# ESTIMATION OF GENETIC PARAMETERS ASSOCIATED WITH EWE REPRODUCTIVE LIFE AND LAMB MORTALITY IN NORTHWESTERN UNITED STATES SHEEP

A Dissertation

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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August 2018

Major Subject: Animal Breeding

ABSTRACT

Ewe reproductive life traits such as longevity and stayability (the probability that a ewe will avoid removal from the flock due to reproductive performance or health) are economically important because of the relationship of removal rates with the value of the cull ewe and cost of replacements. Ewe reproductive life was evaluated as: 1) ewe longevity, 2) ewe stayability to six different ages, and 3) ewe survival. The litter size of a ewe at her birth and her litter size at rearing were investigated for potential effects on these traits. Ewe litter size at rearing was not significant in any analyses ($P > 0.15$), but the ewe's litter size at birth was a significant effect in most analyses. Smaller litter sizes at birth, particularly ewes born as singles, were more often associated with greater mean longevity and stayability to specific ages ($P < 0.05$). Ewes born as singles had survivor functions characterized by higher probability of survival to older ages ($P < 0.05$). Polypay ewes had lower longevity and stayability to different ages than other breeds, as well as a survival function with lower probabilities than other breeds for survival to most older ages. Genetic parameters for these measures were consistently low for longevity (estimates of heritability ranged from 0.06 ± 0.022 in the within breed analysis of Columbia to 0.16 ± 0.024 in within breed analysis of Rambouillet). Estimates of heritability for stayability in general were somewhat higher than those for ewe longevity (ranged from 0.08 ± 0.061 for stayability to 6 yr in Columbia to 0.34 ± 0.027 for stayability to 2 yr in the across breed analyses).

Lamb mortality is important to the sheep industry. Mortality was evaluated as: 1) mortality due to any reason, 2) mortality associated with birth (or at birth), and 3) mortality due to pneumonia. Estimates of heritability ranged from $0.05 \pm 0.022$ in the analysis of overall mortality in Polypay to $0.47 \pm 0.032$ in the analysis of birth mortality in Polypay. Some of these estimates of heritability suggest that selection programs could be effective for these traits.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. David Riley, and my committee members, Dr. James Sanders, Dr. Clare Gill, and Dr. Andy Herring for their guidance and support throughout not only this dissertation research, but through my entire graduate program as well.

I would also like to thank Dr. Lauren Hanna, Dr. Kim Vonnahme, and Dr. Larry Reynolds at North Dakota State University for making this project possible and allowing me to complete the research.

Finally, I would like to thank the USDA, ARS, Range Sheep Production Efficiency Research Unit, U.S. Sheep Experiment Station located near Dubois, ID, specifically Bret Taylor for allowing this project to become possible as well as developing the initial scope of research and Natalie Pierce for the data queries and answering questions regarding the formatting.

# CONTRIBUTORS AND FUNDING SOURCES

This dissertation was supported by a graduate committee consisting of Dr. David G. Riley, Dr. James O. Sanders, Dr. Andy. D. Herring, and Dr. Clare A. Gill. Dr. Riley was responsible for guidance on the methodology and interpretation of the dissertation results. All other professors were responsible for guidance and editing of the writing.

The USDA, ARS, Range Sheep Production Efficiency Research Unit, U.S. Sheep Experiment Station located near Dubois, ID partially funded the original project data, but not the dissertation research. The personnel of USDA as well as those of North Dakota State University helped determine the overall scope of the project.

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# INTRODUCTION

Reproductive life can be defined by both longevity and stayability and is important for all livestock species. Longevity, in terms of productive life, is a result of the combination of fertility, maternal ability, and survival of the dam and her offspring. Longevity is directly related to the profitability and the efficiency of an operation. Stayability is the probability that an animal will survive to a specific age if it is given the opportunity to do so (Hudson and Van Vleck, 1981). This can be measured at any point in an animal's life and does not necessarily cover the entire life of the animal. It does not differentiate between reasons for leaving the flock, such as culling or dying. Prolificacy traits (i.e., gestation, birth, and rearing size) may have potential long-term effects on the lifespan of the ewes, such as reduced longevity, and also may affect the culling decisions of farmers. Reproductive life traits have high economic importance because of the reduction in culling rates, the value of the cull ewe, and the cost of replacement females. As production conditions continue to change, increases in reproductive potential and performance should occur, leading to the question of how to appropriately change these traits without compromising fitness traits (Notter, 2012).

Mortality of sheep and lambs has a significant impact in the sheep industry. According to the National Agricultural Statistics Service (NASS), it has been estimated that the total loss in the United States from both predator and non-predator causes totaled 589,000 in 2016 out of 5.32 million head (NASS, 2016; 2017). Lamb losses accounted for most of the total losses at 63%. In 2010, predator losses resulted in a loss of approximately $20.5 million and non-predator losses resulted in a loss of $36.3 million to farmers and ranchers (NASS, 2010). Non-predator losses include, but are not limited to, causes such as weather conditions, digestive problems, and respiratory problems. Genetic improvement of resistance to disease or other causes of mortality could be an efficient way to improve production. Typically, the focus of mortality studies has not been on the inheritance of very specific causes of death, but there have been observations that genetic variation may differ for distinct causes of death (Gama et al. 1991). Genetic parameters and effects associated with lamb survival have been investigated in the past with a variety of models and differing conclusions (e.g., Gama et al., 1991, Southey et al., 2001, Southey et al., 2004, and Everett-Hincks et al., 2014).

The objectives of this study were to evaluate the impact of different reproductive aspects, such as litter size at birth and rearing litter size, on longevity and stayability and to determine associated genetic parameters. Hypothesis: Larger litter size at birth and rearing litter size will detrimentally impact productivity of the later production of females born or raised in such litters. Previous studies have investigated the effect of a ewe producing different litter and rearing sizes (Zishiri et al., 2013; Douhard et al., 2016), but not the effect of the ewe’s own litter and rearing sizes. It was also an objective of the study to estimate genetic parameters associated with overall lamb mortality, lamb mortality within 24 hr of birth, and lamb mortality associated with pneumonia. Hypothesis: Estimates of genetic parameters will be low for all types of mortality, but larger influences of maternal components will be detected in mortality associated with birth.

# LITERATURE REVIEW

***Ewe Longevity and Stayability***

A study of New Zealand flocks showed that increasing the levels of prolificacy, or the ability to produce multiple offspring early on, are associated with a decay in the ewe's productive lifespan (Douhard et al., 2016). Ewes with lower levels of prolificacy tended to be more likely to be removed from the flock early compared to ewes with higher levels of prolificacy. But as prolificacy got higher, there was a negative effect on the lifespan of the ewes. Including the number of dead lambs during the first two parities of a ewe as a fixed effect, along with the number of live lambs, improved the model for ewes that produced twin and triplet lambs ewes as they relate to stayability. The total number of dead lambs from a ewe also had a negative effect on stayability during the first 2 years of her productive life. Douhard et al. (2016) also showed that ewes with higher levels of early prolificacy had a decrease in rearing ability of the first two parities, impairing the ewe's lifetime production. There also tended to be a greater sensitivity from the environment on a ewe's rearing ability with lower prolificacy; these ewes appeared to prioritize their own survival and maintenance requirements over that of their lambs.

Reproductive traits, including longevity, were evaluated in Dorset, Finnsheep, Romanov, Texel, and Montadale as sire breeds of sheep in fall and spring seasons by Casas et al. (2004, 2005). In both studies, longevity of each ewe was measured as a binary trait based upon the presence or absence of the ewe at the end of the experiment.

In a fall mating season flock (Casas et al., 2004), sire breed, dam breed, and season had influence on longevity. The ewes that had the greatest longevity were sired by Romanov and Montadale, the most productive and one of the least productive sire breeds in terms of weights, respectively. Similar results were seen in the later study (Casas et al., 2005); Romanov-sired ewes had overall greater fertility, prolificacy, and longevity compared to Finnsheep-sired ewes.

Longevity, lifetime performance, and lamb output were compared in Scottish Blackface ewes and crosses (Annett et al., 2011). Of the factors evaluated with the potential to affect ewe survival to the next mating, breed of ewe, age of dam at mating, the dam's body condition score, number of missing teeth, and average daily gain per litter were found to be significant. The probability of surviving to the next mating was highest in ewes with Swaledale sires and Scottish Blackface dams and was lowest in ewes with Lleyn sires and Scottish Blackface dams. Age at mating did not have an effect on the probability of survival up to 3.5 years of age (> 0.900), but the probability was about half of that (0.521) in ewes 5.5 years of age (Annett et al., 2011). Body condition scores on these ewes ranged from 0 to 5, which represented a continuum from emaciated to fat condition. Ewes in good body condition (2.5 or higher) at weaning had high probability of survival to the next mating. Probabilities were much lower for body condition scores below 2.0. Tooth loss was associated with reduced probability of survival. As average daily gain per litter increased, survival probability increased, although this effect was small.

Ewe productivity was evaluated by Notter et al. (2017) with a small emphasis on longevity. Two generations were evaluated and differences in these generations were due to different management practices, such as which breeds of males were castrated, how the ewes were separated, which animals went to feedlots, and number of each mating type. Along with all traits evaluated in the first generation, ewe survival information was used to determine ewe longevity, expressed as a total number of lambings or matings in the second generation over a 4-year period. The model for longevity included fixed effects of the ewe's birth year, ewe breed, lamb's sire breed, and all two-way interactions. The random effect in the model was the sire of the ewe nested within ewe breed and birth year. Romanov–White Dorper × Rambouillet crossbred ewes had the greatest ewe longevity in terms of ewe productivity when compared to both purebred Rambouillet and Polypay ewes. These differences, based upon the breeds and crosses compared, suggest an effect of heterosis for ewe longevity. Romanov–White Dorper × Rambouillet ewes had greater longevity compared to both Rambouillet and Polypay, but the lower longevity of the composite breed Polypay compared to Rambouillet was not consistent with this expected effect of heterosis (Notter et al., 2017).

***Estimates of Genetic Parameters Associated with Longevity and Stayability***

Genetic parameters and genetic relationships of longevity with other traits were evaluated in crossbred Mule ewes (crosses between Bluefaced Leicester sires and hill breed ewes) using Bayesian linear censored models; genetic associations between longevity and culling decisions were also evaluated (Mekkawy et al., 2009). Longevity was defined as the number of years from the age of first lambing at 2 years until culling or death with ewes having the opportunity to produce between 6 and 8 lamb crops. If a ewe remained in the flock after 6 lambings or was missing they were treated as censored data and this accounted for approximately 24% of the records. The model for longevity included the combined effect of year-farm of culling, the additive genetic effect of the animal, the genetic group assignments, and the residual effects. Estimates of heritability for the different farms ranged from 0.22 to 033, with the mean heritability being 0.27. The higher estimates of heritability for this trait were potentially due to the control of husbandry and other environmental effects, the tightly defined culling criteria, and the evaluation of crossbred Mule ewes rather than purebred sheep (Mekkawy et al., 2009). Genetic correlations between ewe longevity and culling traits were high, 0.51 to 0.87, suggesting that selection for longevity will improve other traits associated with teeth, mouth, and udders. On the other hand, the genetic correlations between longevity and growth traits were low and not significant.

Borg et al. (2009) estimated genetic parameters for both productive life (longevity) and stayability on Targhee ewes and lambs and evaluated how these traits are associated with others, such as lamb growth and ewe performance to help improve accuracy of selection, using bivariate and trivariate models. Stayability was measured at eight different points as a binomial trait; overall stayability was the probability that a ewe lambed at ages 3, 4, 5, and 6, given that she lambed at age 2 and marginal stayability was measured as the probability that a ewe that lambed in the current year lambed in the previous year as well. Productive life was evaluated though it did not include all sheep used in the stayability analysis. It was only evaluated for ewes that had the opportunity to remain in the flock until 6 years of age. Stayability was evaluated as a single-trait analysis for each of the conditional stayability ages and the variance components estimated from these were used as priors for a multiple-trait analysis (Borg et al., 2009). Phenotypic variances ranged from 0.158 to 0.239 and heritability estimates ranged from 0.00 to 0.09 for stayability in single-trait analyses. Similar results were reported from the bivariate analyses of stayability with estimates of heritability ranging from 0.04 to 0.10 and slightly higher in trivariate analyses, 0.02 to 0.15.

Zishiri et al. (2013) investigated genetic parameters in Dorper sheep for growth, reproduction, and fitness traits in South Africa. Different components of reproduction and efficiency were evaluated. As indicators of longevity, the number of lambs born alive and the number of lambs that were weaned per ewe throughout her lifetime were used. The productive life of the ewe was defined by the age of the ewe at her last lambing and was used for longevity. Stayability to ages 2, 3, and 4 were evaluated. The random effects included the direct additive, maternal additive, maternal permanent environmental effects, and the covariance between the direct and maternal additive effects. Estimates of heritability for lamb survival to weaning, ewe productive life (longevity), and ewe stayability for ages 2, 3, and 4 were 0.07, 0.05, 0.05, 0.09, and 0.11, respectively. The number of lambs born alive and the number of lambs weaned also had low estimates of heritability of 0.10 and 0.09, respectively. Other traits that are indicative of ewe longevity and vitality, such as number of times lambed (up to 4 years of age) had similarly low estimates of heritability. Genetic correlations between these traits were low to moderate. Genetic correlations between longevity and stayability for each age group ranged from 0.23 to 0.38. There was a moderate genetic correlation, 0.48, between lamb survival and ewe stayability suggesting an improvement could be made to longevity by selecting on lamb survival to weaning (Zishiri et al., 2013). The genetic correlations of stayability with the number of lambs born and number of lambs weaned were low at age 2, 0.16 and 0.19 respectively, but the genetic correlation was moderate for stayability with weaning at age 4, 0.48.

Estimates of genetic parameters for both stayability and productive life of ewes were obtained in another New Zealand sheep population (Lee et al., 2015). Productive life was the total number of years a ewe remained in the flock, which is defined as the age of the ewe when removed from the flock or upon death minus two years (Lee et al., 2015). Only animal of known age when leaving the flock, or animals where this could be inferred were used for analysis of productive life, and all live animals were excluded. Stayability was evaluated as a binary trait, 0 if the ewe was not present and 1 if the ewe was present (Lee et al., 2015), and based on specific years, that is, the probability of a ewe remaining a flock at age 3, 4, 5, etc. given that she was in the flock at age 2. Heritbability estimates of productive life for seedstock and commercial flocks were 0.1 and 0.13, respectively. Heritability estimates for seedstock stayability to 3 and 4 years, 0.087 and 0.089, were higher than stayability for commercial operations, 0.048 and 0.065 (Lee et al., 2015). The heritability estimates for stayability to 5 and 6 years were more similar between the two production systems. Genetic correlations for stayability and productive life between seedstock and commercial flocks were high, from 0.84 to

0.96 and 0.81 to 0.96, respectively. Both of these traits had the highest correlations with the number of lambs born (0.43 and 0.48 for seedstock and commercial respectively) and live weights up to one year of age (0.17 and 0.32 for seedstock and commercial respectively) compared to other traits.

***Effect of Birth Type and Rearing Type***

Birth and rearing types have been shown to be associated with differences in certain traits, especially with weight and growth traits. Inaccuracy of recording birth and rearing types can also affect later genetic evaluations. Birth types and rearing types may differ from each other because of artificial rearing or cross-fostering, where a ewe may rear more or less lambs than she lambed, but the main cause for this difference is due to lamb mortality (McHugh et al., 2017). Typically ewes with lighter lambs born as singles are selected for fostering so that there is less competition for resources between the lambs. It was reported by McHugh et al. (2017) that different rearing types for singles did not have an influence on their growth potential. In analyses of birth and rearing types in relation to growth, lambs that were born and reared as a single had the greatest birth weight, 40-day weight, and average daily gain out of all birth/rear combinations (McHugh et al., 2017). Birth and rearing types of sheep have been shown to have a large influence on growth traits, especially preweaning, and making adjustments to weight records is important to appropriately predict breeding values for weights in sheep (Notter and Brown, 2015).

***Lamb Mortality***

Gama et al. (1991) estimated heritability and phenotypic and genetic correlations for preweaning lamb mortality. Overall mortality (all lambs dead before weaning at 60 d of age), perinatal mortality (all lambs born dead and lambs that died within the first 24 hours of life), postnatal mortality (all lambs dead from day 1 to weaning), respiratory mortality (subdivision of postnatal mortality) and other mortality (subdivision of postnatal mortality) were evaluated for three different breed groups using three different models. All models included the effects of breed, year, sex, age of dam, and interactions. Two of the models included other effects as well; one included the effect of litter size and the other also included birth weight in the model. Estimates of heritability for total mortality differed for each model and were estimated on a binomial scale and transformed into normal scale. The estimates of heritability in the binomial scale, ranged from 0.04 to 0.07 in all three populations for paternal half-sibling relationships whereas the heritability estimate was much higher for full-sibling relationships, upwards of 0.36, indicating maternal effects. The estimates of heritability in the larger models did not change for the paternal breed group (Suffolk and ½ Columbia ¼ Suffolk ¼ Hampshire composite) or the accelerated maternal breed groups (Finnsheep, Dorset, Rambouillet, and ½ Finnsheep ¼ Dorset, ¼ Rambouillet composite) (Gama et al., 1991). In the maternal breed group (Finnsheep, Suffolk, Targhee, and ½ Finnsheep ¼ Suffolk ¼ Targhee composite), the heritability estimates based on paternal half-sibling relationships became almost zero in the other models. Perinatal and postnatal heritability estimates ranged from 0.02 to 0.06 and from 0.015 to 0.07, respectively. There was inconsistency between populations for respiratory mortality ranging from zero (a negative heritability estimate) to 0.07. Normal scale heritability estimates for total mortality remained similar in all three populations. The range of heritability estimates for perinatal mortality was from 0.09 to 0.19; with inclusion of litter size, estimates were from 0.07 to 0.10, and with inclusion of birthweight, the heritability estimates only slightly altered from the binomial scale. Postnatal mortality heritability estimates had a larger range than the other traits in the simplest model with the range from 0.03 to 0.18, and there was only a small decrease in the estimates for the other two models. The range in the simple model for respiratory mortality was from zero (-0.02) to 0.32 and the other two models did not change the estimates significantly.

Southey et al. (2001) evaluated lamb mortality using survival analysis. Lambs that were alive at the end of each period in the study and lambs that were culled were treated as censored in the data. Models included direct additive, maternal genetic, and the covariance between them as random effects. In this study, sex had a significant effect on mortality throughout all periods, where mortality was greater in males than in females. The hazard ratios for sex ranged from 1.22 to 1.59 as a deviation of male lambs from the female lambs. Litter size at birth was also a significant effect on the hazard of mortality, with mortality in twins being higher than singles, for all periods up to weaning. The type of birth did not have a significant effect on survival from either weaning to 1 year of age or 120 days to 1 year of age. Age of dam not detected as significant for survival from weaning to 1 year of age or 120 days to 1 year of age. Estimates of heritability in this study ranged from 0.12 to 0.21 for the survival analysis and 0.08 to 0.11 for the logistic sire model. Heritability estimates were lower in logistic animal and maternal effects models than the previous sire model, ranging from 0.036 to 0.052 and 0.028 to 0.066 (direct) and 0.006 to 0.071 (maternal), respectively.

Southey et al. (2004) also evaluated overall lamb mortality and lamb mortality from specific causes of death (dam-related (dystocia and starvation), pneumonia, disease, and other). Each of these causes of death was assumed to be independent of the others; therefore, mortality was analyzed with a competing risk approach and evaluated from both continuous and discrete-time mortality records. Competing risks analyses account for specific causes of mortality by considering the competition among the causes of mortality. That is, there is a mortality risk associated with each cause for a lamb that is still alive and a lamb that is dead has the risk of mortality due to other causes removed. The difference between the continuous and discrete-time mortality records was due to using either the specific time of mortality (continuous) or using four time intervals with each animal having either the occurrence or nonoccurrence of mortality. Similar results were seen as in the previous study (Southey et al., 2001) in relation to the fixed effects for overall mortality. Male lambs, lambs born in litters of three or more, and lambs out of dams aged 1 and 2 years old had greater hazard of mortality than the other levels. Male lambs had a greater hazard of mortality in both the pneumonia- and dam-related causes of mortality. Dam-related mortality had the highest association with type of birth, with the risk of mortality being greater in lambs born in litters of three of more than in lambs born as twins and greater in lambs born as twins than in lambs born as singles. The lowest risk of mortality associated with birth type was with the disease and pneumonia categories. Lambs from 2-year-old dams had a greater risk of mortality from disease than lambs from 3-year-old dams. The probability of mortality was observed to decrease greatly from the first and second week of age, from 10% to 2%, but did not reflect all the changes from the categories used in this study. The highest specific cause of mortality was dam-related mortality, but it decreased greatly by 2 weeks, 3.8% to 0.3%, and was almost nonexistent after the fourth week up to weaning (Southey et al., 2004). The probability of mortality due to pneumonia was constant throughout the 7-week period. Heritability of mortality due to any cause was 0.159 and 0.328 for the sire and animal models. Heritability of mortality due to disease was 0.293 and 0.161, due to dam related events was 0.736 and 0.411, due to pneumonia was 0.304 and 0.166, and heritability of mortality due to other causes was 0.332 and 0.378, from sire and animal model analyses, respectively. The discrete-time analyses included a third model, the maternal effects model, which incorporated additive genetic, maternal additive genetic and the covariance between the two. The estimates of heritability ranged from 0.082 (direct) to 0.128 (sire model) for overall mortality from the various model parameterizations. The heritability of mortality due to disease ranged from 0.087 (direct) to 0.307 (maternal). Dam-related mortality ranged from 0.159 (direct) to 0.679 (sire model). The pneumonia mortality category had heritability estimates ranging from 0.012 (maternal) to 0.295 (sire model) and the other category had a range from 0.142 (direct) to 0.257 (maternal). The covariance between the additive genetic and the maternal genetic components was negative in all mortality categories except for pneumonia. The covariance estimates ranged from –0.206 (other) to –0.057 (overall) and was 0.102 for pneumonia. The same was seen for the correlation between the additive and maternal components as well, which were negative in all categories except for pneumonia. The correlations ranged from -0.526 (other) to -0.204 (dam related). There was a correlation of 0.941 between the additive and maternal genetic components of mortality due to pneumonia but that estimate had an extremely large standard error associated with the estimate, 4.419. This component is not always easily estimated.

Different genetic effects from introducing meat breeds of sheep into extensive sheep systems in Patagonia and the role this introduction has on lamb growth, survival, and finishing have been investigated (Álvarez et al., 2010). Survival of the lambs to weaning was analyzed using a Bayesian threshold model that included lamb genotype (breed), dam parity and dam BCS at lambing, year, birth litter size, sex, the additive genetic effect of the lamb's sire and maternal grandsire, and the permanent environmental effect of the dam. The parity of the dam did not have a significant effect on a lamb's survival to weaning but higher BCS on dams did show a higher chance for lamb survival. No differences for survival were detected between the sexes, but could be partially attributed to the small difference observed in birth weights by sex. Singleton lambs had a higher survival than twins, but effects of birth size on survival are typically due to birth weights (Álvarez et al., 2010).

Leeds et al. (2012) evaluated lamb survival, along with growth traits, on lambs that were from different breeds of terminal sires. Sheep in this study were from the USDA ARS, U.S. Sheep Experiment Station located near Dubois, ID, the same location as the present study, and therefore the sheep could potentially be a part of the same dataset. Lamb survival was evaluated using sire breed, year, total number born (i.e., single, twin, triplet), the age of the ewe, sex of the lamb, birthweight, and all two-way interactions with sire breed. Sire breed, year, and ewe age were kept in models regardless of significance whereas the remainder of the variables were removed sequentially from the model based upon significance level. Of these variables, the sire breed – ewe age interaction and birth weight were significant effects on lamb survival, the interaction of sire breed with lamb sex was not. Lambs with lighter birth weights from large sire breeds (Columbia and Suffolk) had a greater risk of mortality than the smaller sire breeds (Leeds et al., 2012). Birth weights seemed to explain the same effect as total number born, where the total number born was not significant with birth weight in the model but was significant when birth weight was not modeled. Lambs born to mature (3- to 5-yr old) ewes had higher survival.

The majority of lamb deaths occur in the first 3 days after birth and typically ranges from 5 to 30% for each flock. Everett-Hincks and Dodds (2008) investigated lamb viability at birth, lamb death risks from dystocia, starvation, exposure, and survival to weaning by evaluating the effects of the dam’s body condition (BCS) during pregnancy, the birth weight of lambs, the weather during the lambing period, and maternal behavior (how the ewe responds to shepherd attending her lambs) on singles, twins, and triplets. Lambs that were triplets had the lowest viability at birth, followed by lambs born as singles, and twins had the highest viability. Birth weight was a significant effect on this trait and both lambs that were heavier and lighter than the ideal birth weight (0.5 kg above the mean) were less viable. Lamb dystocia death risks were similar to that of lamb viability. Higher dystocia rates were reported for triplets, ram lambs, and lambs born to 3-year-old dams. Lambs that were in the optimum birth weight category had an overall lower death risk from dystocia. The greatest death risk to dystocia was observed in lambs born as triplets that were 2 kg lighter than the mean birth weight. Lamb death risk to starvation was very similar to the previous mortality causes. Lamb survival to 3 days was lowest in triplets and in lambs that were out of older ewes (5 years old). Lambs born as triplets that were born 2 kg lighter than the mean had the lowest survival to 3 days of age. Lamb survival to weaning was the lowest in lambs born as triplets, ram lambs, and lambs born to 2-year-old ewes. Survival to weaning was 11% greater in twins than in triplets (Everett-Hincks and Dodds, 2008).

Genetic parameter estimates for lamb survival and mortality traits were investigated in New Zealand sheep farms using different random effects models with constant fixed effects (Everett-Hincks et al., 2014). The different models were: a model including direct additive genetic effects, maternal genetic effects, and the covariance between them; a model including those same three effects as well as the temporary environmental effect of the litter (dam within year); a model including the direct additive genetic effects, maternal genetic effects and the permanent environmental effect of the dam; and a model with the direct additive genetic effects, maternal genetic effects, and the temporary environmental effect of the litter. The covariance between the direct additive and maternal genetic components was not included in the latter models because it was not significant in the first two models. These models were used to analyze birth weight, viability at birth (in reference to lung aeration (presence or absence of air in the lungs)), lamb death risk from dystocia, lamb death risk from starvation, lamb survival to 3 days after birth, and lamb survival to weaning. Estimates of heritability for direct additive effects and maternal genetic effects on birth weights ranged from 0.13 to 0.14 and 0.18 to 0.32, respectively. Direct additive genetic effects were all less than 0.01 (as a fraction of the phenotypic variance) for all measures of mortality, and the heritability estimates for maternal genetic effects ranged from 0.01 to 0.08. Approximately half to two-thirds of all of the genetic variation was due to maternal effects (Everett-Hincks et al., 2014). Estimates for total heritability (summation of the direct additive genetic and maternal genetic effect variances divided by total variance) were obtained for these data. Estimating heritability as total heritability has been investigated previously by Lopez-Villalobos and Garrick (1999) and Morris et al. (2000). The estimates of total heritability were still relatively low, ranging from 0.01 to 0.08 for mortality traits and moderate, ranging from 0.32 to 0.43, for birth weights.

Factors associated with the mortality of newborn southern Australian lambs were evaluated by Refshauge et al. (2016). The different causes of death were placed into separate categories based upon postmortem autopsy and analyzed separately. These categories were starvation/mismothering (failure to care for lamb), accounting for 25%, stillbirths, 21%, birth injury, 18%, dystocia, 9%, death *in utero*/premature, 10%, predators, 7%, cold exposure 5%, unknown, 4%, infection, 1%, and misadventure (extraordinary death circumstances, such as stuck between posts, falling in holes, structures collapsing on them, etc.), 1%. All types of mortality were analyzed as binary data using mixed model logistic regression. The model that best explained lamb mortality for dystocia included litter size at birth, birthweight, and body mass index (lamb's birthweight divided by the square crown-rump length) as significant effects. In this model, single born lambs had a significantly higher probability of mortality than both twin and triplet born lambs. Stillbirth mortality was best explained by litter size at birth, birth weight, body mass index, and dam breed. Lambs that were born as singles that were at average weights and from Merino dams were more likely to fall into this mortality category than lambs born as twin and triplets from both Merino and maternal (Border Leicester, South African Mutton Merino, Dohne, Coopworth, and Corriedale) dams. Lambs falling into the category of mortality from birth injury were associated with litter size at birth, body mass index, and age of dam. Female lambs born as twins had the same probability of mortality from this cause as males born as twins but had a higher incidence of mortality than either lambs born as singles or triplets of either sex. Significant effects associated with starvation/mismothering (failure to care for lamb) lambs were litter size at birth, birthweight, body mass index, and sire type (terminal breed versus maternal breed). Starvation probability for lambs born as twins was significantly greater than for lambs born as singles with similar sire types, but lambs born as triplets from sires with more maternal or Merino composition were similar to twin lambs' probabilities of starvation. Breed composition of the dam was the only significant effect for lambs that had mortality associated with predators and it was the highest in lambs whose dams were maternal breeds when compared to Merino dams. Significant effects for lambs that died *in utero*/premature were birth type, birthweight, body mass index, sex, and age of dam. Male lambs born as triplets with average birthweights and body mass index born from 5-year-old ewes had a higher incidence of mortality than twin and single lambs, both male and female. Overall litter size at birth had a significant effect on mortality and mortality was higher in single born lambs for dystocia and stillbirths, higher in twin lambs for birth injury and starvation, and higher in triplets for starvation and death *in utero*.

Holmøy et al. (2017) investigated early lamb mortality and stillbirths in sheep flocks in Norway. Overall, in 81% litters of twins or greater, at least one lamb died after birth, and of these litters, 12% of these litters had stillborn lambs. Of live-born lambs that subsequently died, 80% died within 2 days after birth, 41% died within 24 hours, and 27% died within 3 hours of birth. In 36% of the lambs, infection was the primary cause of death. Among those lambs that died within 3 hours of birth, assigned causes of death included septicemia (48%), pneumonia (25%), gastrointestinal infections (22%), and other infections (5%) (Holmøy et al., 2017). Trauma was the primary cause of mortality in 20% of the lambs; of these, 46% died within 3 hours after birth and 70% died within 24 hours post parturition. Lambs dying from trauma was highest in lambs born as singles and lowest in lambs born as twins. The other causes of mortality, including asphyxia, congenital malformations, starvation, non-infectious gastrointestinal tract diseases, and unknown accounted for 10%, 10%, 6%, 2%, and 16% of deaths, respectively. The main causes of early mortality in sheep were infection and trauma, with most of these deaths occurring shortly after birth indicating that lambing events and immediately after lambing are critical for lamb survival (Holmøy et al., 2017).

## MATERIALS AND METHODS

### *Sheep Populations*

Texas A&M University Institutional Animal Care and Use Committee approval was not obtained for this study because the records were extracted from an existing database. All records on sheep used for this study were from the USDA, ARS, Range Sheep Production Efficiency Research Unit, U.S. Sheep Experiment Station located near Dubois, ID. Records (n = 270,400) were available on purebred and crossbred animals from 1950 to 2015. Breeds represented in this dataset include Columbia, Hampshire, Merino, Polypay, Rambouillet, Suffolk, Targhee, Friesian, Dorper, Texel, Finnsheep, Dorset, Romanov, and a USMARC-Composite developed in the 1970s (Leymaster, 1991). All lambs produced in this population were born from February through May each year. Pedigree information was used to confirm and determine breed proportions for each animal. Animals were grouped based upon purebred breeds, $F_1$, $F_2$, etc., and crossbreds were grouped based upon a majority breed (i.e., greater than 50% Columbia is a Columbia crossbred). Analyses focused on five major breeds, Columbia, Polypay, Rambouillet, Suffolk, and Targhee, across all years of records. These breeds were chosen as they were present in the flock longer than other breeds.

### *Culling Criteria*

All ewes in this dataset were removed from the flock after they weaned their lambs at age 7. Ewes that were still present in the dataset with records after the age of 7 were part of other experiments and trials but were not reflective of typical production practices. Ewes were culled prior to that age for various reasons, including failure to conceive and give birth after 2 years of age, unsoundness, or nonconformity with breed standards. Ewes also exited the flock due to death; in most cases cause of death was recorded.

***Longevity and Stayability***

Typically, analyses of longevity have some censored records, where events determining when an animal leaves the herd or flock may not have had the chance to happen yet. Right censored data, in relation to longevity, are observations where only the initial or lower bound of longevity is known, which is typical for animals that are still alive, because they have not reached the end of their productive life yet. On the other hand, left censoring is where the information before a certain time period is not known on an animal, such as an animal that was brought in from an outside herd or an animal that was present in the herd before a study started; the information about the earlier years of that animal are not known. Based upon the culling criteria of these sheep, all records involving animals that were not born in the flock and all animals that did not yet have the opportunity to make it 7 years of age (animals born at the end of the data set and have not been alive long enough to have the opportunity to reach 7 years of age) were excluded from analysis. Traits were evaluated similarly to Borg et al. (2009) and Zishiri et al. (2013).

Longevity and stayability were evaluated using six data sets, one of which was records from 1982 to 2002 (across breeds) that included 4 of the 5 evaluated breeds in every year and the others not limited by year being breed specific (within breed) analyses for Columbia, Polypay, Rambouillet, Suffolk, and Targhee. Longevity was analyzed using ASReml (Gilmour et al., 2015) as univariate analyses defined by the last age a ewe had a record in the herd, up to the possible 7 yr based upon previous culling practices, ranging from 1 to 7 yr of age. Stayability was evaluated assuming a binomial distribution and a logit link function using generalized linear mixed models with ASReml (Gilmour et al., 2015). Stayability was measured at multiple points in the ewe's lifetime, starting at 1 yr of age; analyses were conducted distinctly for stayability to ages 2 through 7. Each ewe was assigned a value of 1 if present in the flock at each age, each conditional on the ewe lambing (and not necessarily the lamb surviving) at 1 year of age, and a value of 0 if not present. All ewes had records of stayability at each stage even after they had left the flock. Fixed effects investigated for both traits were ewe breed, the litter size that the ewe was born as, the litter size the ewe was reared as, and the birth year. Effects were kept in the model if the corresponding $F$-statistic had a probability $P < 0.15$. Random effects considered for both traits were additive genetic, maternal additive genetic, the covariance between these two, and the maternal permanent environmental effects. The final random effect structure for each model and analysis of longevity and stayability were determined by likelihood ratio tests.

***Survival Analyses***

Survival curves were generated in SAS (SAS Inst., Inc., Cary, NC) using PROC LIFETEST and the survival analysis methodology described by Allison (2010). This methodology provides a method for testing for differences in survivor functions for multiple groups (strata). A total of 11 survival curves were generated, allowing visualization of the probability of survival for each analysis and corresponding significant fixed effects (strata) at $P < 0.15$. Some of the data was singly Type I right censored (Allison, 2010). The censoring time was fixed at 7 yr of age for all animals; all ewes present that did not have an end of life event at the end of 7 yr were censored.

***Lamb Mortality***

Lamb mortality was evaluated assuming a binomial distribution and a logit link function using generalized linear mixed models with ASReml (Gilmour et al., 2015). Fixed effects investigated were lamb breed, lamb litter size at birth (i.e., single, twin, triplet), sex of the lamb, age group of dam, and the year of record. Wethers and rams were combined into a single sex category. Age groups of dams were yearlings, 2-yr-olds, 3 to 5 yr (young adults), and 6 yr and older (older adults). Detailed death records or reason for leaving the flock were available for each animal. Mortality was evaluated in distinct analyses as mortality due to all causes of death (**overall mortality**), as mortality associated with birth (**birth mortality**), and for a specific cause of mortality (**pneumonia**). Lambs that died were given a value of 1 and those alive or that died from other causes were given a value of 0. Random effects considered were additive genetic, maternal additive genetic, the covariance of these two, and maternal permanent environmental effects. Likelihood ratio tests were used to determine the final random effects structure for each model for each type of mortality.

***Data Editing***

Analyses focused strictly on purebred Columbia, Polypay, Rambouillet, Suffolk and Targhee as the other breeds were only present in the flock for more limited time periods. Records of crossbred dams, dams with missing age, dams that were born before the start of the dataset (before 1950), and ewes with parities that were inconsistent with age (not within 2 years of age) were removed. A total of 26,656 records were then available for evaluating ewe longevity and stayability. Records from 1982 to 2002 that contained 4 of the 5 breeds in every year with at least 20 records per breed per year were available. The number of records available for longevity and stayability are in Table 1 and Table 2, respectively.

Mortality records of crossbred lambs were removed as well as records with missing sex classifications on the lambs and missing dam ages, resulting in 102,481 records. Records from 1978 to 2004 that contained 4 of the 5 breeds in each year with at least 20 records per breed per year were kept for across breed analyses of mortality. Distinct subsets of data were used for breed specific analysis of Columbia, Polypay, Rambouillet, Suffolk, and Targhee, using years that had at least 20 records available in that year for that breed. The number of records in each of these subsets and by each mortality category are in Table 3.

**Table 1.** Number of records evaluated for longevity

| | | Longevity (yr) | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Data set | Total Records | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Across breed[1] | 11,550 | 2,800 | 1,671 | 1,523 | 1,464 | 1,248 | 1,007 | 1,837 |
| Within breed | | | | | | | | |
| Columbia | 4,398 | 695 | 653 | 669 | 576 | 492 | 433 | 880 |
| Polypay | 4,534 | 1,226 | 743 | 637 | 604 | 456 | 353 | 515 |
| Rambouillet | 5,922 | 913 | 869 | 786 | 822 | 700 | 607 | 1,225 |
| Suffolk | 213 | 36 | 40 | 26 | 29 | 34 | 30 | 18 |
| Targhee | 6,482 | 1,175 | 867 | 959 | 890 | 732 | 619 | 1,240 |

[1]Across breed analysis was limited to years 1982 to 2002

**Table 2.** Number of records evaluated for stayability

| | | Stayability to age | | | | | |
|---|---|---|---|---|---|---|---|
| Data set | Total Records | 2 | 3 | 4 | 5 | 6 | 7 |
| Across breed[1] | 11,550 | 8,750 | 7,079 | 5,556 | 4,092 | 2,844 | 1,837 |
| Within breed | | | | | | | |
| Columbia | 4,389 | 3,694 | 3,043 | 2,375 | 1,802 | 1,313 | 880 |
| Polypay | 4,534 | 3,308 | 2,565 | 1,928 | 1,324 | 868 | 515 |
| Rambouillet | 5,922 | 5,009 | 4,140 | 3,354 | 1,832 | 1,225 | 2,532 |
| Suffolk | 213 | 177 | 137 | 111 | 82 | 48 | 18 |
| Targhee | 6,482 | 5,307 | 4,440 | 3,481 | 2,591 | 1,859 | 1,240 |

[1]Across breed analysis was limited to years 1982 to 2002

**Table 3.** Number of records for evaluation of mortality

| | | Mortality | | | | | |
|---|---|---|---|---|---|---|---|
| Data set | Total records | Overall | % | Birth | % | Pneumonia | % |
| Across breed[1] | 61,989 | 13,345 | 21.5 | 2,420 | 3.9 | 749 | 1.2 |
| Within breed | | | | | | | |
| Columbia | 6,957 | 1,412 | 20.3 | 329 | 4.7 | 111 | 1.6 |
| Polypay | 27,604 | 6,754 | 24.5 | 1,404 | 5.1 | 267 | 1.0 |
| Rambouillet | 11,708 | 2,358 | 20.1 | 423 | 3.6 | 140 | 1.2 |
| Suffolk | 1,271 | 403 | 31.7 | 76 | 6.0 | 22 | 1.7 |
| Targhee | 13,641 | 2,980 | 21.8 | 455 | 3.3 | 204 | 1.5 |

[1]Across breed analysis was limited to years 1978 2004

## RESULTS AND DISCUSSION

### ***Longevity***

The litter size that a ewe was reared in did not explain substantial variation in the analyses of longevity in the across breed data nor in the breed-specific data (*P* > 0.15). The year of birth of the ewe was highly significant in all analyses of longevity. In all analyses, the additive genetic component was included as a random variable, but the addition of other random components was not supported by likelihood ratio tests, and in all analyses the estimates of the added random components were 0.

***Across Breed*.** Breed was a significant effect in the overall analysis of longevity (*P* = 0.038) as was the ewe's litter size at birth (*P* = 0.003; Table 4). Rambouillet had greater longevity than both Polypay and Targhee ewes (*P* < 0.020; Table 5). This lower longevity of the Polypay compared to Rambouillet was consistent with previous comparisons of ewe longevity in evaluation of Rambouillet, Polypay, Romanov-White Dorper × Rambouillet from the US Sheep Experiment Station in Dubois, ID (Notter et al., 2017). The longevity of Columbia ewes was intermediate to those but did not differ from the other breed groups (*P* > 0.05). Ewes that were born as singles had greater longevity (3.61 ± 0.048 yr) than ewes born as twins or triplets (*P* < 0.005, Table 5). The estimate of heritability for longevity from this analysis was low (0.16 ± 0.016), and was consistent with estimates of heritability previously reported in seedstock and commercial flocks in New Zealand (Lee et al., 2015), slightly higher than estimated in purebred Dorper in South Africa (Zishiri et al., 2013), and slightly lower than previously estimated in crossbred Mule ewes (crosses between Bluefaced Leicester sires and hill breed ewes) in England, Scotland, and Wales (Mekkawy et al., 2009).

***Within Breed.*** The ewe's litter size at birth was influential in the analyses of longevity of Polypay, Rambouillet, and Targhee ewes, ($P < 0.107$; Table 4). Polypay and Rambouillet ewes that were born as single lambs had greater longevity ($P < 0.035$) than ewes (within each breed) that were born as triplets (Table 5). Within each breed those ewes born as twins had intermediate longevity means. Targhee ewes born as singles had greater longevity ($P = 0.012$) than those born as twins but did not differ in longevity from those born as triplets ($P > 0.05$), likely due to the small number of Targhee ewes born as triplets (Table 4). Estimates of heritability of longevity ranged from 0.06 ± 0.022 in Columbia ewes to 0.16 ± 0.024 in Rambouillet ewes (Table 6). These estimates of heritability are similar to those reported previously for purebred Dorper ewes (Zishiri et al., 2013) and lower than estimates obtained from crossbred ewes (Mekkawy et al., 2009). Also, the estimate of heritability from the Suffolk analysis was similar to both the Columbia and the Polypay results, but is not reliable as there were not sufficient records to adequately estimate the additive genetic component (n = 213).

**Table 4.** Distributions of records for litter size at birth in the tested models and *P*-values

| | | Litter size at birth | | |
|---|---|---|---|---|
| Data set | *P*-value[1] | Single | Twin | Triplet |
| Across breed | 0.003 | 2,695 | 7,256 | 1,599 |
| Within breed | | | | |
| Columbia | 0.791 | 1,508 | 2,594 | 287 |
| Polypay | 0.107 | 622 | 2,643 | 1,269 |
| Rambouillet | 0.064 | 2,206 | 3,380 | 336 |
| Suffolk | 0.949 | 60 | 135 | NA |
| Targhee | 0.014 | 2,204 | 3,944 | 334 |

[1]*P*-value of *F*-statistics for litter size at birth in each analysis.

**Table 5.** Longevity means and SE for fixed effects

| | Data set | | | |
|---|---|---|---|---|
| Fixed effects | Across breed | Polypay | Rambouillet | Targhee |
| Ewe breed | | | | |
| Columbia | $3.51^{ab} \pm 0.072$ | | | |
| Polypay | $3.40^{a} \pm 0.062$ | | | |
| Rambouillet | $3.63^{b} \pm 0.064$ | | | |
| Targhee | $3.43^{a} \pm 0.060$ | | | |
| Litter size at birth | | | | |
| Single | $3.61^{a} \pm 0.048$ | $3.32^{a} \pm 0.086$ | $4.01^{a} \pm 0.059$ | $3.86^{a} \pm 0.070$ |
| Twin | $3.47^{b} \pm 0.036$ | $3.18^{ab} \pm 0.048$ | $3.91^{ab} \pm 0.051$ | $3.73^{b} \pm 0.064$ |
| Triplet | $3.40^{b} \pm 0.061$ | $3.11^{b} \pm 0.064$ | $3.74^{b} \pm 0.120$ | $3.94^{ab} \pm 0.126$ |

[a-b]Means in column within each fixed effect that do not share a superscript differ ($P$ < 0.05).

**Table 6.** Estimates of additive genetic variance ($\sigma_a^2$) and heritability ($\mathrm{h}^2$) for ewe longevity

| | Data set | | | | | |
|---|---|---|---|---|---|---|
| Parameter | Across breed | Columbia | Polypay | Rambouillet | Suffolk | Targhee |
| $\sigma_a^2$ | 0.74 ± 0.076 | 0.26 ± 0.091 | 0.28 ± 0.085 | 0.68 ± 0.103 | 0.31 ± 0.492 | 0.54 ± 0.088 |
| $\mathrm{h}^2$ | 0.16 ± 0.016 | 0.06 ± 0.022 | 0.07 ± 0.021 | 0.16 ± 0.024 | 0.09 ± 0.133 | 0.13 ± 0.021 |

***Stayability***

The ewe's litter size at rearing was not important in either across breed or within breed analyses of stayability (*P* > 0.15). Year was significant in all analyses of stayability except in the analyses of stayability to 3, 5, 6, and 7 years in Suffolk (*P* > 0.15), but it was retained in final models. As in the analysis of longevity, the additive genetic component was the only random variable included, as addition of other random components was not supported.

***Across Breed.*** Ewe breed was an important fixed effect in the analyses of ewe stayability to different years of age (Table 7). Polypay ewes had lower stayability to 2 yr of age (*P* < 0.008) than ewes of other breeds, and had lower stayability to 3 yr than Rambouillet and Columbia ewes (*P* < 0.003; Table 8). Rambouillet ewes had greater stayability to ages 4 through 7 (*P* < 0.025) than ewes of all breed groups except for Columbia ewes to 6 yr of age (*P* = 0.077). Litter size at birth of the ewe was detected as a significant fixed effect in analyses of stayability to ages 2, 3, and 7 yr (Table 7). Ewes born as single lambs had greater stayability (*P* < 0.040) to ages 2 and 3 than ewes born in litters (Table 8), and had greater stayability to age 7 (*P* = 0.011) than ewes born as triplets. Estimates of heritability for stayability to different ages were high (Table 9) relative to previously reported estimates of stayability (Borg et al., 2009; Lee et al., 2015). These high estimates more closely resemble the high estimates of heritability obtained for longevity reported for Mule ewes (Mekkawy et al., 2009).

**Table 7.** *P*-values of *F*-statistics of fixed effects for stayability

| | Stayability to age | | | | | |
|---|---|---|---|---|---|---|
| Data set | 2 | 3 | 4 | 5 | 6 | 7 |
| Across breed | | | | | | |
| Ewe breed | 0.001 | 0.004 | 0.001 | 0.002 | 0.023 | 0.012 |
| Litter size at birth | 0.001 | 0.011 | 0.196 | 0.153 | 0.199 | 0.041 |
| Within breed | | | | | | |
| Litter size at birth | | | | | | |
| Columbia | 0.528 | 0.139 | 0.172 | 0.607 | 0.643 | 0.147 |
| Polypay | 0.043 | 0.169 | 0.791 | 0.515 | 0.279 | 0.265 |
| Rambouillet | 0.146 | 0.410 | 0.414 | 0.139 | 0.439 | 0.063 |
| Suffolk | 0.962 | 0.675 | 0.662 | 0.782 | 0.608 | 0.593 |
| Targhee | 0.147 | 0.046 | 0.049 | 0.055 | 0.511 | 0.042 |

**Table 8.** Across breed means and SE for fixed effects in analyses of stayability

| | Stayability to age | | | | | |
|---|---|---|---|---|---|---|
| Fixed effects | 2 | 3 | 4 | 5 | 6 | 7 |
| Ewe breed | | | | | | |
| Columbia | $0.80^a \pm 0.012$ | $0.64^a \pm 0.015$ | $0.47^b \pm 0.014$ | $0.34^b \pm 0.013$ | $0.24^{ab} \pm 0.011$ | $0.15^b \pm 0.009$ |
| Polypay | $0.73^b \pm 0.012$ | $0.58^b \pm 0.013$ | $0.45^b \pm 0.012$ | $0.33^b \pm 0.011$ | $0.22^b \pm 0.009$ | $0.14^b \pm 0.008$ |
| Rambouillet | $0.79^a \pm 0.012$ | $0.64^a \pm 0.014$ | $0.52^a \pm 0.013$ | $0.39^a \pm 0.012$ | $0.27^a \pm 0.011$ | $0.17^a \pm 0.009$ |
| Targhee | $0.77^a \pm 0.011$ | $0.61^{ab} \pm 0.013$ | $0.47^b \pm 0.012$ | $0.33^b \pm 0.011$ | $0.23^b \pm 0.009$ | $0.14^b \pm 0.008$ |
| Litter size at birth | | | | | | |
| Single | $0.80^a \pm 0.009$ | $0.64^a \pm 0.011$ | --[1] | -- | -- | $0.16^a \pm 0.008$ |
| Twin | $0.76^b \pm 0.007$ | $0.60^b \pm 0.008$ | -- | -- | -- | $0.15^{ab} \pm 0.005$ |
| Triplet | $0.75^b \pm 0.013$ | $0.60^b \pm 0.015$ | -- | -- | -- | $0.13^b \pm 0.009$ |

[a-b]Means in column within each fixed effect that do not share a superscript differ ($P < 0.05$).

[1]Mean not estimated due to non-significance of the fixed effect.

**Table 9.** Estimates of additive genetic variance ($\sigma_a^2$) and heritability ($\mathrm{h}^2$) for ewe stayability from across breed analyses

| | Stayability to age | | | | | |
|---|---|---|---|---|---|---|
| Parameter | 2 | 3 | 4 | 5 | 6 | 7 |
| $\sigma_a^2$ | 0.51 ± 0.062 | 0.40 ± 0.048 | 0.29 ± 0.043 | 0.26 ± 0.044 | 0.27 ± 0.051 | 0.31 ± 0.066 |
| $\mathrm{h}^2$ | 0.34 ± 0.027 | 0.28 ± 0.025 | 0.23 ± 0.026 | 0.20 ± 0.028 | 0.21 ± 0.031 | 0.24 ± 0.038 |

***Within Breed.*** Litter size at birth of the ewe was significant for stayability to 3 and 7 yr in Columbia, to 2 yr in Polypay, to 2, 5, and 7 yr in Rambouillet, and to 2, 3, 4, 5, and 7 yr in Targhee ($P < 0.15$). Litter size at birth was significant in the analysis of Columbia for stayability to 3 and 7 yr, but no differences between the ewe litter sizes at birth were detected ($P > 0.05$; Table 10). Polypay ewes born as singles had greater stayability to 2 yr than Polypay ewes born as either twins or triplets ($P < 0.05$). A difference between the ewe litter sizes at birth was detected for Rambouillet stayability to 7 yr. Rambouillet ewes born as singles had greater stayability to 7 yr than ewes born as twins ($P = 0.048$), but neither was different from ewes born as triplets ($P > 0.05$), which could be due to the small number of triplet records for Rambouillet. No differences between litter sizes at birth were detected in analyses of stayability to 2 or 5 yr in Targhee ($P > 0.05$), but in stayability to other ages, Targhee ewes born as singles had greater stayability than ewes born as twins ($P < 0.040$), but were not different from ewes born as triplets. As with Rambouillet, Targhee ewes born as triplets were also not different from those born as twins.

**Table 10**. Within breed stayability means and SE for of ewe birth litter size born

| | Stayability to age | | | | | |
|---|---|---|---|---|---|---|
| Litter size at birth | 2 | 3 | 4 | 5 | 6 | 7 |
| Columbia | | | | | | |
| Single | --[1] | $0.71^{a} \pm 0.015$ | -- | -- | -- | $0.19^{a} \pm 0.011$ |
| Twin | -- | $0.70^{a} \pm 0.013$ | -- | -- | -- | $0.20^{a} \pm 0.009$ |
| Triplet | -- | $0.75^{a} \pm 0.028$ | -- | -- | -- | $0.15^{a} \pm 0.022$ |
| Polypay | | | | | | |
| Single | $0.72^{a} \pm 0.128$ | -- | -- | -- | -- | -- |
| Twin | $0.67^{b} \pm 0.134$ | -- | -- | -- | -- | -- |
| Triplet | $0.65^{b} \pm 0.137$ | -- | -- | -- | -- | -- |
| Rambouillet | | | | | | |
| Single | $1.00^{a} \pm 0.016$ | -- | -- | $0.43^{a} \pm 0.014$ | -- | $0.20^{a} \pm 0.011$ |
| Twin | $0.99^{a} \pm 0.019$ | -- | -- | $0.41^{a} \pm 0.012$ | -- | $0.18^{b} \pm 0.009$ |
| Triplet | $0.99^{a} \pm 0.021$ | -- | -- | $0.36^{a} \pm 0.029$ | -- | $0.15^{ab} \pm 0.020$ |
| Targhee | | | | | -- | |
| Single | $0.99^{a} \pm 0.207$ | $0.83^{a} \pm 0.640$ | $0.48^{b} \pm 0.431$ | $0.34^{a} \pm 0.313$ | -- | $0.09^{a} \pm 0.086$ |
| Twin | $0.99^{a} \pm 0.233$ | $0.81^{b} \pm 0.639$ | $0.45^{a} \pm 0.406$ | $0.32^{a} \pm 0.293$ | -- | $0.08^{b} \pm 0.074$ |
| Triplet | $0.99^{a} \pm 0.210$ | $0.84^{ab} \pm 0.639$ | $0.50^{a} \pm 0.447$ | $0.37^{a} \pm 0.339$ | -- | $0.10^{ab} \pm 0.092$ |

[a-b]Means of each breed within each fixed effect that do not share a superscript differ ($P < 0.05$).

[1]Mean not estimated due to non-significance of the fixed effect.

Estimates of heritability from the within breed analyses appeared to be (although no statistical comparison was made) lower for Columbia and Polypay ewe stayability to different ages than other breeds (Table 11). These estimates were lower than those from the across breed analyses. The few records for Suffolk ewe stayability did not support the estimation of heritability. The other estimates of heritability were surprisingly large (Table 11). The estimates of heritability for Columbia ranged from 0.08 ± 0.061 for stayability to 6 yr to 0.22 ± 0.068 for stayability to 2 yr. The estimates for heritability in Polypay ewes ranged from 0.10 ± 0.057 for stayability to 5 yr to 0.28 ± 0.048 for stayability to 2 yr. Rambouillet estimates ranged from 0.21 ± 0.039 for stayability to 5 yr to 0.83 ± 0.041 for stayability to 3 yr and Targhee estimates of heritability ranged from 0.17 ± 0.039 for stayability to 5 yr to 0.32 ± 0.045 for stayability to 2 yr. These estimates of heritability are much higher than previously estimated (Borg et al., 2009; Lee et al., 2015; Zishiri et al., 2013).

**Table 11.** Estimates of additive genetic variance ($\sigma_a^2$) and heritability ($h^2$) for ewe stayability from within breed analyses

| | Stayability to age | | | | | |
|---|---|---|---|---|---|---|
| Data set | 2 | 3 | 4 | 5 | 6 | 7 |
| Columbia | | | | | | |
| $\sigma_a^2$ | 0.29 ± 0.113 | 0.25 ± 0.081 | 0.14 ± 0.066 | 0.14 ± 0.068 | 0.09 ± 0.072 | 0.10 ± 0.090 |
| $h^2$ | 0.22 ± 0.068 | 0.20 ± 0.052 | 0.12 ± 0.050 | 0.13 ± 0.052 | 0.08 ± 0.061 | 0.09 ± 0.074 |
| Polypay | | | | | | |
| $\sigma_a^2$ | 0.38 ± 0.092 | 0.13 ± 0.066 | 0.14 ± 0.065 | 0.11 ± 0.070 | 0.18 ± 0.090 | 0.17 ± 0.123 |
| $h^2$ | 0.28 ± 0.048 | 0.12 ± 0.051 | 0.12 ± 0.050 | 0.10 ± 0.057 | 0.15 ± 0.065 | 0.14 ± 0.090 |
| Rambouillet | | | | | | |
| $\sigma_a^2$ | 0.30 ± 0.101 | 0.40 ± 0.080 | 0.27 ± 0.064 | 0.26 ± 0.062 | 0.32 ± 0.071 | 0.39 ± 0.087 |
| $h^2$ | 0.23 ± 0.060 | 0.28 ± 0.041 | 0.22 ± 0.039 | 0.21 ± 0.039 | 0.24 ± 0.041 | 0.28 ± 0.045 |
| Targhee | | | | | | |
| $\sigma_a^2$ | 0.46 ± 0.096 | 0.35 ± 0.072 | 0.23 ± 0.060 | 0.21 ± 0.058 | 0.27 ± 0.068 | 0.31 ± 0.083 |
| $h^2$ | 0.32 ± 0.045 | 0.26 ± 0.040 | 0.18 ± 0.040 | 0.17 ± 0.039 | 0.21 ± 0.042 | 0.24 ± 0.048 |
| Suffolk | | | | | | |
| $\sigma_a^2$ | 0.05 ± 0.619 | 0.30 ± 0.403 | 0.12 ± 0.362 | 0.19 ± 0.387 | 0.20 ± 0.472 | --[1] |
| $h^2$ | 0.05 ± 0.557 | 0.23 ± 0.236 | 0.11 ± 0.290 | 0.16 ± 0.270 | 0.17 ± 0.326 | -- |

[1]Estimates not obtained due to variance component of zero.

***Survival Analyses***

The statistical analyses and software used (SAS, SAS Inst. Inc., Cary, NC) permitted the statistical censoring of records. Many of the records in these data were right censored and are summarized in Tables 12 and 13 for the across breed and within breed survival analyses respectively.

**Table 12.** Number and percentages of censored records from across breed survival analyses

| Data set | Total records | Censored | Percent censored |
|---|---|---|---|
| Across breed | 11,550 | 265 | 2.29 |
| Ewe breed | | | |
| Columbia | 2,577 | 39 | 1.51 |
| Polypay | 2,936 | 43 | 1.46 |
| Rambouillet | 2,817 | 99 | 3.51 |
| Targhee | 3,220 | 84 | 2.61 |
| Litter size at birth | | | |
| Single | 2,695 | 68 | 2.52 |
| Twin | 7,256 | 157 | 2.16 |
| Triplet | 1,599 | 40 | 2.50 |

**Table 13.** Summary of censored records from within breed survival analyses

| Data set | Total records | Censored | Percent censored |
|---|---|---|---|
| Columbia | 4,389 | 331 | 7.54 |
| Litter size at birth | | | |
| Single | 1,508 | 140 | 9.28 |
| Twin | 2,594 | 180 | 6.94 |
| Triplet | 287 | 11 | 3.83 |
| Polypay | 4,534 | 74 | 1.63 |
| Rambouillet | 5,922 | 510 | 8.61 |
| Litter size at birth | | | |
| Single | 2,206 | 243 | 11.02 |
| Twin | 3,380 | 249 | 7.37 |
| Triplet | 336 | 18 | 5.36 |
| Targhee | 6,482 | 458 | 7.07 |
| Litter size at birth | | | |
| Single | 2,204 | 202 | 9.17 |
| Twin | 3,944 | 245 | 6.21 |
| Triplet | 334 | 11 | 3.29 |
| Suffolk | 213 | 5 | 2.35 |

***Across Breed.*** . The across breed survival function accounting for no strata (fixed effect) is presented in Figure 1. Survival curves differed by ewe breed ($P < 0.001$, Figure 2) and by ewe litter size at birth ($P = 0.008$, Figure 3).

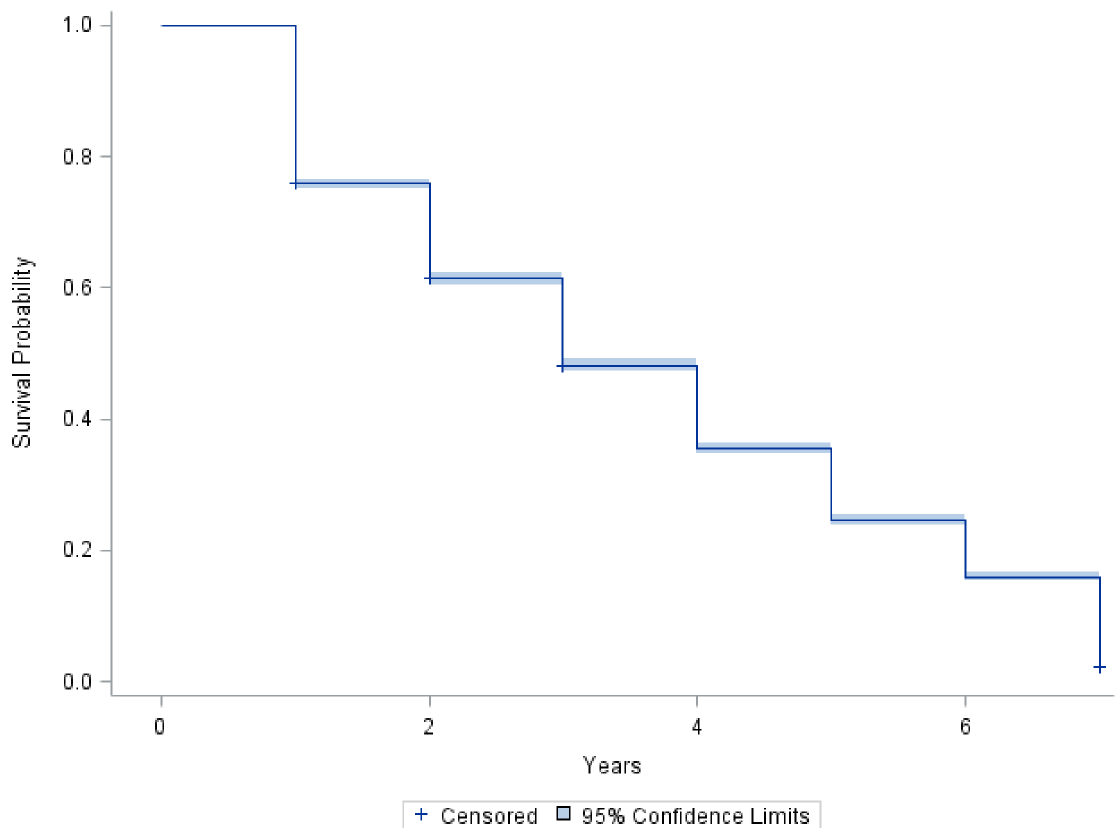


**Figure 1.** Survival curve for across breed analysis. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

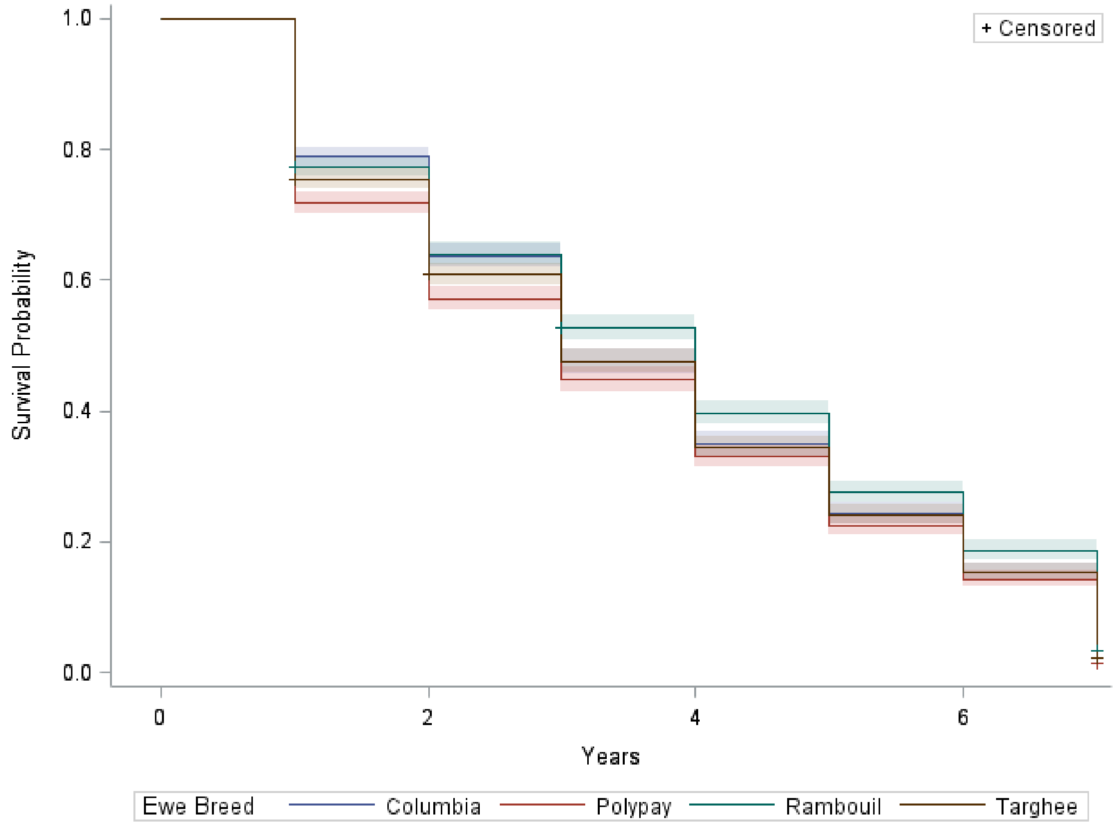


**Figure 2.** Survival curve for across breed analysis by ewe breed. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

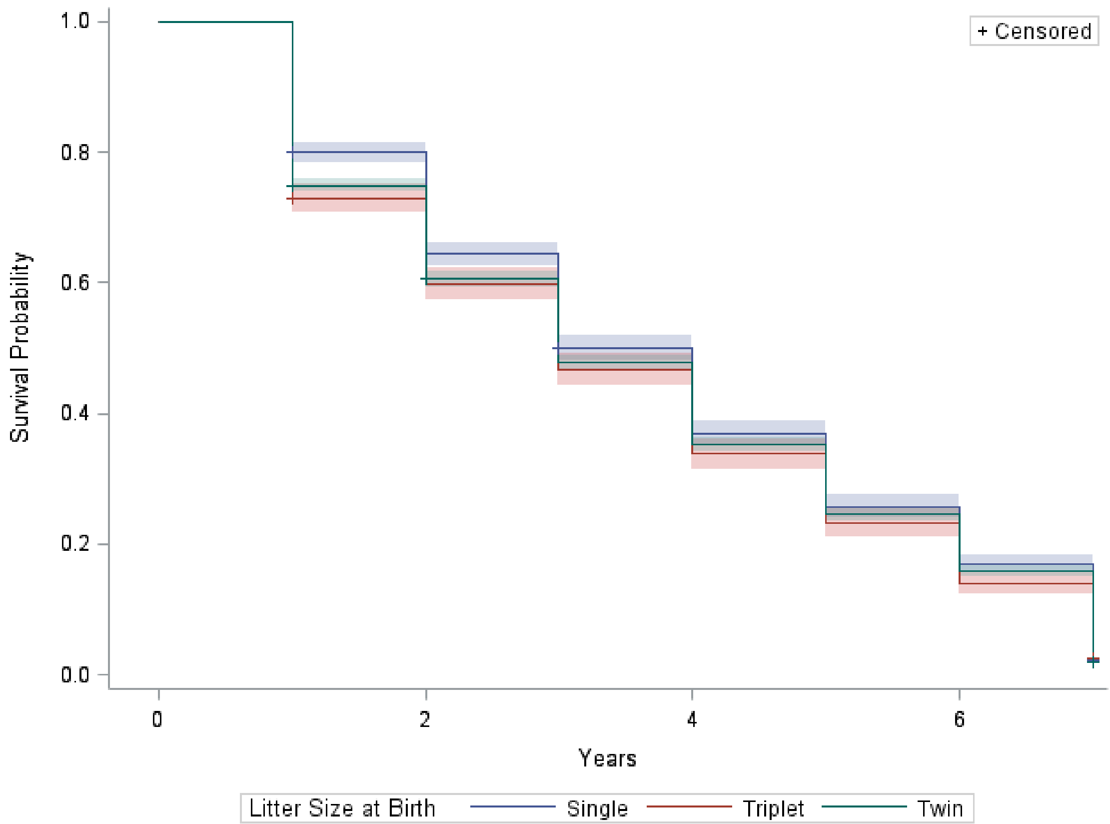


**Figure 3.** Survival curve for across breed analysis by ewe litter size at birth. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

The fixed effect means estimated from the survival functions (Table 14) are somewhat similar to the means estimated for the analysis of longevity. It should be noted that the hypothesis tested in survival analyses is for homogeneity of survival functions over strata (different levels of the classification variable, which in the present case is ewe litter size at birth) rather than comparisons of means. The probability of survival to 2 and 3 years was visually greater in Columbia than in Polypay (Figure 2) and was supported by the corresponding probabilities of survival (0.79 ± 0.008 and 0.64 ± 0.010 for

Columbia; 0.72 ± 0.008 and 0.57 ± 0.009 for Polypay, Table 14). Rambouillet had the highest mean survival to later years and Polypay had the lowest mean survival. Probabilities of survival ranged from 0.14 ± 0.007 for survival in Polypay from 6 to 7 yr to 0.79 ± 0.008 for survival in Columbia to 1 to 2 yr across all functions. Survival curves of ewe litter size at birth indicated that ewes born as singles had greater probability of survival than ewes born as triplets to most ages (Figure 3). The probability of survival due to litter size at birth ranged from 0.14 ± 0.009 for survival to 7 yr in ewes born as triplets to 0.80 ± 0.008 in survival to 2 yr in lambs born as singles. Ewes born as single lambs appeared to have larger probabilities of survival supporting their estimated survival function. Álvarez et al. (2010) reported greater survival to weaning of lambs born as singles; but the effect of the ewe's own birth litter size on her survival as a mature producing ewe has not been previously assessed.

**Table 14.** Mean survival age and probabilities of survival by ewe breed and ewe litter size at birth from across breed analyses[1]

| | | Probability of survival | | | | | |
|---|---|---|---|---|---|---|---|
| Data set | Age | 1 to 2 yr | 2 to 3 yr | 3 to 4 yr | 4 to 5 yr | 5 to 6 yr | 6 to 7 yr |
| Across breed | 3.61 ± 0.020 | 0.76 ± 0.004 | 0.61 ± 0.005 | 0.48 ± 0.005 | 0.35 ± 0.005 | 0.25 ± 0.004 | 0.16 ± 0.003 |
| Ewe breed | | | | | | | |
| Columbia | 3.65 ± 0.041 | 0.79 ± 0.008 | 0.64 ± 0.010 | 0.48 ± 0.010 | 0.35 ± 0.009 | 0.24 ± 0.009 | 0.15 ± 0.007 |
| Polypay | 3.44 ± 0.040 | 0.72 ± 0.008 | 0.57 ± 0.009 | 0.45 ± 0.009 | 0.33 ± 0.009 | 0.23 ± 0.008 | 0.14 ± 0.007 |
| Rambouillet | 3.80 ± 0.413 | 0.77 ± 0.008 | 0.64 ± 0.009 | 0.53 ± 0.009 | 0.40 ± 0.009 | 0.28 ± 0.008 | 0.19 ± 0.007 |
| Targhee | 3.58 ± 0.038 | 0.76 ± 0.008 | 0.61 ± 0.009 | 0.48 ± 0.009 | 0.34 ± 0.008 | 0.24 ± 0.008 | 0.15 ± 0.006 |
| Litter size at birth | | | | | | | |
| Single | 3.74 ± 0.041 | 0.80 ± 0.008 | 0.64 ± 0.009 | 0.50 ± 0.001 | 0.37 ± 0.009 | 0.26 ± 0.008 | 0.17 ± 0.007 |
| Twin | 3.59 ± 0.025 | 0.75 ± 0.005 | 0.61 ± 0.006 | 0.48 ± 0.006 | 0.35 ± 0.006 | 0.25 ± 0.005 | 0.16 ± 0.004 |
| Triplet | 3.51 ± 0.054 | 0.73 ± 0.011 | 0.60 ± 0.012 | 0.47 ± 0.013 | 0.34 ± 0.012 | 0.23 ± 0.011 | 0.14 ± 0.009 |

[1]Probabilities were obtained from survival functions specific to each level of fixed effects. The hypothesis tested was that of homogeneity of survival functions; probabilities extracted from those functions (like those presented here) were not statistically compared.

***Within Breed.*** Columbia survival curves (Figure 4) differed by ewe litter size at birth (*P* = 0.002, Figure 5). However, litter size at birth was not significant in the analysis of longevity nor for most stayability ages for this breed. Columbia ewes born as singles appeared to have the greatest mean survival and ewes born as triplets had the lowest probabilities of survival (Figure 5; Table 15).

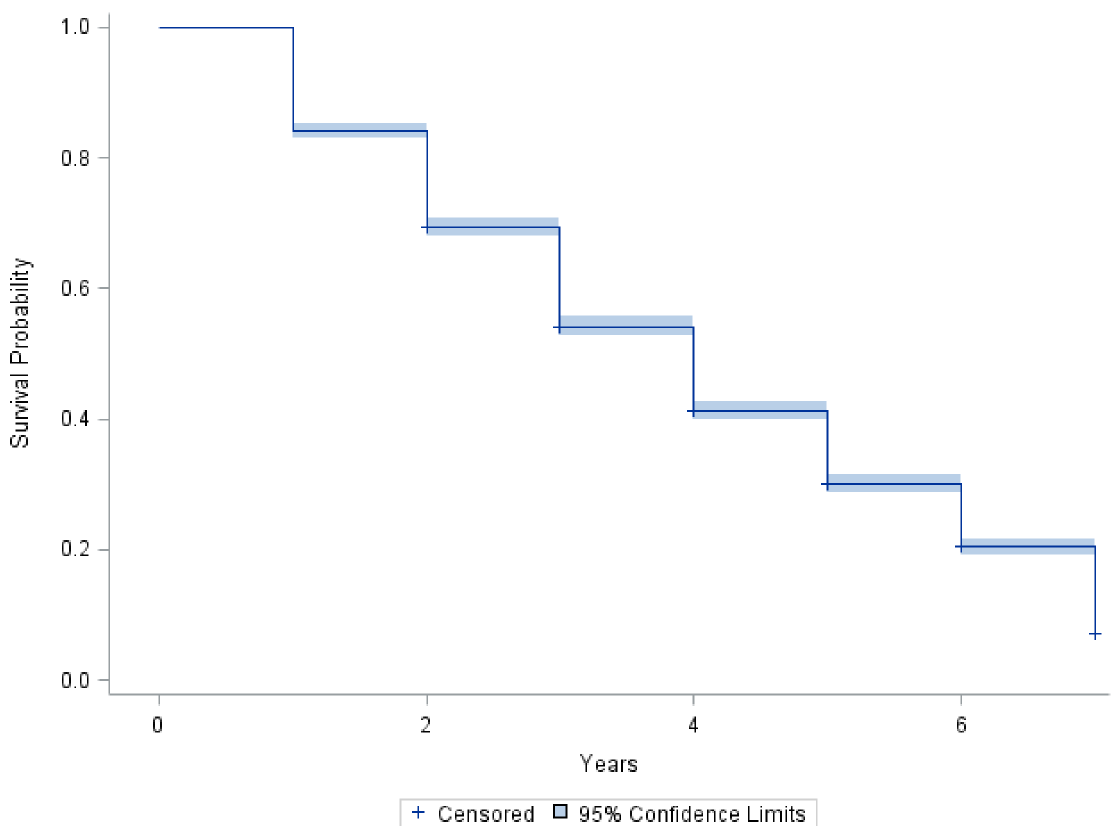


**Figure 4.** Survival curve for analysis of Columbia. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

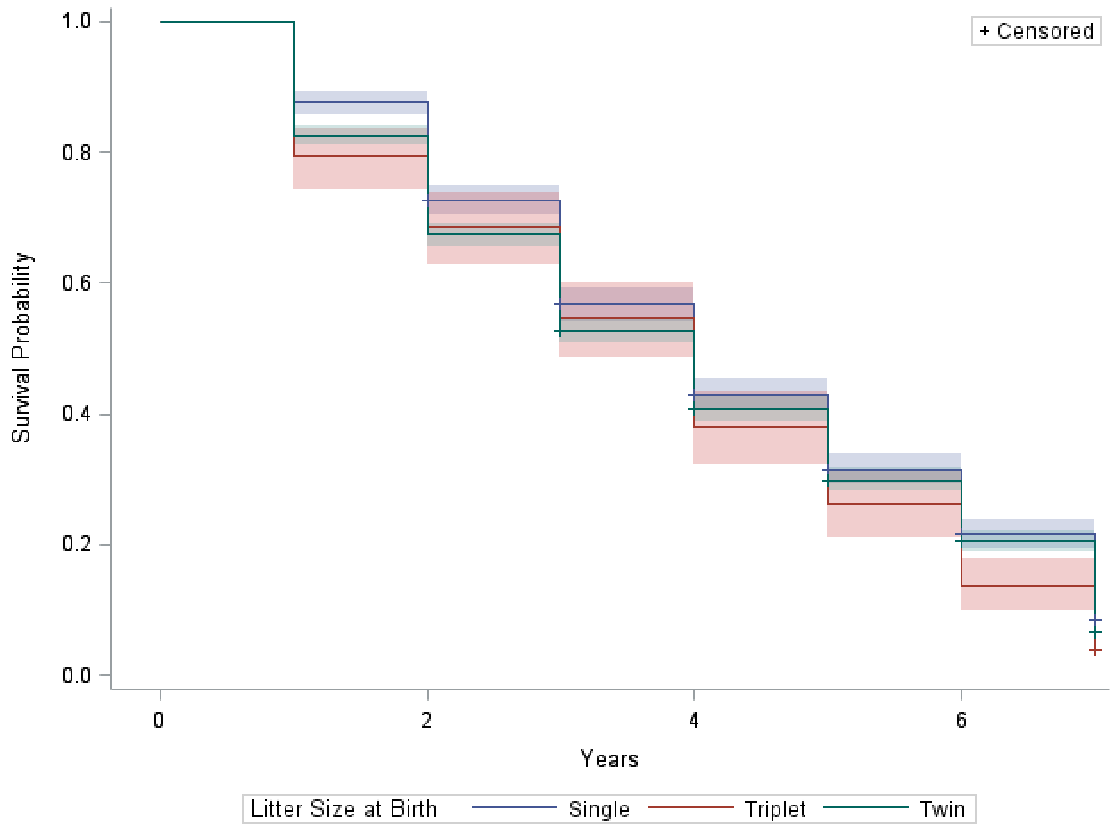


**Figure 5.** Survival curve for analysis of Columbia by ewe litter size at birth. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

**Table 15.** Mean survival age and the probability of survival by ewe litter size at birth of Columbia[1]

| | | Probability of survival | | | | | |
|---|---|---|---|---|---|---|---|
| Data set | Age | 1 to 2 yr | 2 to 3 yr | 3 to 4 yr | 4 to 5 yr | 5 to 6 yr | 6 to 7 yr |
| Columbia | 4.00 ± 0.032 | 0.84 ± 0.006 | 0.69 ± 0.007 | 0.54 ± 0.008 | 0.41 ± 0.007 | 0.30 ± 0.007 | 0.20 ± 0.006 |
| Litter size at birth | | | | | | | |
| Single | 4.13 ± 0.053 | 0.87 ± 0.008 | 0.72 ± 0.012 | 0.57 ± 0.013 | 0.43 ± 0.013 | 0.31 ± 0.012 | 0.22 ± 0.011 |
| Twin | 3.94 ± 0.042 | 0.83 ± 0.007 | 0.67 ± 0.009 | 0.53 ± 0.010 | 0.41 ± 0.010 | 0.30 ± 0.009 | 0.21 ± 0.008 |
| Triplet | 3.80 ± 0.122 | 0.79 ± 0.024 | 0.68 ± 0.027 | 0.54 ± 0.029 | 0.38 ± 0.029 | 0.26 ± 0.026 | 0.14 ± 0.020 |

[1]Probabilities were obtained from survival functions specific to each level of fixed effects. The hypothesis tested was that of homogeneity of survival functions; probabilities extracted from those functions (like those presented here) were not statistically compared.

Survival curves for Rambouillet analyses are presented in Figures 6 and 7. Litter size at birth of Rambouillet ewes was detected as an important class variable in analyses of ewe survival ($P < 0.001$). However, there was a large 95% confidence band associated with Rambouillet ewes born as triplets, similarly to Columbia ewes. Rambouillet ewes born as singles had a high probability of survival from 1 to 2 yr, especially in comparison to Rambouillet ewes born as triplets (Table 16).

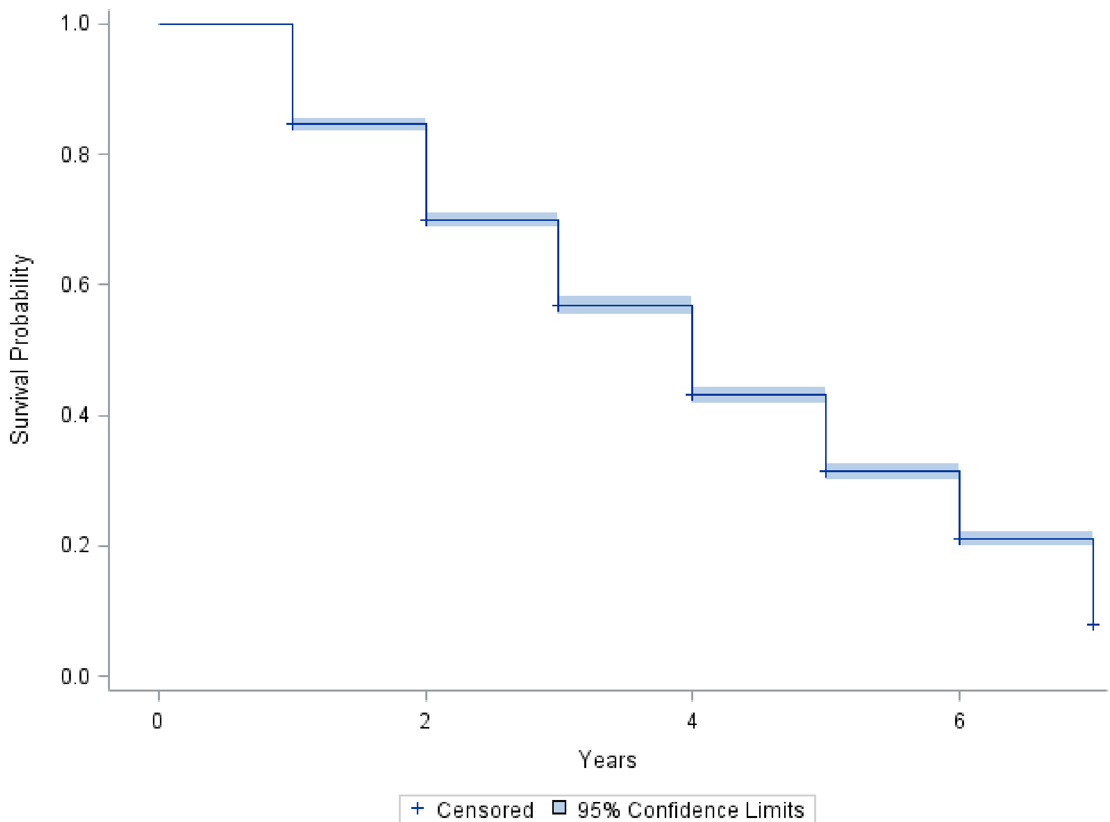


**Figure 6.** Survival curve for analysis of Rambouillet. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

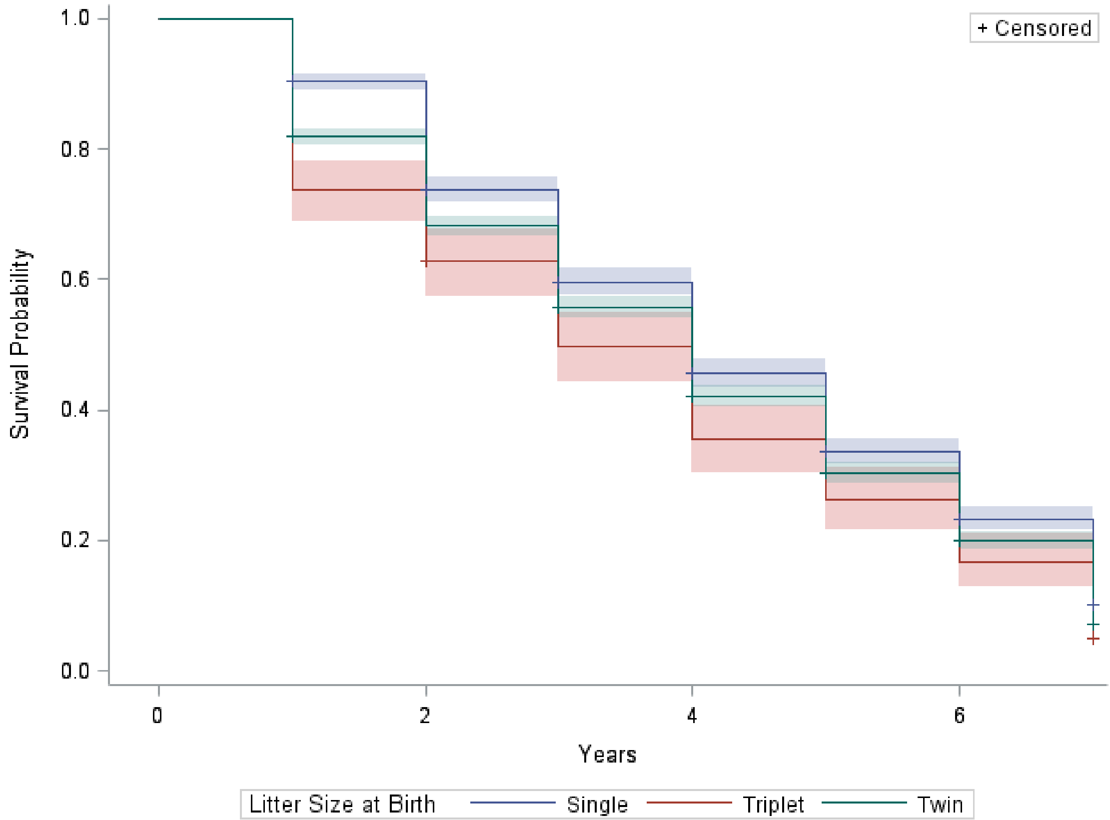


**Figure 7.** Survival curve for analysis of Rambouillet by ewe litter size at birth. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

**Table 16.** Mean survival age and the probability of survival by ewe litter size at birth of Rambouillet[1]

| | | Probability of survival | | | | | |
|---|---|---|---|---|---|---|---|
| Data set | Age | 1 to 2 yr | 2 to 3 yr | 3 to 4 yr | 4 to 5 yr | 5 to 6 yr | 6 to 7 yr |
| Rambouillet | 4.07 ± 0.028 | 0.85 ± 0.005 | 0.70 ± 0.006 | 0.57 ± 0.006 | 0.43 ± 0.006 | 0.31 ± 0.006 | 0.21 ± 0.005 |
| Litter size at birth | | | | | | | |
| Single | 4.26 ± 0.044 | 0.90 ± 0.006 | 0.74 ± 0.009 | 0.60 ± 0.011 | 0.46 ± 0.011 | 0.34 ± 0.010 | 0.23 ± 0.009 |
| Twin | 4.00 ± 0.037 | 0.82 ± 0.007 | 0.68 ± 0.008 | 0.56 ± 0.009 | 0.42 ± 0.009 | 0.30 ± 0.008 | 0.20 ± 0.007 |
| Triplet | 3.65 ± 0.120 | 0.74 ± 0.024 | 0.63 ± 0.026 | 0.50 ± 0.027 | 0.36 ± 0.026 | 0.26 ± 0.024 | 0.17 ± 0.020 |

[1]Probabilities were obtained from survival functions specific to each level of fixed effects. The hypothesis tested was that of homogeneity of survival functions; probabilities extracted from those functions (like those presented here) were not statistically compared.

The Targhee ewe survival function is presented in Figure 8. Ewe litter size at birth was significant for ewe survival ($P < 0.001$, Figure 9). The probabilities of survival (especially to the early ages) were greater in ewes born as singles than both ewes born as both twins and triplets (Figure 9, Table 17).

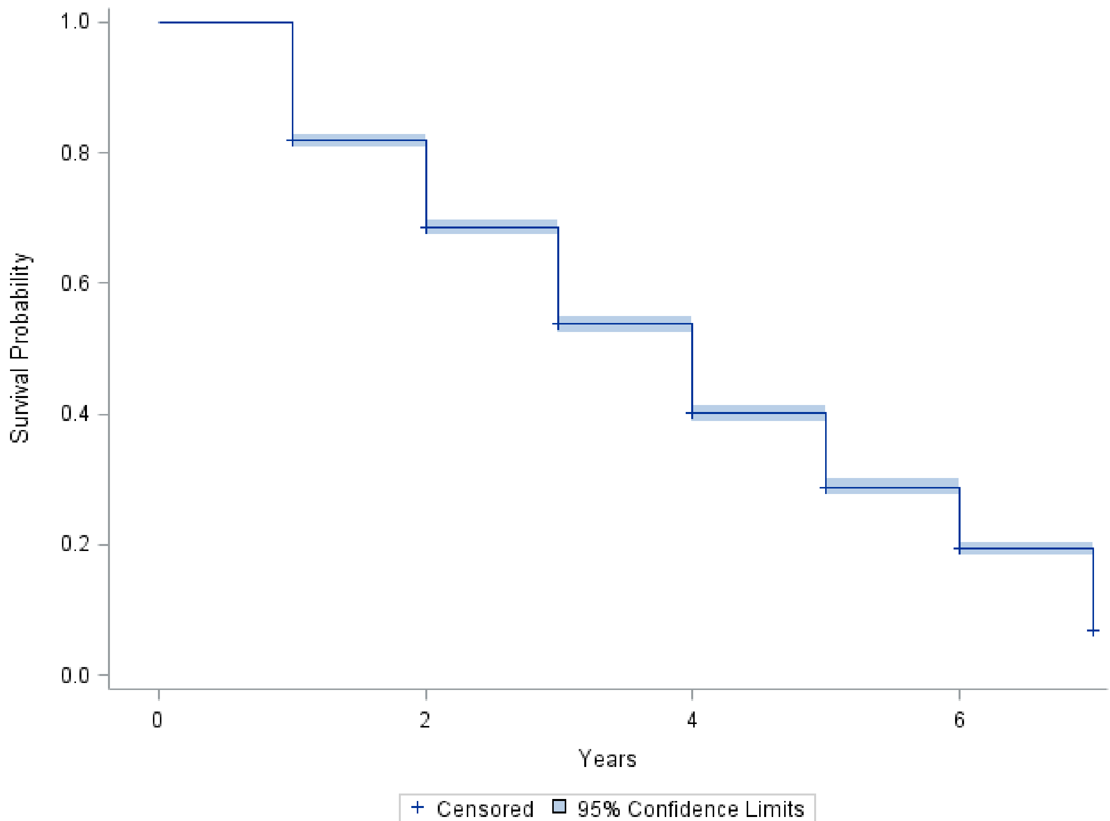


**Figure 8.** Survival curve for analysis of Targhee. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

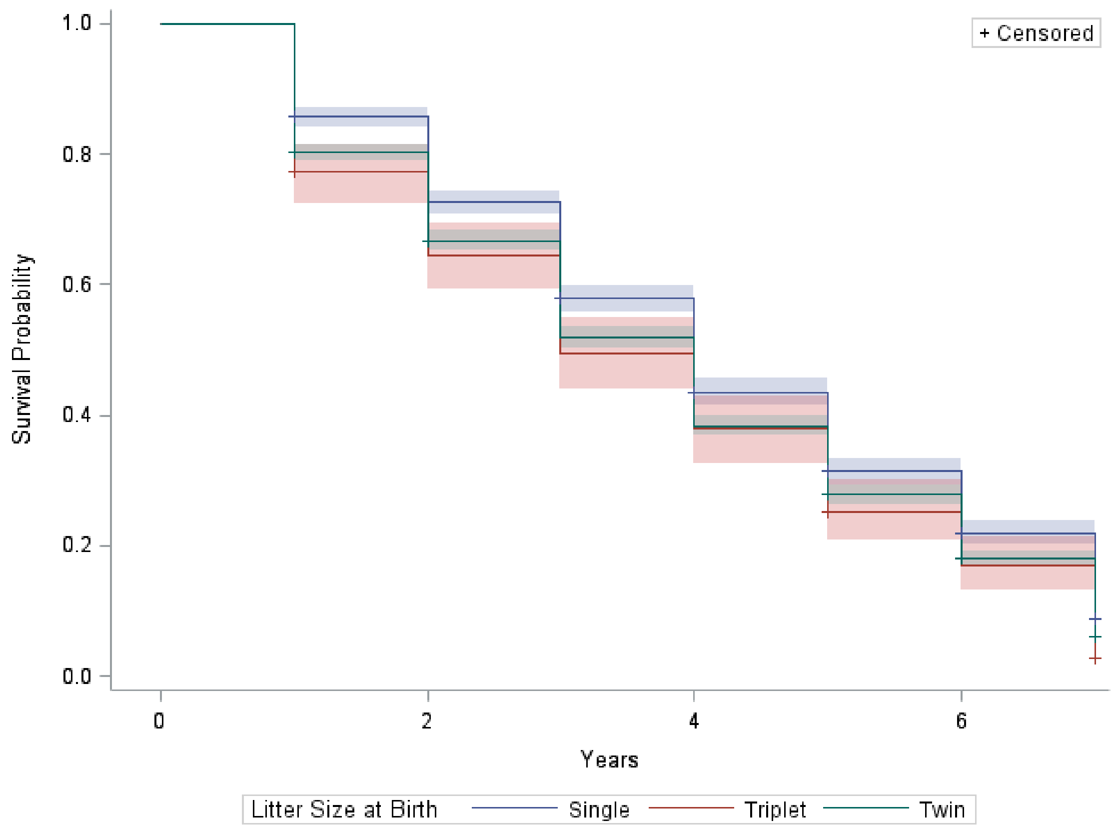


**Figure 9.** Survival curve for analysis of Targhee by ewe litter size at birth. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

**Table 17.** Mean survival age and the probability of survival by ewe litter size at birth of Targhee[1]

| | | Probability of survival | | | | | |
|---|---|---|---|---|---|---|---|
| Data set | Age | 1 to 2 yr | 2 to 3 yr | 3 to 4 yr | 4 to 5 yr | 5 to 6 yr | 6 to 7 yr |
| Targhee | 3.93 ± 0.027 | 0.82 ± 0.005 | 0.69 ± 0.006 | 0.54 ± 0.006 | 0.40 ± 0.006 | 0.29 ± 0.006 | 0.19 ± 0.005 |
| Litter size at birth | | | | | | | |
| Single | 4.13 ± 0.045 | 0.86 ± 0.008 | 0.73 ± 0.010 | 0.58 ± 0.011 | 0.44 ± 0.011 | 0.31 ± 0.010 | 0.22 ± 0.009 |
| Twin | 3.83 ± 0.034 | 0.80 ± 0.006 | 0.67 ± 0.008 | 0.52 ± 0.008 | 0.38 ± 0.008 | 0.28 ± 0.007 | 0.18 ± 0.006 |
| Triplet | 3.72 ± 0.118 | 0.77 ± 0.023 | 0.65 ± 0.026 | 0.50 ± 0.027 | 0.38 ± 0.027 | 0.25 ± 0.024 | 0.17 ± 0.021 |

[1]Probabilities were obtained from survival functions specific to each level of fixed effects. The hypothesis tested was that of homogeneity of survival functions; probabilities extracted from those functions (like those presented here) were not statistically compared.

Differences in survival due to ewe litter sizes at birth were not detected for either Polypay or Suffolk ($P > 0.15$, Figure 10 and 11). There was a very low probability of survival for Polypay ewes at early years (0.73 ± 0.007, Table 18), relative to other breeds. Suffolk ewes also had extremely low probability of survival to 7 yr (0.08 ± 0.019, Table 18).

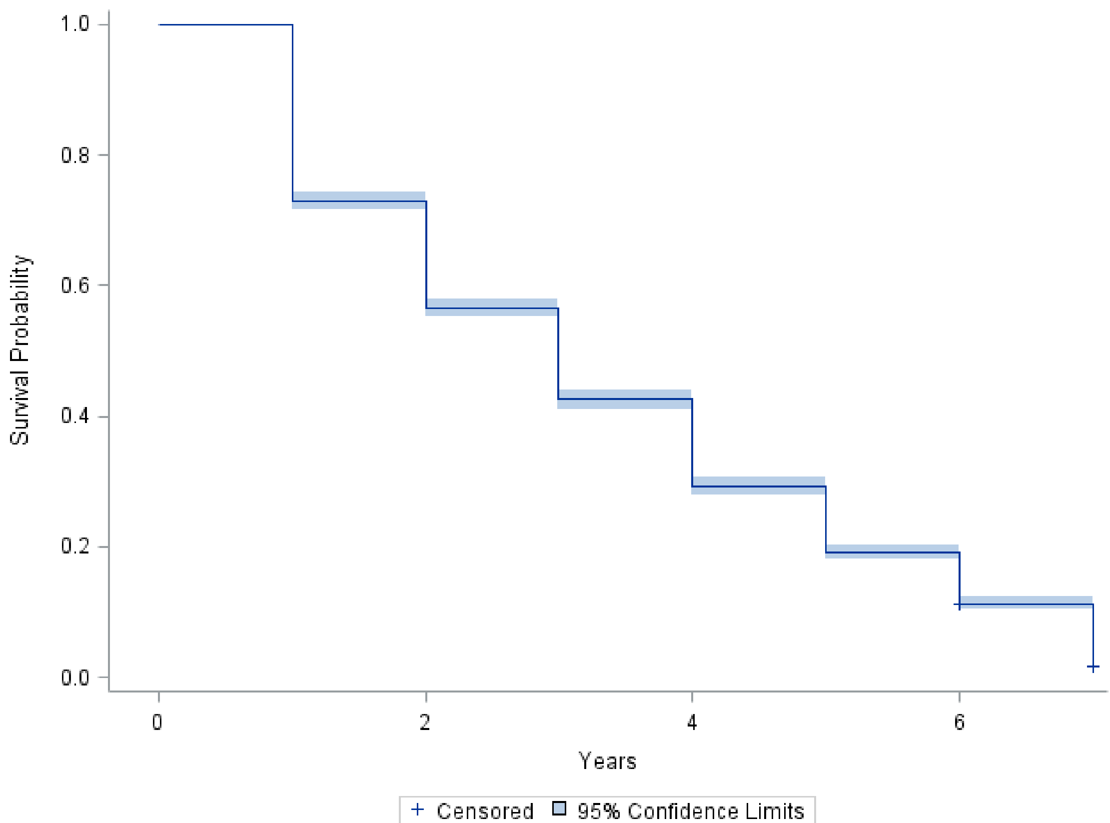


**Figure 10.** Survival curve for analysis of Polypay. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

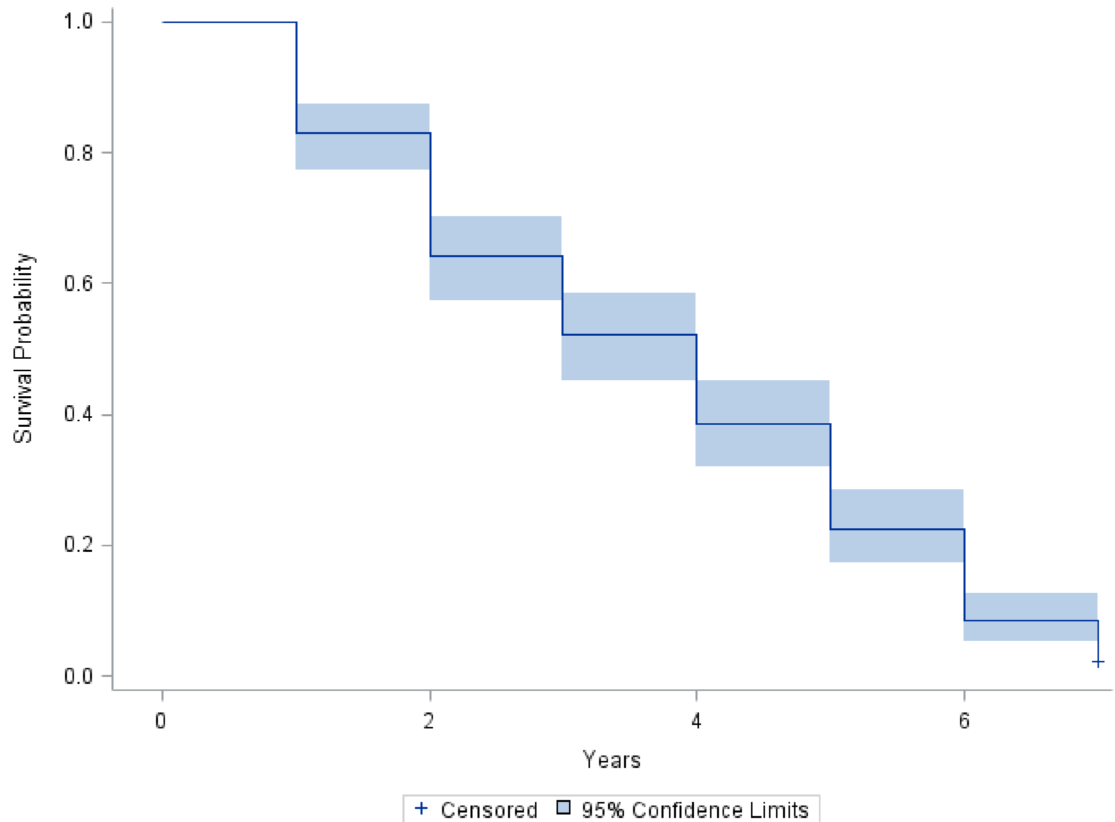


**Figure 11.** Survival curve for analysis of Suffolk. The x axis represents the age in years and the y axis represents the probability of survival. The colored bands around the probabilities represent the 95% confidence intervals for each curve.

**Table 18.** Mean survival age and the probability of survival of Polypay and Suffolk[1]

| | | Probability of survival | | | | | |
|---|---|---|---|---|---|---|---|
| Data set | Age | 1 to 2 yr | 2 to 3 yr | 3 to 4 yr | 4 to 5 yr | 5 to 6 yr | 6 to 7 yr |
| Polypay | 3.32 ± 0.030 | 0.73 ± 0.007 | 0.57 ± 0.007 | 0.43 ± 0.007 | 0.29 ± 0.007 | 0.19 ± 0.006 | 0.11 ± 0.005 |
| Suffolk | 3.69 ± 0.134 | 0.83 ± 0.026 | 0.64 ± 0.033 | 0.52 ± 0.034 | 0.39 ± 0.033 | 0.23 ± 0.029 | 0.08 ± 0.019 |

[1]Probabilities were obtained from survival functions specific to each level of fixed effects. The hypothesis tested was that of homogeneity of survival functions; probabilities extracted from those functions (like those presented here) were not statistically compared.

### *Lamb Mortality*

***Across Breed.*** Record counts by level of each fixed effect are available in Table 19. All fixed effects were significant except sex in the birth mortality analysis ($P$ = 0.542, Table 20) and year in the analysis of pneumonia ($P$ = 0.292). Likelihood ratio tests were used to determine the random effects structure for each model for each type of mortality; log-likelihood values for each are presented in Table 21. Likelihood ratio tests indicated a common structure for analyses of each mortality trait using the across breed data: the additive genetic component and the permanent environmental effect of the dam as random effects.

**Table 19.** Number of records for levels of fixed effects and numbers of deaths by mortality classification from across breed analyses

| | | Traits | | |
|---|---|---|---|---|
| Fixed effect | Total records | Overall mortality | Birth mortality | Pneumonia mortality |
| Lamb breed | | | | |
| Columbia | 11,688 | 2,472 | 538 | 170 |
| Polypay | 19,087 | 4,374 | 781 | 195 |
| Rambouillet | 14,669 | 2,945 | 527 | 169 |
| Targhee | 16,545 | 3,554 | 574 | 215 |
| Litter size at birth | | | | |
| Single | 12,411 | 1,981 | 354 | 155 |
| Twin | 38,623 | 7,630 | 1,256 | 462 |
| Triplet | 10,955 | 3,734 | 810 | 132 |
| Sex | | | | |
| Ram | 31,078 | 7,284 | 1,193 | 421 |
| Ewe | 30,911 | 6,061 | 1,227 | 328 |
| Dam age group | | | | |
| 1 yr | 7,287 | 2,179 | 290 | 160 |
| 2 yr | 12,584 | 2,663 | 470 | 162 |
| 3 to 5 yr | 30,399 | 5,972 | 1,166 | 300 |
| 6 yr and older[1] | 11,719 | 2,531 | 494 | 127 |

[1]Not limited to 7 yr of age

**Table 20.** *P*-values of *F*-statistics of fixed effects for each type of mortality from across breed analyses

| | Mortality | | |
|---|---|---|---|
| Fixed effects | Overall | Birth | Pneumonia |
| Lamb breed | < 0.001 | < 0.001 | < 0.001 |
| Litter size at birth | < 0.001 | < 0.001 | < 0.001 |
| Sex | < 0.001 | 0.542 | < 0.001 |
| Dam age group | < 0.001 | < 0.001 | < 0.001 |
| Year | < 0.001 | < 0.001 | 0.292 |

**Table 21.** Log-likelihood values for random effect models in across breed analyses

| | Log-likelihood | | |
|---|---|---|---|
| Random effects[1] | Overall mortality | Birth mortality | Pneumonia mortality |
| A | –29516.24 | –124595.12 | –154628.40 |
| A + M | –29335.94 | – 16320.95 | – 13534.27 |
| A + M + AM | –29373.69 | – 16349.95 | – 12888.60 |
| A+ PE | –28894.66 | – 15096.94 | – 12572.61 |
| A +M + PE | –29015.13 | – 15096.94 | – 12572.62 |
| A + M + AM + PE | –29062.73 | --[2] | – 11975.90 |

[1]Additive genetic (A), maternal additive genetic (M), covariance between additive and maternal (AM), and maternal permanent environmental effects (PE).
[2]The system of equations failed to converge for this trait and random effects structure.

Polypay lambs had the lowest mortality ($P < 0.03$, Table 22) in all analyses. Lambs born as triplets had greater mortality in all analyses than lambs born as twins and lambs born as singles ($P < 0.015$). This is similar to previous reports (Southey et al., 2001; 2004; Everett-Hincks and Dodds, 2008). Ram lambs had greater mean overall mortality and mortality due to pneumonia than ewe lambs ($P < 0.001$), and these results were consistent with other work (Southey et al., 2001; Southey et al., 2004). No sex effect was detected in the analysis of birth mortality ($P = 0.542$). Young dams (1-yr-old) had the greatest mortality in their lambs compared to all other ages in all analyses, whereas more mature dams had lower mortality in their lambs ($P < 0.03$). This has been previously reported in both composite and purebred sheep (Southey et al., 2004; Leeds et al., 2012).

**Table 22.** Across breed means and SE for fixed effects in analyses of lamb mortality

| | Mortality | | |
|---|---|---|---|
| Fixed effect | Overall | Birth | Pneumonia |
| Lamb breed | | | |
| Columbia | 0.318$^{a}$ ± 0.013 | 0.056$^{a}$ ± 0.005 | 0.016$^{a}$ ± 0.003 |
| Polypay | 0.192$^{c}$ ± 0.006 | 0.032$^{c}$ ± 0.002 | 0.009$^{b}$ ± 0.001 |
| Rambouillet | 0.276$^{c}$ ± 0.009 | 0.042$^{b}$ ± 0.003 | 0.013$^{a}$ ± 0.002 |
| Targhee | 0.298$^{ac}$ ± 0.009 | 0.043$^{b}$ ± 0.003 | 0.016$^{a}$ ± 0.002 |
| Litter size at birth | | | |
| Single | 0.155$^{c}$ ± 0.004 | 0.027$^{c}$ ± 0.002 | 0.009$^{c}$ ± 0.001 |
| Twin | 0.241$^{b}$ ± 0.005 | 0.034$^{b}$ ± 0.002 | 0.013$^{b}$ ± 0.001 |
| Triplet | 0.466$^{a}$ ± 0.009 | 0.084$^{a}$ ± 0.005 | 0.017$^{a}$ ± 0.002 |
| Sex | | | |
| Ram | 0.293$^{a}$ ± 0.006 | --[2] | 0.015$^{a}$ ± 0.001 |
| Ewe | 0.244$^{b}$ ± 0.005 | -- | 0.011$^{b}$ ± 0.001 |
| Dam age group | | | |
| 1 yr | 0.434$^{a}$ ± 0.010 | 0.057$^{a}$ ± 0.004 | 0.026$^{a}$ ± 0.003 |
| 2 yr | 0.250$^{b}$ ± 0.006 | 0.040$^{b}$ ± 0.003 | 0.013$^{b}$ ± 0.001 |
| 3 to 5 yr | 0.200$^{d}$ ± 0.004 | 0.036$^{b}$ ± 0.002 | 0.009$^{c}$ ± 0.001 |
| 6 yr and older[1] | 0.219$^{c}$ ± 0.006 | 0.040$^{b}$ ± 0.003 | 0.010$^{bc}$ ± 0.001 |

[a- b]Means in column within each fixed effect that do not share a superscript differ ($P < 0.05$).

[1]Not limited to 7 yr of age

[2]Mean not estimated due to fixed effect non-significance

Estimates of heritability and the maternal permanent environment effects as a proportion of the phenotypic variance ($c^2$) are presented in Table 23. These estimates were mostly of low magnitude and this is consistent with what has been previously observed in the literature (Southey et al., 2004; Everett-Hincks et al., 2014). The analysis of birth mortality yielded a high estimate for $c^2$, 0.38 ± 0.028, and it has been previously noted that the maternal component can account for a large percentage (over one half) of the genetic variation for dam related mortality events (Everett-Hincks et al., 2014). A large estimate of $h^2$ was observed in analysis of pneumonia mortality and unlike previous studies attempting to analyze respiratory disease (Southey et al., 2004), this estimate did not have high SE.

**Table 23.** Estimates of genetic parameters for lamb mortality from across breed analyses

| | Mortality | | |
|---|---|---|---|
| Parameter[1] | Overall | Birth | Pneumonia |
| $\sigma_a^2$ | 0.13 ± 0.019 | 0.34 ± 0.071 | 0.80 ± 0.185 |
| $\sigma_c^2$ | 0.15 ± 0.018 | 0.84 ± 0.070 | 0.27 ± 0.165 |
| $h^2$ | 0.10 ± 0.014 | 0.16 ± 0.030 | 0.39 ± 0.074 |
| $c^2$ | 0.12 ± 0.014 | 0.38 ± 0.028 | 0.13 ± 0.075 |

[1]Additive variance ($\sigma_a^2$), maternal permanent environmental variance ($\sigma_c^2$), additive heritability ($h^2$), and maternal permanent environmental variance as a proportion of the phenotypic variance ($c^2$).

***Within Breed.*** Number of records within levels of fixed effects are detailed in Table 24. Year was significant in all within breed analyses of mortality, except for the analysis of birth and pneumonia mortality in Suffolk ($P > 0.15$; Table 25), but it was maintained within the model. Sex was not significant ($P > 0.15$) in analyses of birth and pneumonia mortality for all breeds. The lamb's litter size at birth was a significant effect in all analyses and breeds except for analysis of pneumonia in Columbia and Suffolk ($P > 0.15$). No fixed effects were significant in the analysis of pneumonia mortality in Suffolk, possibly due to the smaller number of records compared to the rest of the breeds in the analyses (n = 1,277).

**Table 24**. Number of records of all levels of fixed effects for within breed analysis of mortality

| | Data set | | | | |
|---|---|---|---|---|---|
| Fixed effects | Columbia | Polypay | Rambouillet | Suffolk | Targhee |
| Litter size at birth | | | | | |
| Single | 1,591 | 3,424 | 2,643 | 301 | 3,313 |
| Twin | 4,367 | 15,004 | 7,613 | 856 | 8,957 |
| Triplet | 999 | 9,176 | 1,452 | 120 | 1,371 |
| Sex | | | | | |
| Ram | 3,418 | 13,828 | 5,909 | 643 | 6,884 |
| Ewe | 3,539 | 13,776 | 5,799 | 634 | 6,757 |
| Dam age group | | | | | |
| 1 yr | 738 | 6,123 | 1,044 | 251 | 1,007 |
| 2 yr | 1,518 | 5,959 | 2,092 | 252 | 2,830 |
| 3 to 5 yr | 3,503 | 11,940 | 5,936 | 585 | 6,881 |
| 6 yr and older[1] | 1,198 | 3,582 | 2,636 | 189 | 2,923 |

[1]Not limited to 7 yr of age

**Table 25.** *P*-values of *F*-statistics of fixed effects for each type of mortality for within breed analyses

| | Mortality | | |
|---|---|---|---|
| Data set | Overall | Birth | Pneumonia |
| Columbia | | | |
| Litter size at birth | < 0.001 | < 0.001 | 0.214 |
| Sex | < 0.001 | 0.200 | 0.342 |
| Dam age group | < 0.001 | 0.149 | < 0.001 |
| Year | < 0.001 | 0.001 | 0.067 |
| Polypay | | | |
| Litter size at birth | < 0.001 | < 0.001 | 0.084 |
| Sex | < 0.001 | 0.242 | 0.053 |
| Dam age group | < 0.001 | < 0.001 | < 0.001 |
| Year | < 0.001 | <0.001 | < 0.001 |
| Rambouillet | | | |
| Litter size at birth | < 0.001 | < 0.001 | 0.038 |
| Sex | < 0.001 | 0.848 | 0.913 |
| Dam age group | < 0.001 | 0.035 | 0.014 |
| Year | < 0.001 | < 0.001 | < 0.001 |
| Suffolk | | | |
| Litter size at birth | < 0.001 | 0.017 | 0.784 |
| Sex | 0.148 | 0.580 | 0.307 |
| Dam age group | < 0.001 | < 0.001 | 0.717 |
| Year | 0.011 | 0.173 | 0.743 |
| Targhee | | | |
| Litter size at birth | < 0.001 | < 0.001 | 0.004 |
| Sex | < 0.001 | 0.246 | 0.378 |
| Dam age group | < 0.001 | < 0.001 | < 0.001 |
| Year | 0.111 | < 0.001 | < 0.001 |

The log-likelihood values for within breed analysis of mortality are shown in Table 26. Likelihood ratio tests from all within breed analyses of mortality, except for pneumonia analyses and analyses of the Suffolk, indicated that the best model include only the additive genetic component and the permanent environmental effect of the dam. The analyses of overall mortality in Suffolk incorporated the additive genetic effect, the maternal additive genetic effect, and the covariance of the two as random effects.

Although more effects were supported by the likelihood ratio tests, in the Targhee analysis of pneumonia only the additive genetic component was included in the random effects. Inclusion of further random effects resulted in components with a variance of zero.

Columbia rams had a greater mean overall mortality than ewes ($P < 0.001$; Table 27) but this sex effect was not kept in the final models for birth and pneumonia mortality ($P > 0.20$). This sex difference is consistent with previous studies (Southey et al., 2001; 2004). Columbia lambs born as triplets had higher overall and birth mortality than lambs born as twins, and mortality of twins was greater than that of lambs born as singles ($P < 0.001$), and these results were consistent with previous studies (Everett-Hincks and Dodds, 2008). Lambs out of young ewes (1-yr-old) had greater mortality than lambs out of older ewes ($P < 0.040$), consistent with other work in Columbia, Suffolk, Texel, and crosses (Southey et al., 2004; Leeds et al., 2012). No effect of litter size at birth was detected ($P > 0.30$) as an effect in analysis of pneumonia mortality.

**Table 26.** Log-likelihood values for random effect models for within breed analysis of mortality

| | Log-likelihood | | |
|---|---|---|---|
| Random effects[1] | Overall mortality | Birth mortality | Pneumonia mortality |
| Columbia | | | |
| A | –3311.54 | –1909.46 | –7304.02 |
| A + M | –3278.15 | –1919.60 | –1867.25 |
| A + M + AM | –3282.22 | –1919.27 | –1966.90 |
| A+ PE | –3192.62 | –1788.30 | –1942.16 |
| A +M + PE | –3193.51 | –1803.83 | –1867.25 |
| A + M + AM + PE | --[2] | –1792.31 | –1969.67 |
| Polypay | | | |
| A | –9053.97 | –3632.65 | –83025.70 |
| A + M | –3558.21 | –4606.58 | – 9035.57 |
| A + M + AM | –3528.68 | –4610.47 | – 8742.64 |
| A+ PE | –3450.28 | –7757.37 | – 7907.67 |
| A +M + PE | –3471.94 | –7912.43 | – 7907.67 |
| A + M + AM + PE | –3442.41 | –7905.13 | -- |
| Rambouillet | | | |
| A | –6931.65 | –4291.69 | –3408.24 |
| A + M | –5589.78 | –4340.38 | –3408.23 |
| A + M + AM | –5577.85 | –4317.86 | -- |
| A+ PE | –5475.40 | –2894.92 | –3113.06 |
| A +M + PE | –5509.40 | –2894.92 | –3113.06 |
| A + M + AM + PE | –5503.77 | -- | -- |
| Suffolk | | | |
| A | –1721.81 | –2571.25 | -- |
| A + M | – 652.76 | –2597.62 | -- |
| A + M + AM | – 651.89 | -- | -- |
| A+ PE | – 652.05 | – 449.62 | -- |
| A +M + PE | – 652.76 | – 452.10 | -- |
| A + M + AM + PE | – 651.89 | -- | -- |
| Targhee | | | -- |
| A | –6424.88 | –3812.94 | –5944.82 |
| A + M | –6400.76 | –3831.85 | –4201.35 |
| A + M + AM | –6408.99 | –3794.14 | –4243.17 |
| A+ PE | –6281.02 | –3449.05 | –3317.59 |
| A +M + PE | –6310.02 | –3537.94 | –3317.59 |
| A + M + AM + PE | –6320.42 | –3489.85 | -- |

[1]Additive genetic (A), maternal additive genetic (M), covariance between additive and maternal (AM), and maternal permanent environmental effects (PE).
[2]The system of equations failed to converge for this trait and random effects structure.

**Table 27.** Means and SE for fixed effects from analyses of Columbia lamb mortality

| | Mortality | | |
|---|---|---|---|
| Fixed effect | Overall | Birth | Pneumonia |
| Litter size at birth | | | |
| Single | $0.15^{c} \pm 0.013$ | $0.03^{c} \pm 0.005$ | -- |
| Twin | $0.23^{b} \pm 0.015$ | $0.04^{b} \pm 0.006$ | -- |
| Triplet | $0.40^{a} \pm 0.026$ | $0.08^{a} \pm 0.013$ | -- |
| Sex | | | -- |
| Ram | $0.27^{a} \pm 0.017$ | --[2] | -- |
| Ewe | $0.22^{b} \pm 0.015$ | -- | -- |
| Dam age group | | | |
| 1 yr | $0.44^{a} \pm 0.029$ | $0.06^{a} \pm 0.008$ | $0.03^{a} \pm 0.008$ |
| 2 yrs | $0.22^{b} \pm 0.018$ | $0.05^{ab} \pm 0.012$ | $0.01^{b} \pm 0.003$ |
| 3 to 5 yrs | $0.18^{bc} \pm 0.013$ | $0.04^{b} \pm 0.006$ | $0.01^{b} \pm 0.003$ |
| 6 yrs and older[1] | $0.19^{bc} \pm 0.016$ | $0.04^{ab} \pm 0.007$ | $0.01^{b} \pm 0.002$ |

[a- b]Means in column within each fixed effect that do not share a superscript differ ($P <$ 0.05).

[1]Not limited to 7 yr of age

[2] Mean not estimated due to non-significance of the fixed effect.

Polypay lambs born as singles had greater mortality associated with them in all analyses ($P < 0.040$, Table 28). The sex difference detected in the analysis of overall mortality is in line with previous studies (Southey et al., 2001; 2004) but was not detected in the analysis of birth mortality ($P = 0.242$). Sex was detected to be significant in the analysis of pneumonia ($P = 0.053$). Similarly to the other within breed analyses of mortality and other studies, lambs out of 1-yr-old dams had the greatest mortality in all analyses ($P < 0.001$).

**Table 28.** Means and SE for fixed effects from analyses of Polypay lamb mortality

| | Mortality | | |
|---|---|---|---|
| Fixed effect | Overall | Birth | Pneumonia |
| Litter size at birth | | | |
| Single | $0.10^{c} \pm 0.005$ | $0.03^{c} \pm 0.003$ | $0.003^{b} \pm 0.001$ |
| Twin | $0.18^{b} \pm 0.005$ | $0.04^{b} \pm 0.003$ | $0.003^{ab} \pm 0.001$ |
| Triplet | $0.40^{a} \pm 0.008$ | $0.07^{a} \pm 0.006$ | $0.005^{a} \pm 0.001$ |
| Sex | | | |
| Ram | $0.22^{a} \pm 0.005$ | --[2] | $0.004^{a} \pm 0.001$ |
| Ewe | $0.19^{b} \pm 0.006$ | -- | $0.003^{a} \pm 0.001$ |
| Dam age group | | | |
| 1 yr | $0.36^{a} \pm 0.009$ | $0.07^{a} \pm 0.006$ | $0.008^{a} \pm 0.002$ |
| 2 yr | $0.19^{b} \pm 0.006$ | $0.04^{b} \pm 0.004$ | $0.003^{b} \pm 0.001$ |
| 3 to 5 yr | $0.14^{c} \pm 0.005$ | $0.03^{c} \pm 0.003$ | $0.003^{b} \pm 0.001$ |
| 6 yr and older[1] | $0.17^{d} \pm 0.007$ | $0.03^{bc} \pm 0.004$ | $0.002^{b} \pm 0.001$ |

[a- c]Means in column within each fixed effect that do not share a superscript differ (*P* < 0.05).

[1]Not limited to 7 yr of age

[2] Mean not estimated due to non-significance of the fixed effect.

Rambouillet ram lambs had greater overall mortality than ewe lambs (*P* < 0.001, Table 29), but sex was not influential (*P* > 0.80) for mortality at birth or pneumonia mortality in this breed. Lambs born as triplets had greater mortality (P < 0.03) of all types than lambs born as singles or twins. Lambs born as twins also had greater overall mortality than lambs born as singles (*P* < 0.001), but birth and pneumonia mortality of these two groups did not differ (*P* > 0.05). These birth litter type results were consistent with results from other breeds in the present study and with work from other investigators (Everett Hincks and Dodds, 2008; Refshauge et al., 2016). All categories of ewe age differed for overall mortality (*P* < 0.05; Table 29), in which ewes from 3 to 5 yr of age had lower mortality in their lambs than the other groups, which is in line with others (Southey et al., 2004). The effect of dam age was not as pronounced in analyses of birth or pneumonia mortality as in overall mortality.

**Table 29.** Means and SE for fixed effects from analyses of Rambouillet lamb mortality

| | Mortality | | |
|---|---|---|---|
| Fixed effect | Overall | Birth | Pneumonia |
| Litter size at birth | | | |
| Single | $0.13^{c} \pm 0.008$ | $0.02^{b} \pm 0.003$ | $0.006^{b} \pm 0.002$ |
| Twin | $0.24^{b} \pm 0.009$ | $0.03^{b} \pm 0.003$ | $0.007^{b} \pm 0.002$ |
| Triplet | $0.43^{a} \pm 0.019$ | $0.08^{a} \pm 0.011$ | $0.012^{a} \pm 0.004$ |
| Sex | | | |
| Ram | $0.27^{a} \pm 0.010$ | --[2] | -- |
| Ewe | $0.22^{b} \pm 0.009$ | -- | -- |
| Dam age group | | | |
| 1 yr | $0.42^{a} \pm 0.023$ | $0.03^{ab} \pm 0.007$ | $0.013^{a} \pm 0.004$ |
| 2 yr | $0.23^{b} \pm 0.012$ | $0.04^{ab} \pm 0.006$ | $0.009^{ac} \pm 0.003$ |
| 3 to 5 yr | $0.17^{d} \pm 0.007$ | $0.03^{b} \pm 0.003$ | $0.005^{b} \pm 0.002$ |
| 6 yr and older[1] | $0.20^{c} \pm 0.010$ | $0.04^{a} \pm 0.005$ | $0.006^{bc} \pm 0.002$ |

[a-d]Means in column within each fixed effect that do not share a superscript differ (*P* < 0.05).

[1]Not limited to 7 yr of age

[2] Mean not estimated due to non-significance of the fixed effect.

The few records of Suffolk restricted analyses of mortality to overall and birth mortality, as no fixed effect was detected as significant in the analysis of pneumonia mortality (Table 30). Greater overall and birth mortality was associated with increasing litter size ($P < 0.03$), but birth mortality of lambs born as singles or twins were not different ($P = 0.081$). No sex effect was detected in the analysis of birth mortality ($P = 0.580$), and although retained in the model for overall mortality ($P = 0.145$), the difference was not large. The youngest dams (1-yr-old) had the greatest mean overall lamb mortality ($P < 0.001$), greater than lambs of either of the older dam age categories, which did not differ from each other ($P$ > 0.10). No other birth mortality differences were detected among ewe age categories ($P$ > 0.06). These dam age results are consistent with reports for overall lamb mortality (Southey et al., 2004; Leeds et al., 2012) but not for birth mortality, as it has been shown that lambs from older ewes are more susceptible to mortality at birth (Everett-Hincks and Dodds, 2008).

**Table 30.** Means and SE for fixed effects from analyses of Suffolk lamb mortality[1]

| | Mortality | | |
|---|---|---|---|
| Fixed effect | Overall | Birth | Pneumonia |
| Litter size at birth | | | |
| Single | $0.20^{c} \pm 0.026$ | $0.03^{b} \pm 0.008$ | -- |
| Twin | $0.38^{b} \pm 0.024$ | $0.05^{b} \pm 0.009$ | -- |
| Triplet | $0.63^{a} \pm 0.052$ | $0.12^{a} \pm 0.037$ | -- |
| Sex | | | |
| Ram | $0.41^{a} \pm 0.028$ | --[2] | -- |
| Ewe | $0.37^{a} \pm 0.027$ | -- | -- |
| Dam age group | | | |
| 1 yr | $0.68^{a} \pm 0.040$ | $0.22^{a} \pm 0.043$ | -- |
| 2 yr | $0.38^{b} \pm 0.039$ | $0.05^{b} \pm 0.014$ | -- |
| 3 to 5 yr | $0.25^{c} \pm 0.024$ | $0.02^{b} \pm 0.007$ | -- |
| 6 yr and older[1] | $0.29^{bc} \pm 0.037$ | $0.03^{b} \pm 0.010$ | -- |

[1]No fixed effect was detected as significant in analyses of Suffolk pneumonia mortality.
[a-d]Means in column within each fixed effect that do not share a superscript differ ($P$ < 0.05).
[1]Not limited to 7 yr of age
[2] Mean not estimated due to non-significance of the fixed effect.

Targhee lambs born as triplets had greater ($P$ < 0.009) overall, birth, and pneumonia mortality than lambs born as twins or singles (Table 31). Lambs born as twins had greater ($P$ < 0.001) overall mortality than lambs born as singles, but those did not differ ($P$ > 0.08) in analyses of birth or pneumonia mortality in this breed. Ram lambs had greater overall mortality than ewe lambs ($P$ < 0.001), which was consistent with the sex difference reported by Southey et al. (2004); however, no sex effect was detected ($P > 0.20$) for birth or pneumonia mortality. Lambs born to 1-yr-old ewes had higher overall, birth, and pneumonia mortality than all other dam age categories; pneumonia mortality results associated with young dams are similar to those of Southey et al. (2004). Lambs born to ewes that were 3 to 5 yr of age had lower overall mortality than lambs born to ewes of other ages ($P < 0.003$) and this is in line with results from other lamb mortality studies (Southey et al., 2004; Leeds et al., 2012).

**Table 31.** Means and SE for fixed effects from analyses of Targhee lamb mortality

| | Mortality | | |
|---|---|---|---|
| Fixed effect | Overall | Birth | Pneumonia |
| Litter size at birth | | | |
| Single | $0.17^{c} \pm 0.009$ | $0.03^{b} \pm 0.003$ | $0.006^{b} \pm 0.002$ |
| Twin | $0.28^{b} \pm 0.011$ | $0.03^{b} \pm 0.003$ | $0.010^{a} \pm 0.002$ |
| Triplet | $0.49^{a} \pm 0.021$ | $0.08^{a} \pm 0.011$ | $0.015^{a} \pm 0.004$ |
| Sex | | | |
| Ram | $0.32^{a} \pm 0.013$ | --[2] | -- |
| Ewe | $0.27^{b} \pm 0.011$ | -- | -- |
| Dam age group | | | |
| 1yr | $0.49^{a} \pm 0.024$ | $0.07^{a} \pm 0.011$ | $0.019^{a} \pm 0.005$ |
| 2 yr | $0.27^{b} \pm 0.014$ | $0.04^{b} \pm 0.005$ | $0.010^{b} \pm 0.003$ |
| 3 to 5 yr | $0.22^{c} \pm 0.010$ | $0.03^{b} \pm 0.003$ | $0.007^{b} \pm 0.002$ |
| 6-yrs and older[1] | $0.25^{b} \pm 0.012$ | $0.03^{b} \pm 0.004$ | $0.007^{b} \pm 0.002$ |

[a-c]Means in column within each fixed effect that do not share a superscript differ ($P < 0.05$).
[1]Not limited to 7 yr of age
[2] Mean not estimated due to non-significance of the fixed effect.

Estimates of heritability of overall mortality from the Columbia data subset were low (Table 32), consistent with previously published estimates in New Zealand sheep and crossbred (50% Columbia, 25% Hampshire, and 25% Suffolk) sheep (Everett-

Hincks et al., 2014; Southey et al., 2001). The estimates of additive genetic variance and heritability were also greater in the subset analyses, birth and pneumonia than in overall mortality, though no statistical comparison was made. There was a more moderate estimate of $c^2$ (the maternal permanent environment as a proportion of the phenotypic variance), 0.39 ± 0.078, and a moderate estimate of $h^2$ in the pneumonia analysis, 0.26 ± 0.210. Although notably higher, the large SE of the estimates of $h^2$ and $c^2$ from analyses of pneumonia mortality necessitate cautious interpretation. The estimate of $h^2$ for pneumonia mortality was consistent with the range of heritability estimates from previous studies (Gama et al., 1991; Southey et al., 2004).

**Table 32.** Estimates of genetic parameters for Columbia lamb mortality

| | Mortality | | |
|---|---|---|---|
| Parameter[1] | Overall | Birth | Pneumonia |
| $\sigma_a^2$ | 0.10 ± 0.061 | 0.33 ± 0.204 | 0.47 ± 0.450 |
| $\sigma_m^2$ | --[2] | -- | 0.35 ± 0.326 |
| $\sigma_c^2$ | 0.26 ± 0.066 | 0.85 ± 0.196 | -- |
| | | | |
| $h^2$ | 0.08 ± 0.043 | 0.15 ± 0.087 | 0.26 ± 0.210 |
| $m^2$ | -- | -- | 0.19 ± 0.173 |
| $c^2$ | 0.19 ± 0.043 | 0.39 ± 0.078 | -- |

[1]Additive variance ($\sigma_a^2$), maternal additive variance ($\sigma_m^2$), maternal permanent environmental variance ($\sigma_c^2$), additive heritability ($h^2$), maternal additive variance as a proportion of the phenotypic variance ($m^2$), and maternal permanent environmental variance as a proportion of the phenotypic variance ($c^2$).
[2]Genetic parameter not was supported by likelihood ratio test.

Polypay analyses included the most complete random effects model (Table 33). The other analyses of mortality were similar in model terms to other within and across breed analyses. All estimates of heritability for the analysis of overall mortality were low and consistent with other reports from other studies (Southey et al., 2004; Everett-Hincks et al., 2014) ranging from 0.05 ± 0.022 for $h^2$ to 0.08 ± 0.030 for $m^2$. This was the only analysis with a correlation between the additive genetic and maternal additive genetic component estimated, which was negative and close to zero (–0.05 ± 0.023). Unlike the other breed birth mortality analyses, analysis of Polypay only supported inclusion of the additive genetic component. This estimate was very large for this trait, but a maternal component was not supported for estimation as in the other analyses, therefore some of the variance likely was accounted for in the additive genetic component. Both estimates of heritability for pneumonia mortality were large and had high SE associated with them.

**Table 33.** Estimates of genetic parameters for Polypay lamb mortality

| | Mortality | | |
|---|---|---|---|
| Parameter[1] | Overall | Birth | Pneumonia |
| $\sigma_a^2$ | 0.06 ± 0.027 | 0.89 ± 0.113 | 0.06 ± 0.264 |
| $\sigma_m^2$ | 0.10 ± 0.035 | --[2] | -- |
| $\sigma_{am}$ | –0.05 ± 0.027 | -- | -- |
| $\sigma_c^2$ | 0.06 ± 0.028 | -- | 0.52 ± 0.288 |
| | | | |
| $h^2$ | 0.05 ± 0.022 | 0.47 ± 0.032 | 0.38 ± 0.163 |
| $m^2$ | 0.08 ± 0.030 | -- | -- |
| $r_{am}$ | –0.05 ± 0.023 | -- | -- |
| $c^2$ | 0.05 ± 0.024 | -- | 0.33 ± 0.154 |

[1]Additive variance ($\sigma_a^2$), maternal additive variance ($\sigma_m^2$), covariance between additive and maternal ($\sigma_{am}$), maternal permanent environmental variance ($\sigma_c^2$), additive heritability ($h^2$), maternal additive variance as a proportion of the phenotypic variance ($m^2$), correlation between additive and maternal ($r_{am}$), and maternal permanent environmental variance as a proportion of the phenotypic variance ($c^2$).
[2]Genetic parameter was not supported by likelihood ratio test.

Likelihood ratio tests supported only the inclusion of the additive genetic component and permanent environmental effect of the dam in analyses of Rambouillet lamb mortality (Table 34). Estimates of heritability in the overall mortality analysis were low and ranged from 0.05 ± 0.030 to 0.16 ± 0.034, which are within the range of previous estimates (Gama et al., 1991; Southey et al., 2001; Southey et al., 2004; Everett-Hincks et al., 2014) and are similar to previous analyses in this study. Birth mortality had the large estimate for $c^2$, 0.41 ± 0.069. This is consistent with what was reported by Everett-Hincks et al. (2014) who concluded that maternal effects can account for large portions of genetic variation, especially when the mortality is more dam-related (Southey et al., 2004). Pneumonia mortality had a low estimate of $h^2$, 0.17 ± 0.195, and was moderate for the maternal permanent environment effect, 0.24 ± 0.197. More moderate estimates have been previously estimated in other analyses of pneumonia (Southey et al., 2004), but both of these estimates have large SE.

**Table 34.** Estimates of genetic parameters for Rambouillet lamb mortality

| | Mortality | | |
|---|---|---|---|
| Parameter[1] | Overall | Birth | Pneumonia |
| $\sigma_a^2$ | 0.06 ± 0.039 | 0.25 ± 0.168 | 0.28 ± 0.354 |
| $\sigma_c^2$ | 0.21 ± 0.048 | 0.85 ± 0.173 | 0.40 ± 0.375 |
| | | | |
| $h^2$ | 0.05 ± 0.030 | 0.12 ± 0.075 | 0.17 ± 0.195 |
| $c^2$ | 0.16 ± 0.034 | 0.41 ± 0.069 | 0.24 ± 0.197 |

[1]Additive variance ($\sigma_a^2$), maternal permanent environmental variance ($\sigma_c^2$), additive heritability ($h^2$), and maternal permanent environmental variance as a proportion of the phenotypic variance ($c^2$).

The number of Suffolk records were not sufficient to support estimation of the parameters reported in Table 35. Estimates were similar to that in the other breeds, but had high SE associated with them, and therefore are unreliable.

**Table 35.** Estimates of genetic parameters for Suffolk lamb mortality

| | Mortality | | |
|---|---|---|---|
| Parameter[1] | Overall | Birth | Pneumonia |
| $\sigma_a^2$ | 0.09 ± 0.171 | 0.05 ± 0.497 | -- |
| $\sigma_m^2$ | 0.22 ± 0.201 | -- | -- |
| $\sigma_{am}$ | –0.11 ± 0.208 | -- | -- |
| $\sigma_c^2$ | --[2] | 0.64 ± 0.415 | -- |
| | | | |
| $h^2$ | 0.08 ± 0.136 | 0.03 ± 0.278 | -- |
| $m^2$ | 0.19 ± 0.164 | -- | -- |
| $r_{am}$ | –0.09 ± 0.162 | -- | -- |
| $c^2$ | -- | 0.38 ± 0.229 | -- |

[1]Additive variance ($\sigma_a^2$), maternal additive variance ($\sigma_m^2$), covariance between additive and maternal ($\sigma_{am}$), maternal permanent environmental variance ($\sigma_c^2$), additive heritability ($h^2$), maternal additive variance as a proportion of the phenotypic variance ($m^2$), correlation between additive and maternal ($r_{am}$), and maternal permanent environmental variance as a proportion of the phenotypic variance ($c^2$).
[2]Genetic parameter was not supported by likelihood ratio test.

A low estimate of heritability was detected in the analysis of Targhee overall mortality, 0.10 ± 0.031 for $h^2$ and a low estimate of $c^2$, 0.18 ± 0.030 (Table 36). There was a moderate estimate of heritability in the birth mortality analysis, 0.41± 0.071, but the other estimates were low. The additive genetic component was the only random effect supported by likelihood ratio tests for inclusion in the pneumonia analysis and this estimate of heritability was low, with a large standard error associated with it, 0.06 ±

0.204. These estimates are similar to previous reports (Everett-Hincks and Dodds, 2014; Southey et al., 2004; Southey et al., 2001) and similar to other estimates in this study.

**Table 36.** Estimates of genetic parameters for Targhee lamb mortality

| | Mortality | | |
|---|---|---|---|
| Parameter[1] | Overall | Birth | Pneumonia |
| $\sigma_a^2$ | 0.14 ± 0.046 | 0.20 ± 0.168 | 0.06 ± 0.235 |
| $\sigma_c^2$ | 0.25 ± 0.046 | 0.84 ± 0.170 | --[2] |
| | | | |
| $h^2$ | 0.10 ± 0.031 | 0.10 ± 0.078 | 0.06 ± 0.204 |
| $c^2$ | 0.18 ± 0.030 | 0.41 ± 0.071 | -- |

[1]Additive variance ($\sigma_a^2$), maternal permanent environmental variance ($\sigma_c^2$), additive heritability ($h^2$), and maternal permanent environmental variance as a proportion of the phenotypic variance ($c^2$).
[2]Genetic parameter was not supported by likelihood ratio test.

# CONCLUSIONS

## ***Ewe Lifetime Traits***

Estimates of genetic parameters and least squares means for ewe productive life were investigated. Of the main effects of interest, the ewe's litter size at birth was determined to have a significant effect on longevity in some analyses, but the ewe's litter size at rearing did not have a significant effect on longevity in any analyses. The smaller litter sizes at birth were associated with higher longevity in most of the analyses; that is, it may be that less competition for nourishment and development early in life positively impacts ewe productivity and how long the ewe will remain in the flock. Though most of the analyses had sufficient records, only the additive genetic component could be estimated; any further terms attempted in the random structure of the model resulted in a zero variance for that parameter. These low estimates of heritability were expected as this is typical of reproductive traits. The estimates of heritability in the analyses ranged from $0.06 \pm 0.022$ for the within breed analysis of Columbia to $0.16 \pm 0.024$ for the within breed analysis of Rambouillet.

Results of analyses of stayability were similar results to those of longevity, with litter size at rearing not a significant effect in any analysis and litter size at birth being a significant effect, although not significant in stayability to all ages. In the analyses that included litter size at birth as a significant effect, smaller litter sizes again tended to have greater stayability to each age associated with them, but this was not the case for all analyses. Likelihood ratio tests supported the inclusion of only the additive genetic component, just as in longevity. Estimates of heritability were lower for stayability to older ages. The estimates were slightly higher than previous estimates of heritability that have been reported. Most of the estimates were higher and more moderate than the estimates of heritability for longevity, ranging from 0.08 ± 0.061 for stayability to 6 yr in Columbia to 0.34 ± 0.027 for stayability to 2 yr in the across breed analyses.

The probability of survival was lower at stayability to later ages. In the analyses of longevity and stayability, ewes born as singles had the highest mean survival age in all models, though these values were not statistically tested for differences. The survival curves were able to detect significant fixed effects and each was analyzed separately. The ewe's litter size at birth was detected to be significant for survival in Columbia, which was not the case for longevity and most of the stayability in Columbia. Polypay ewe litter size at birth was not detected to be important to survival analysis ($P > 0.15$), in contrast to the analyses of longevity and stayability. Large confidence intervals were associated with some of the survival curves, these being the analyses or level of fixed effect that did not have large number of records.

Overall, these results show that selection for longevity and stayability could be implemented, though these traits are lowly heritable. Selection for stayability to the early years of life seems much more probable based upon the higher estimates of heritability. Other studies have attempted to look for genetic correlations between other traits and survival to help in this selection. Some of the breed specific comparisons suggest that prolificacy may have played a part in longevity and stayability, as well, and warrant further investigation, as Polypay ewes tended to have lower lifetime productivity than some of the other breeds. In general, ewes born as single lambs had higher lifetime reproductive performance measured as longevity, stayability, and survival than ewes born in litters.

***Lamb Mortality***

The lamb's litter size at birth was a significant effect on most of the evaluated mortality traits and as mortality was greater in lambs born as triplets than the other litter sizes. Sex was never detected as an important influence on birth or pneumonia mortality, but was influential on overall mortality as ram lambs had greater mortality than ewe lambs. Young dams were also consistently associated with greater mortality in their lambs than older dam categories for most analyses.

Estimates of heritability ($h^2$) and the maternal permanent environment as a proportion of the phenotypic variance ($c^2$) were similar from analyses of the different data sets; most were low, especially for the analysis of overall mortality. Estimates of $c^2$ ($> 0.3$) were obtained in all analyses of birth mortality indicating the importance of maternal influence on this trait. Most estimates of heritability from the analyses of pneumonia suggest that a large portion of the variation is due to additive genetic effects, but the standard errors in most analyses were very large.

There is potential for effective selection programs for these traits. There were breeds and specific litter sizes at birth that were more susceptible to mortality. Inclusion of crossbred records in the next evaluations will be an important step in identification of appropriate selection and crossbreeding strategies for improvement of lamb mortality.

# LITERATURE CITED


Allison, P. D. 2010. Survial analysis using SAS: A practical guide, Second Edition. Cary, NC: SAS Insitute Inc.

Álvarez, M., R. M. Rodríguez Iglesias, J. García Vinent, H. Giorgetti, and M. Baselga. 2010. Introduction of meat sheep breeds in extensive systems of Patagonia: Lamb growth and survival. J. Anim. Sci. 88: 1256–1266.

Annett, R. W., A. F. Carson, L. E. R. Dawson, D. Irwin, A. W. Gordon, and D. J. Kilpatrick. 2011. Comparison of the longevity and lifetime performance of Scottish Blackface ewes and their crosses within hill sheep flocks. Animal 5: 347–355.

Borg, R. C., D. R. Notter, and R. W. Kott. 2009. Genetic analysis of ewe stayability and its association with lamb growth and adult production. J. Anim. Sci. 87: 3515–3524.

Casas, E., B. A. Freking, and K. A. Leymaster. 2004. Evaluation of Dorset, Finnsheep, Romanov, Texel, and Montadale breeds of shep: II. Reproduction of $F_1$ ewes in fall mating seasons. J. Anim. Sci. 82: 1280-1289.

Casas, E., B. A. Freking, and K. A. Leymaster. 2005. Evaluation of Dorset, Finnsheep, Romanov, Texel, and Montadale breeds of sheep: V. Reproduction of $F_1$ ewes in spring mating seasons. J. Anim. Sci. 83: 2743-2751.

Douhard, F., N. B. Jopson, N. C. Friggens, and P. R. Amer. 2016. Effects of the level of early productivity on the lifespan of ewes in contrasting flock environments. Animal 10: 2034–2042.

Dwyer, C. M., J. Conington, F. Corbiere, I. H. Holmøy, K. Muri, R. Nowak, J. Rooke, J. Vipond, and J. M. Gautier. 2016. Invited review: Improving neonatal survival in small ruminants: science into practice. Animal. 10: 449–459.

Everett-Hincks, J. M., and K. G. Dodds. 2008. Management of maternal-offspring behavior to improve lamb survival in easy care sheep systems. J. Anim. Sci. 86(E. Suppl.): E259–E270.

Everett-Hincks, J. M., H. C. Mathias-Davis, G. J. Greer, B. A. Auvray, and K. G. Dodds. 2014. Genetic parameters for lamb birth weight, survival and death risk traits. J. Anim. Sci. 92: 2885–2895.

Gama, L. T., G. E. Dickerson, L. D. Young, and K. A. Leymaster. 1991. Genetic and phenotypic variation in sources of preweaning lamb mortality. J. Anim. Sci. 69: 2744–2753.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. 2015. ASReml User Guide Release 4.1 Structural Specification. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK.

Holmøy, I. H. S. Waage, E. G. Granquist, T. M. L'Abée-Lund, C. Ersdal, L. Hektoen, and R. Sørby. 2017. Early neonatal lamb mortality: postmortem findings. Animal. 11: 295–305.

Hudson, G. F. S., and L. D. Van Vleck. 1981. Relationship between production and stayability in Holstein cattle. J. Dairy Sci. 64: 2246–2250.

Lee, M. A., N. G. Cullen, S. A. N. Newman, K. G. Dodds, J. C. McEwan, and G. H. Shackell. 2015. Genetic analysis and genomic selection of stayability and productive life in New Zealand ewes. J. Anim. Sci.: 3268–3277.

Leeds, T. D., D. R. Notter, K. A. Leymaster, M. R. Mousel, and G. S. Lewis. 2012. Evaluation of Columbia, USMARC-Composite, Suffolk, and Texel rams as terminal sires in an extensive rangeland production system: I. Ewe productivity and crossbred lamb survival and preweaning growth. J. Anim. Sci. 90: 2931–2940.

Leymaster, K. A. 1991. Straightbred comparison of a composite population and the Suffolk breed for performance traits of sheep. J. Anim. Sci. 69: 993–999.

Lopez-Villalobos, N., and D. J. Garrick. 1999. Genetic parameter estimates for lamb survival in Romney sheep. Proc. N. Z. Soc. Anim. Prod. 59: 121–124.

McHugh, N., T. Pabiou, K. McDermott, E. Wall, and D. P. Berry. 2017. Impact of birth and rearing type, as well as inaccuracy of recording, on pre-weaning lamb phenotypic and genetic merit for live weight. Transl. Anim. Sci. 1: 137–145.

Mekkawy, W. et al. 2009. Genetic relationship between longevity and objectively or subjectively assessed performance traits in sheep using linear censored models. J. Anim. Sci. 87: 3482–3489.

Morris, C. A., S. M. Hickey, and J. N. Clarke. 2000. Genetic and environmental factors affecting lamb survival at birth and through to weaning. N. Z. J. Agri. Res. 43: 515–524.

National Agricultural Statistics Service (NASS). 2010. Sheep and goats death loss. http://usda.mannlib.cornell.edu/usda/current/sgdl/sgdl-05-27-2010.pdf. Accessed 10 March 2017.

National Agricultural Statistics Service (NASS). 2016. Sheep and goats. http://usda.mannlib.cornell.edu/usda/nass/SheeGoat//2010s/2016/SheeGoat-01-29-2016.pdf Accessed 15 December 2017.

National Agricultural Statistics Service (NASS). 2017. Sheep and goats. http://usda.mannlib.cornell.edu/usda/current/SheeGoat/SheeGoat-01-31-2017.pdf Accessed 15 December 2017.

Notter, D. R. 2012. Genetic improvement of reproductive efficiency of sheep and goats. Anim. Reprod. Sci. 130: 147–151.

Notter, D. R., and D. J. Brown. 2015. Effects of birth-rearing type on weaning weights in meat sheep are systematically associated with difference in mean performance among flocks. Gen. Sel. Evol. 47: 57–70.

Notter, D. R., M. R. Mousel, G. S. Lewis, K. A. Leymaster, and J. B. Taylor. 2017. Evaluation of Rambouillet, Polypay, and Romanov−White Dorper & Rambouillet ewes mated to terminal sires in an extensive rangeland production system: Lamb production. J. Anim. Sci. 95: 3851–38622.

Refshauge, G., F. D. Brien, G. N. Hinch, and R. van de Ven. 2016. Neonatal mortality: factors associated with the death of Australian lambs. Anim. Prod. Sci. 56: 726–735.

Southey, B. R., S. L. Rodriguez-Zas, and K. A. Leymaster. 2001. Survival analysis of lamb mortality in a terminal sire composite population. J. Anim. Sci. 79: 2298–2306.

Southey, B. R., S. L. Rodriguez-Zas, and K. A. Leymaster. 2004. Competing risks analysis of lamb mortality in a terminal sire composite population. J. Anim. Sci. 82: 2892–2899.

Zishiri, O. T., S. W. P. Cloete, J. J. Olivier, and K. Dzama. 2013. Genetic parameters for growth, reproduction and fitness traits in the South African Dorper sheep breed. Small Rumin. Res. 112: 39–48.