Chapter 4 Evaluation of lamb survival using survival analysis techniques

4.1 INTRODUCTION

Lamb survival is a complex trait influenced by many different factors associated with management, climate, behavior of the ewe and lamb, and other environmental effects (Smith, 1977; Christley et al., 2003; Everett-Hincks et al., 2005). Improving lamb survival through genetic selection is challenging because of the large number of environmental factors influencing the trait, as well as the challenge of properly evaluating a binomially expressed trait. Heritability estimates are typically low (0.00 to 0.11; Safari et al., 2005), hindering the rate of genetic improvement. Cundiff et al. (1982) suggested selecting on correlated traits that are more reliably evaluated to make genetic improvement in lamb survival. However, genetic relationships between lamb survival and other traits must exist for successful response to selection on correlated traits.

Survival analysis procedures have been adapted for the study of time and occurrence of death in livestock (Smith and Quass, 1984; Ducrocq et al., 1988). Survival analysis models have been used to evaluate survival in many different livestock species (Ducrocq et al., 2000; Vukasinovic et al., 2001; Caraviello et al., 2004; Rogers et al., 2004; Serenius and Stalder, 2004; Sewalem et al., 2005; Sawalha et al., 2007). Difference between survival analysis models and more conventional survival evaluation models are that time-dependent variables and censored records may be incorporated into survival analysis models. Time-dependent effects include factors that have a changing effect on survival as the length of exposure to that factor increases. Censored records are those from animals that entered the study but were either removed for reasons other than death or were still alive at the end of the study.

Incorporation of censored records in a survival analysis is theoretically superior to evaluations that exclude these records (Kalbfleisch and Prentice, 1980; Allison, 1997; Klein and Moeschberger 1997). However, selective censoring potentially introduces bias into the evaluations. In lamb survival data, selective censoring occurs when producers preferentially remove small, poor doing lambs in general, and less vigorous lambs from large litters in the flock. The objective of this study was to use survival analysis techniques to evaluate the influence of selective censoring on estimation of factors influencing lamb survival to weaning.

4.2 MATERIALS AND METHODS

4.2.1 Data

The data set included 20,082 spring-born Polypay lambs from 410 sires and 3,690 dams managed in a range environment at the U.S. Sheep Experiment Station, Dubois Idaho. Lambs were born between 1978 and 2005, primarily in April and under shed lambing conditions. Management practices for this population were similar to those described in Ercanbrack and Knight (1998). Ewes were individually penned with their lambs 1 to 2 d immediately after birth. Ewes were then moved with their lambs to outdoor grouping lots and kept close to the station headquarters until being moved to summer mountain range in mid-June. Lambs were typically weaned in mid-August at approximately 120 d of age.

Lambs were typically nursed by their birth dam. However, lambs were removed from their original litter when they appeared unhealthy and could not compete with littermates, or when the ewe was subjectively judged to be unable to successfully nurse the entire litter. Lambs that were not nursed by the birth dam or orphaned for artificial rearing were assumed to be removed from the flock at the time they were removed from their litter, and records from these lambs were considered censored. When possible, lambs that were removed from their litter were nursed by a different ewe within the flock, but in order to avoid unknown environmental effects on lamb survival and because the time of cross-fostering was not recorded, data were edited to remove lambs that were cross-fostered within the flock (4.9 %). Lambs born in litters of more than 4 lambs (0.2 %) were also excluded from the analysis. Lamb records included year of birth, age of dam at lambing, number of lambs born and nursed by the dam, lamb sex, lamb body weight at birth (**BWT**), and day of age when a lamb was either removed from the flock or died. Age of dam was recorded in years of age at the time of lambing. Ewes that were greater than 6 yrs of age at lambing were grouped into a common 7+ age grouping. Lamb sex included ewes, rams, and wethers. Male lambs judged to have no potential as breeding animals (33.0% of total male lambs) were castrated within 2 d of birth by elastration banding. All male lambs removed from their original litter were castrated.

4.2.2 Statistical Analysis

Lamb survival from birth to weaning was analyzed with a Weibull proportional hazards model using the Survival Kit V3.12 software from Ducrocq and Solkner (2000). Lamb survival was recorded as the age of death, in days, between birth and weaning with day of birth equal to 1 d of age. Lambs that did not have a recorded age of death were assumed to be censored. Censored lamb records were included in the data set because survival analysis models account for known lamb survival time until death or a censoring event (Cox, 1972). Retaining censored records accounts for known lamb survival to a given age and more appropriately incorporates all available data into the evaluation, compared to linear and logistic analyses (Kalbfleisch and Prentice, 1980; Allison, 1997; Klein and Moeschberger, 1997). Lambs that remained in the flock to weaning were considered censored at their weaning age. The censoring event associated with weaning corresponded to the end of the survival evaluation and therefore was considered to represent a successful record. Live lambs that were removed from the flock before weaning were censored at the day of removal. This censoring included lambs that were recorded as missing from the flock while on pasture because no lamb or carcass was found and the age of death could not be determined. Records for lambs that died due to accidental deaths (0.1% of lambs born) or lambs removed from the flock for unknown reasons before weaning (2.9% of lambs born) were also treated as censored.

Kaplan-Meier survival curves were estimated using all the available data for each day between birth and weaning. The resulting survival curve represents the probability of lamb death at a specific day. Kaplan-Meier curves are calculated as

$$S(t_i) = \left[1 - \frac{\#\mathbf{Dead}(t_i)}{\#\mathbf{Lambs}(t_i)}\right]$$

where $S(t_i)$ = Kaplan-Meier survival estimate at time (t_i), **# Dead** = number of dead lambs at time (t_i) , **# Lambs** = total number of lambs that could have died at time (t_i), adapted from Klein and Moeschberger (1997). This survival function does not account for fixed effects on lamb survival.

Hazard models evaluate the risk of lamb death that corresponds to exploratory variables included in the model. The risk of death associated with each level of a variable was expressed as a risk ratio, which describes the proportional risk of death associated with a particular level of the variable, holding all other variables constant. The risk associated with different levels of exploratory variables were compared to risk ratios that were set to 1.00 for ewe lambs born in single litters from 3 yr old ewes. Risk ratios greater than 1.00 correspond to a greater risk of death while smaller ratios indicate a reduced risk of death.

The hazard function for an individual lamb at day t, given that the lamb was known to be alive prior to day t was modeled as:

$$h(t) = h_0(t) \exp\{\beta`X + u`Z\}$$

where

$h(t)$ = the hazard function describing the risk of lamb death after t days of age;

$h_0(t)$ = the baseline hazard function for lamb death rate;

β = a vector of effects of exploratory variables;

X = an incidence matrix for levels of exploratory variables;

u = a vector of random effect terms; and

Z = an incidence matrix associated with random effects.

The baseline hazard function was described as $h_0(t) = \lambda\rho(\lambda t)^{\rho-1}$ with scale (**λ**) and shape (**ρ**) parameters estimated from the data. The model was tested without exploratory variables to estimate the log likelihood value of the baseline hazard function ($H_0 = \beta_i = 0$). Variables were sequentially added to the model and tested with likelihood ratio tests for significance ($P < 0.05$) (Ducrocq and Solkner, 2000). Table 4.1 lists the models that were considered. Significance of each model was determined by likelihood ratio tests after removing each variable from the model. Four different models were chosen; all included year of birth and lamb sex as discrete effects, as well as different combinations of main effects and interactions involving age of dam and litter size as discrete variables and BWT as a continuous linear and quadratic effect. Model estimates for each fixed effect level were tested with a Wald's chi-square statistic (square of regression estimate/standard error of the estimate) at a significance level of $P < 0.05$. Risk ratios were determined by exponentiation of model estimates for each discrete fixed effect level where the model estimates correspond to the regression coefficients used in the hazard function. Model estimates for BWT (continuous measure) were expressed as risk ratios using the procedures described by Parmar and Machin (1995), where risk of death was relative to the overall average BWT and calculated as,

$$\text{Risk ratio}_{(BWT)} = \exp\left[\beta_{BWT}(BWT - Ave_{BWT}) + \gamma_{BWT}(BWT^2 - Ave_{BWT}^{\ 2})\right]$$

where the risk ratio $_{BWT}$ expresses the relative risk of death at a given BWT compared to the group average BWT, $\boldsymbol{\beta}_{BWT}$ is the model estimates for the linear BWT effects, $\boldsymbol{\gamma}_{BWT}$ is the model estimate for the quadratic BWT effect, and $\mathbf{Ave}_{BWT}$ is the group average BWT.

Lambs born dead were assumed to have died on d 1. Because only non-castrated male lambs were dead at birth, lamb sex was incorporated into the model as a time-dependent effect on lamb survival. All male lambs began day 1 as ram lambs. The lamb sex variable changed to wether on the day of castration. Ram lambs that were censored after 2 d of age were assumed to be castrated at the time of censoring. Time-dependent effects of number of lambs nursing on lamb survival were also considered, however, the solution vectors for models that attempted to include both birth rank and time-dependent nursing effects did not converge.

4.2.3 Early censoring versus early death

Informative censoring describes the preferential censoring of records based on factors that may influence future survival (Allison, 1995). To evaluate effects of selective censoring of lambs at young ages an additional analysis was performed assuming that all lambs removed from the flock before 3 d of age died at the time of removal. This early death group (**ED**) and the original early censoring group (**EC**) were compared to gauge the potential impact of informative censoring on estimates of fixed effects on lamb survival. All models in Table 4.1 were used to evaluate the ED group. Risk ratios were compared with those estimated from the EC group to evaluate the effect of censoring small, weak, or surplus lambs on estimates of risk.

4.2.4 Genetic analysis

Genetic variation in lamb survival to weaning was not detected from the survival analyses models and multiple-trait evaluations were not possible in the survival analysis approach. Therefore, a linear animal model was used to analyze lamb BWT and survival for both the EC and ED groups. For genetic evaluation, lamb survival at 3 d of age was recorded as a binary trait (1 for lambs alive and 0 for dead or, for group ED, censored lambs). Lamb records that were censored by d 3 were assumed to be missing in the EC group analysis. Survival and BWT evaluations included fixed effects from model 1 (Table 4.1). Genetic parameters were estimated using multiple trait, derivative-free MTDFREML software (Boldman et al., 1993). Convergence of the solutions was assumed to have occurred when the variance of -2 times the log likelihoods across iterates was less than 1 X 10^{-9}. Once convergence was attained, each run was re-started with the converged estimates used as priors to ensure global convergence. The model for survival and BWT also included random additive direct and maternal effects with a mean of 0 and variances of $\mathbf{A}\sigma^2_a$ and $\mathbf{A}\sigma^2_m$, respectively, where **A** is the additive numerator relationship matrix and σ^2_a and σ^2_m are additive direct and maternal variances, respectively. Additive direct and maternal covariances for BWT and survival, as well as the covariance between additive direct effects on trait *i* and additive maternal effects on trait *j* were assumed to be zero (r_{am} = 0) (Notter and Hough, 1997; van Vleck et al., 2003). Random permanent environmental effects of the dam, temporary environmental effects of the litter, and residual effects were included for all traits with mean 0 and variances $\mathbf{I_d}\sigma^2_{pe}$, $\mathbf{I_l}\sigma^2_{te}$ and $\mathbf{I_n}\sigma^2_e$, respectively, where $\mathbf{I_d}$, $\mathbf{I_l}$, and $\mathbf{I_n}$ are identity matrices with orders equal to the number of dams, litters, and individual records, respectively, and σ^2_{pe}, σ^2_{te}, and σ^2_e are maternal permanent environmental, litter temporary environmental, and residual variances, respectively.

Bivariate analyses of lamb birth weight and survival were conducted using variance component estimates from single-trait analysis as starting values. Survival for both EC and ED groups was analyzed in bivariate analyses with BWT to estimate relationships between random effects on lamb survival at 3 d of age and BWT. Significance of covariances in bivariate analyses was determined by likelihood ratio tests after setting each covariance to 0.

4.3 RESULTS AND DISCUSSION

4.3.1 General

Numbers of ewes lambing at different ages and the average litter size for each ewe age group are listed in Table 4.2. The overall lamb drop was 1.99 lambs born per ewe lambing. Although 1-yr-old ewes had the lowest prolificacy, they contributed more lambs per year than other age groups (23.2%). After data editing, lambs born in litters of size 1, 2, 3, and 4 lambs made up 12.9%, 54.8%, 28.7% and 3.6% of the lamb crop, respectively.

Table 4.3 lists percentages of lambs born dead, weaned, and censored before weaning for each ewe age, litter size, and lamb sex group. Lambs recorded as dead at birth accounted for 4.6% of all lambs, which was similar to other reports of death losses at birth from ¼-Finnsheep crossed ewes (4.6%, Cochran et al., 1984; 3.9 %, Ercanbrack and Knight, 1985). The overall weaning rate of lambs was 77.11 % (number of lambs weaned/number of lamb born) which was similar to other reports of lamb survival in range environments (Ercanbrack and Knight, 1985; Kott and Thomas, 1987). A greater portion of single and twin born lambs survived to weaning age compared to lambs from larger litters. Castrated lambs had a much lower survival rate to weaning than ewe and ram lambs. This is partially due to the preferential castration of male lambs that appear weak, unhealthy, or smaller than their littermates.

Lambs censored before weaning represent those lambs removed from the flock or missing for unknown reason. By weaning, 13.3% of the lamb records had been censored. Fewer single and twin born lambs were censored compared to lambs from larger litters. Ram lambs that were voluntarily removed from the flock were castrated, so the frequency of censoring prior to weaning was lower for ram versus ewe and wether lambs.

Least squares means for BWT from model 1 are presented in Table 4.3. Average birth weight increased as ewe age increased through 6 yr and then declined. Litter size effects on BWT were significant ($P < 0.05$) with larger BWT for lambs from smaller litters. These results were consistent with BWT records reported for Targhee sheep elsewhere in this dissertation (Chapter 2).

4.3.2 Survival Curve

Scale parameter (**ρ**) for the baseline hazard function indicates the rate of death with **ρ** < 1 indicating that the risk of death is highest at early ages and decreases with time. The scale parameter for the baseline hazard in this data ranged from 0.33 ± 0.005 to 0.37 ± 0.008 with an average age of lamb death equal to 13.7 d when lambs removed early are assumed censored. The Kalpan-Meier survival curve for lamb survival between birth and weaning is presented in Figure 4.1. This survival function shows the unadjusted lamb survival rate, illustrates greater risk of lamb death at early ages, and estimates the probability of lamb survival at a given point in time.

4.3.3 Risk Ratios

Risk ratios for fixed effects on lamb survival and the associated model estimates and standard errors are presented in Table 4.4 for models 1 and 2. Risk ratios are used to interpret the risk of lamb death associated with each level of fixed effect. For example, the risk ratios for lambs from 2 and 3 yr old ewes of 1.28 and 1.00, respectively, mean that lambs born from 2-yr-old ewes have a 28% greater risk of death than lambs born to 3-yr-old ewes. Ratios less than 1.00 indicate a reduced risk of death. Five-yr-old ewes have a risk ratio of 0.88 relative to 3-yr-old ewes; thus lambs born to 5-yr-old ewes have a 12% lower risk of death relative to lambs from 3-yr-old ewes.

The risk of lamb death was highest for lambs born to yearling ewes. The relative risk of death decreased with age through 5 yrs, but increased again for the oldest ewe age groups ($P < 0.05$ for 7+ ewes) in both model 1 and 2. Sawalha et al. (2007) showed a similar trend in ewe age effects on lamb survival in Scottish Blackfaced sheep, with the greatest risk of lamb death between 1 and 14 d of age found in the youngest (2 yr) and oldest (6 yr) ewe age groups. Morris et al. (2000) reported higher lamb mortality in lambs born from 2- and 5-yr-old ewes from three experimental populations of Romney sheep in New Zealand. Other studies have reported that lamb survival improves with ewe age (Smith 1977; Ercanbrack and Knight, 1985; Cloete et al., 2001; Southey et al., 2001). However, Hohenboken et al. (1976) found no ewe age influence on lamb survival in purebred and crossbred Suffolk and Hampshire lambs reared under favorable conditions.

When effects of BWT were not included in the model (model 1), lamb sex had no effect on lamb survival, but litter size effects were significant. Triplets and quadruplets had a much greater risk of death ($P < 0.05$) than single and twin lambs. When linear and quadratic effects of BWT were considered (model 2), the risk of lamb death was higher for ram lambs than for ewe and wether lambs of the same birth weight, and a dramatic decrease was observed in risk associated with lambs born in large litters. At the same BWT singles had a 34%, 6%, and 16% greater risk of death than twins, triplets, and quadruplets, respectively. Smith (1977) reported that after adjusting for birth weight, pre-weaning survival of purebred and cross-bred lambs was 19% less for lambs born in litters of two or more compared to single born lambs. Birth weight had a significant effect on lamb survival ($P < 0.001$), and the inclusion of linear and quadratic BWT effects indicates an intermediate optimum BWT associated with minimum lamb mortality. Similar effects of BWT on lamb survival have been reported elsewhere

(Notter and Copenhaver, 1980; Morris et al., 2000; Holst et al., 2002; Sawalha et al., 2007).

Ewe age by litter size interactions were included to account for nonlinear effects associated with changes in prolificacy as ewe age increases. Based on likelihood ratio tests, inclusion of a ewe age by litter size interaction led to a significantly better fit for lamb survival than the main-effects models (models 1 and 2). Risk ratios are presented in Figure 4.2 comparing the risk of lamb mortality associated with each ewe age by litter size combination when BWT is not included (model 3) and after accounting for BWT differences (model 4). Yearling ewes had the greatest risk of lamb death at all litter sizes. Differences between risk ratios from model 3 and model 4 were small for single and twin lambs born to ewes 2 yrs of age and older. However, a greater risk of death was associated with triplet and quadruplet lambs when BWT was not accounted for in the model (model 3) indicating that BWT had a larger effect on survival for lambs born of large litters. When adjusting to the same BWT risk ratio estimates were more consistent among the ewe age by litter size groups, with the largest risk associated with triplets born to older ewes. The linear and quadratic regression coefficients for BWT in model 4 were -2.68 and 0.24, respectively, and the lowest risk of mortality was associated with a birth weight of 5.64 kg. The mean BWT for these Polypay lambs was 3.95 kg, well below the optimal level for mortality, and larger birth weights are therefore not expected to pose a threat to lamb survival. Shelton (2002) reached a similar conclusion for highly prolific sheep, suggesting that only a small portion of ewes have heavy weight lambs at birth and that increases in BWT should improve lamb survival.

Figure 4.3 illustrates least squares means for BWT across different ewe age and litter sizes groups. Differences in BWT of single, twin, triplet, and quadruplet lambs were observed over all ewe age groups, with smaller litters having heavier BWT. Birth weights were lighter for all litter size groups in lambs born from less mature 1 and 2-yr-old ewes. Changes in birth weight as ewe age increased were consistent for each litter size group. However, the change in BWT between 1 and 2-yr-old ewes was less for singles (+ 0.40 kg) compared to twins, triplets, and quadruplets (+ 0.52, + 0.58, and + 0.70, respectively). Also, BWT of quadruplets from ewes over 6 yrs of age showed a slightly larger decrease relative to other litter size groups. These slight nonlinear changes in BWT for different ewe age by litter size combinations contributed to the better fit of models 3 and 4 compared to models 1 and 2.

4.3.4 Early censoring versus early death

Informative censoring of young lambs that were unhealthy or relatively smaller than their littermates is a potential source of bias in the survival evaluation due to removal of lambs that would have likely died if left in the production system. Table 4.5 lists the number of lambs removed from the flock at 1, 2 and 3 d of age for each ewe age, litter size, and lamb sex group. A total of 78.6% of lamb removed from the flock for unknown reasons before weaning age were censored within 3 d of age. Given the relatively high mortality rates at early lamb ages reported in the literature (Cochran et al., 1984; Hall et al., 1995; Morris et al., 2000; Sawalha et al., 2007), it is likely that the factors influencing early censoring were informative relative to the survival analysis. Combining dead and censored lambs in the ED group led to a younger average age of death (8.7 d) compared to EC records (13.7 d). More triplet and quadruplet lambs were removed from the flock at early ages in ED which corresponds to the higher death rates expected for these litter size groups.

Table 4.6 presents risk ratio estimates from the ED group for models 1 and 2. Results of risk ratios in Table 4.6 corresponded closely with the portion of lamb records censored by 3 d of age (Table 4.5). Compared to results from the EC group (Table 4.3), risk ratios were relatively unchanged for ewe age effects in the ED group. However, ewe age and litter size groups that experienced more censoring at early ages also had an increase in risk of lamb death between the EC and ED evaluations. For example, the relative risk associated with lambs born to ewes older than 6 yrs of age was smaller than that estimated with EC. This reduction in risk for older ewes appears to be the result of a higher risk associated with 3 yr old ewes due to a greater proportion of censored lamb records. In both EC and ED evaluations, triplet and quadruplet lambs had higher risks of in model 1, indicating that BWT strongly influences survival in lamb from large litters. Based on these results, informative censoring did impact the estimates of risk associated with fixed effects on lamb survival. Risk ratios for lambs born in large litters still differed between EC and ED after accounting for BWT (model 4). This result indicates that the censoring that occurred within 3 d of birth was not only based on body weight of the lamb but also other subjective factors associated with large litters. For example, removing lambs from large litters may be common when foster ewes are available to nurse additional lambs or the dam appears to have poor milking ability.

Linear and quadratic effects of BWT on lamb survival from model 4 are displayed in Figure 4.4 for both EC and ED groups. Estimates were converted to risk ratio values relative to the mean BWT of 3.95 kg (Parmar and Machin, 1995). In all evaluations including BWT, both linear and quadratic effects were significant ($P < 0.001$). Similar quadratic BWT effects on lamb mortality have been reported (Smith, 1977; Notter and Copenhaver, 1980; Hall et al., 1995; Morris et al., 2000; Holst et al., 2002; Sawalha et al., 2007), indicating an intermediate optimal range for lamb birth weights. The informative censoring that occurs within the first 3 d of age influenced estimates of BWT effects on survival. The lowest risk of death was associated with 5.6 kg and 7.1 kg for the EC and ED groups, respectively. The relative risk of lamb death increased as lamb weight decreased in a generally similar manner for both EC and ED groups. However, as BWT increased, only the EC group had a clear intermediate optimal BWT, with increasing risk of death at BWT greater than 7 kg. Figure 4.4 shows a slight decrease in risk of death at light weights and relatively little risk for heavy BWT in the ED evaluation. Predicting the extent of bias from informative censoring is difficult (Allison, 1995) and may lead to incorrect inferences regarding factors influencing survival. However, given the range of BWT values (1.8 to 7.8 kg) the impact of censoring appeared to have only a modest impact on the interpretation risk ratios associated with BWT effects in the current population.

4.3.5 Genetic analysis

Estimated variance components for BWT and lamb survival to 3 d of age (**SUV3**) from bivariate models are presented in Table 4.7. The proportions of variance in BWT associated with additive, additive maternal, permanent environmental dam, and temporary environmental litter effects were 0.15, 0.20, 0.09, and 0.14, respectively. These estimates were consistent with those reported in Bromley et al. (2000) and Van Vleck et al. (2005). Temporary environmental effects of the litter were included for both BWT and SUV3 evaluations, and account for common environmental effects of the litter as well as non-additive effects in full-sibs. In relatively prolific sheep, Al-Shorepy and Notter (1998) suggested that maternal effects are more accurately estimated for BWT if random effects of litter are included in the model. In the current evaluation, litter effects accounted for 14% of the phenotypic variation in BWT.

The probability of survival to 3 d of age was 10 % lower in the ED evaluation. Variance components for SUV3 were small, ranging from 0.00 to 0.01 for heritability and maternal heritability in both EC and ED, although the heritability estimate of 0.01 was significantly different from zero in the ED group. Random litter effects on SUV3 in the EC group were significantly different from zero ($P < 0.01$). The low heritability estimates for SUV3 are consistent with the lack of sire effects on lamb survival in Merino crossbred lambs (Holst et al., 2002). However, larger estimates of heritability for lamb survival have been reported at birth (0.05, Sawalha et al., 2007), 1 d of age (0.03, Morris et al., 2000), 3 d of age (0.05, Hall et al., 1995), and 14 d of age (0.20, Sawalha et al., 2007). The significant litter effect in EC may reflect the assumption of a linear relationship between BWT and SUV3, with more light lambs from large litters preferentially removed from the flock at an early age.

Table 4.8 lists the estimated correlations between BWT and SUV3. Phenotypic correlations were 0.23 and 0.26 for EC and ED. Smith (1977) reported an antagonistic phenotypic correlation between birth weight and lamb mortality of 0.23 indicating that heavier birth weights were associated with higher death loss, but a favorable genetic correlation of -0.28, suggesting a correlated response in survival from selection on BWT. Sawalha et al. (2007) estimated genetic and residual correlations between BWT and survival at birth of -0.21 and 0.25, respectively. Direct additive and direct maternal correlations in the current study were significantly different from zero ($P < 0.05$) between BWT and SUV3 for the ED and EC groups, respectively. All significant correlations between BWT and SUV3 were positive indicating that increases in BWT would result in higher lamb survival. However, given the small portion of genetic variance in SUV3, the potential impact of these genetic relationships between BWT and survival is small.

4.4 IMPLICATIONS

Improvements in lamb survival are likely through implementation of management practices that give special care to lambs born to groups that are at a higher risk of death rather than through selection for genetic improvement in the trait. Given the high prolificacy of the Polypay breed, selection for increased birth weight may improve lamb survival, however, this relationship likely results from heaver lambs being less susceptible to antagonistic environmental factors at a phenotypic level and not from a particularly strong pleiotropic genetic relationship. In time-dependent survival analysis, relationships involving lamb survival may be more appropriately estimated when less preferential censoring occurs at early ages.

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Table 4.1 Listing of fixed effects included in different hazards models.

	Fixed effects included in the model [1]
Model 1.	BYEAR + EAGE + LITSIZE + SEX
Model 2.	BYEAR + EAGE + LITSIZE + SEX + BWT + QBWT
Model 3.	BYEAR + (EAGE x LITSIZE) + SEX
Model 4.	BYEAR + (EAGE x LITSIZE) + SEX + BWT + QBWT

1. BYEAR = year of birth, EAGE = age of dam at lambing, LITSIZE = number of lambs born within a litter, SEX = lamb gender (ewe, ram, wether), BWT = linear term for lamb birth weight, QBWT = quadratic term for lamb birth weight.

Table 4.2 Summary of number of ewes lambing and prolificacy level for each ewe age group [1].

Ewe age	No. of Ewes	Litter size
1	3009	1.55
2	2068	2.00
3	1709	2.19
4	1291	2.27
5	915	2.29
6	640	2.30
7+	462	2.20
Total	10094	1.99

1. Ewe age = Age of dam at the time of birth, No. of Ewes = total number of ewes lambing in each ewe age group, % Lamb crop = number of lambs born per ewe lambing within each ewe age group.

Table 4.3 Summary of the number of lambs born, proportion of lambs weaned or censored, and least squares (LS) means for birth weight (BWT)[1].

Item		Lambs Born	Born Dead %	Weaned % [2]	Censored prior to weaning % [3]	BWT (kg) LS Mean	BWT (kg) s.e.
Ewe age	1	4507	4.46	72.06	15.40	3.22	0.01
	2	4006	4.04	78.93	12.03	3.69	0.01
	3	3534	4.27	79.46	12.20	3.96	0.01
	4	2775	5.59	77.62	12.58	4.09	0.02
	5	1934	4.29	78.59	13.55	4.11	0.02
	6	1370	5.50	74.89	14.89	4.14	0.02
	7+	930	6.13	75.81	11.94	4.07	0.03
Litter size	1	2465	3.49	84.67	5.27	4.85	0.02
	2	10433	3.04	82.95	9.03	4.18	0.01
	3	5462	7.41	64.76	22.32	3.55	0.01
	4	696	10.78	49.57	34.77	3.00	0.03
Sex	Ewe	9508	4.89	78.88	11.12	3.77	0.01
	Ram	6397	4.35	82.91	5.77	4.10	0.01
	Wether [4]	3151	NA	57.73	35.10	3.81	0.02
Overall		19056	4.62	77.11	14.76	3.98	-

1. See Table 1 for trait definitions.
2. Percentage of lambs born that remained in the flock at weaning.
3. Percentage of censored lambs removed from the flock before weaning.
4. Total number of male lambs is the sum of numbers of ram and wether lambs, wethers were castrated at 2 d of age, so percentage dead at birth pertains only to ram lambs and is not available (NA) for wethers.

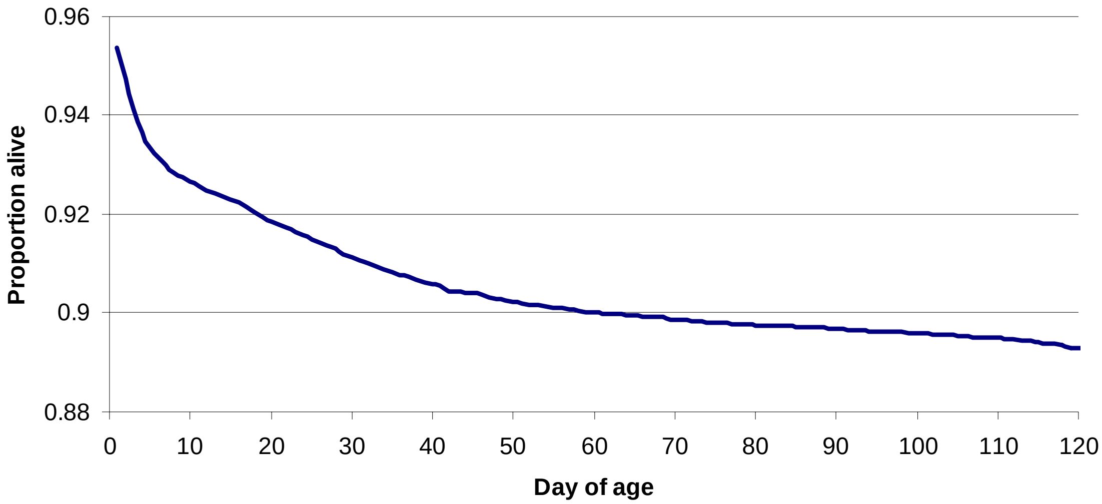

Figure 4.1 Kaplan-Meier survival function illustrating the proportion of lambs in the flock on each day of age from birth to weaning.

Table 4.4 Listing of hazard ratios and associated model estimates for effects included in models 1 and 2[1,2].

Item		Model 1			Model 2		
		Risk ratio	Model estimate	s.e.	Risk ratio	Model estimate	s.e.
Ewe age	1	2.770	1.019	0.080	1.267	0.237	0.083
	2	1.279	0.246	0.080	0.971	-0.029	0.080
	3	1.000	0.000	*	1.000	0.000	*
	4	1.112	0.106	0.085	1.196	0.179	0.085
	5	0.878	-0.123	0.100	0.988	-0.012	0.101
	6	1.183	0.168	0.104	1.258	0.229	0.105
	7+	1.548	0.436	0.112	1.673	0.515	0.112
Litter Size	1	1.000	0.000	*	1.000	0.000	*
	2	1.103	0.098	0.076	0.657	-0.420	0.077
	3	2.652	0.975	0.085	0.943	-0.059	0.090
	4	3.834	1.344	0.126	0.839	-0.175	0.133
Lamb sex	Ewe	1.000	0.000	*	1.000	0.000	*
	Ram	1.071	0.069	0.049	1.322	0.280	0.050
	Wether	0.997	-0.003	0.086	1.014	0.014	0.085
Birth weight [3]	BWT				*	-2.566	0.138
	QBWT				*	0.220	0.019

1. See Table 1 and 2 for model and trait definitions.
2. Risk ratio = estimates of the proportional difference in risk of death associated with a fixed effect level relative to the fixed effect level with a value of 1.00, Model estimate = coefficients for the fixed effect in the hazard model and are equal to the natural log of the risk ratio, s.e. = standard errors of the model estimate.
3. Model estimates for continuous measures are regression coefficients for the birth weight term in the hazards model.

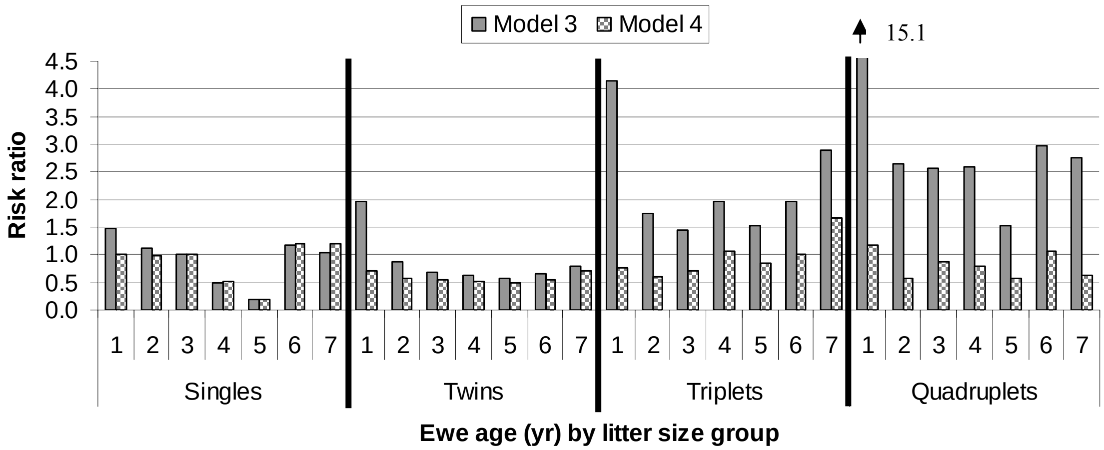

Figure 4.2 Risk ratios for lamb survival for each ewe age by litter size combination in models with (model 4) and without (model 3) linear and quadratic birth weight effects.

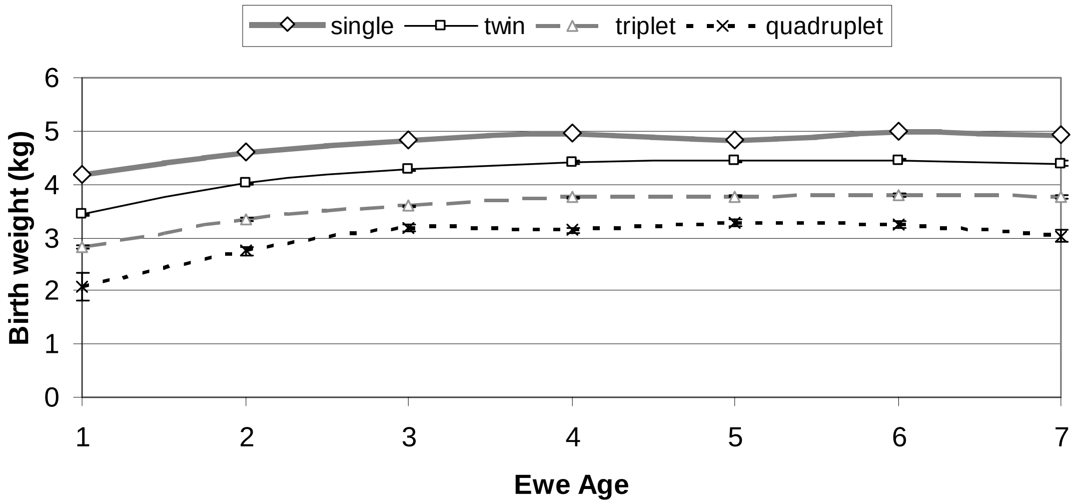

Figure 4.3 Least squares means of birth weight for lambs born as singles, twins, triplets, and quadruplets from different ewe age groups. Standard error bars indicate significance at a *P* < 0.05 level.

Table 4.5 Number of lambs censored between birth and 3 d of age, and total number of lambs censored before weaning.

Item		Number of censored lambs censored at: Day 1	Day 2	Day 3	Prior to weaning [1]	% of lambs censored by Day 3 [2]
Total		369	1310	312	2533	78.60
Ewe age, yr	1	104	368	65	694	77.38
	2	71	256	62	482	80.71
	3	67	215	63	431	80.05
	4	50	182	51	349	81.09
	5	40	135	34	262	79.77
	6	22	106	18	204	71.57
	7+	15	48	19	111	73.87
Litter size	1	7	88	7	130	78.46
	2	95	511	95	942	74.42
	3	226	579	182	1219	80.97
	4	41	132	28	242	83.06
Sex	Ewe	165	585	105	1058	80.81
	Ram	5	234	24	369	71.27
	Wether	199	491	183	946	78.93

1. Includes lambs censored at 1, 2, and 3 d of age.
2. Proportion of the total number of lambs censored between birth and weaning that were censored within 3 d of age.

Table 4.6 Listing of hazard ratios and associated model estimates for effects included in models 1 and 2 assuming lambs censored prior to 3 d of age were dead at the time of censoring[1,2].

Item		Model 1			Model 2		
		Risk ratio	Model estimate	s.e.	Risk ratio	Model estimate	s.e.
Ewe age	1	2.876	1.057	0.056	1.352	0.301	0.057
	2	1.260	0.232	0.055	0.964	-0.037	0.055
	3	1.000	0.000	*	1.000	0.000	*
	4	1.055	0.054	0.059	1.161	0.149	0.059
	5	0.944	-0.058	0.066	1.073	0.071	0.066
	6	1.110	0.104	0.072	1.233	0.210	0.072
	7+	1.284	0.250	0.083	1.389	0.329	0.083
Litter Size	1	1.000	0.000	*	1.000	0.000	*
	2	1.417	0.348	0.061	0.823	-0.195	0.062
	3	4.359	1.472	0.066	1.496	0.403	0.069
	4	7.287	1.986	0.086	1.556	0.442	0.091
Lamb sex	Ewe	1.000	0.000	*	1.000	0.000	*
	Ram	1.269	0.238	0.034	1.582	0.459	0.035
	Wether	1.025	0.024	0.060	1.077	0.074	0.060
Birth weight [3]	BWT				*	-1.773	0.112
	QBWT				*	0.113	0.016

1. See Table 1 and 2 for model and trait definitions.
2. Risk ratio = estimates of the proportional difference in risk of death associated with a fixed effect level relative to the fixed effect level with a value of 1.00, Model estimate = coefficients for the fixed effect in the hazard model and are equal to the natural log of the risk ratio, s.e. = standard errors of the model estimate.
3. Model estimates for continuous measures are regression coefficients for the birth weight term in the hazards model.

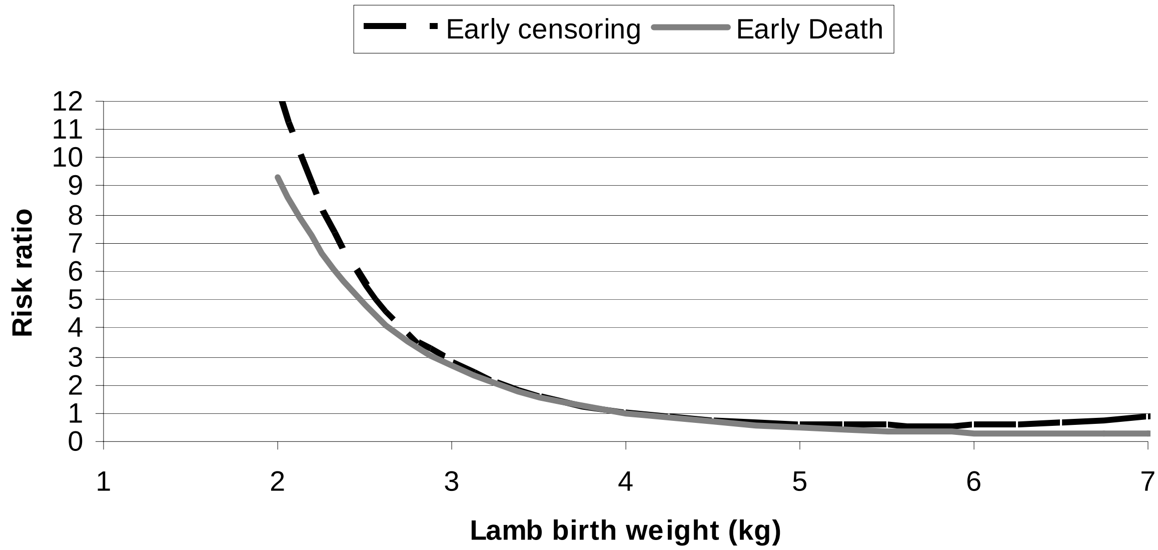

Figure 4.4 Changes in risk ratios associated with birth weight after accounting for effects of ewe age, litter size and lamb sex. Risk ratio lines were created from linear and quadratic model estimates for birth weight from model 4 (including ewe age and litter size interaction). Baseline risk ratio was set to the phenotypic mean of birth weight (3.95 kg). Early censoring = censoring of lambs removed within 3 d of age, Early death = assumed all lambs removed within 3 d of age were dead.

Table 4.7 Estimated variance components from two-trait analysis including birth weight and lamb survival to 3 d of age [1, 2, 3].

		Survivability	
Item	BWT	EC	ED
No. Records	19056	17067	19056
Mean	3.952	0.935	0.837
h^2	0.15 ***	0.00	0.01 *
m^2	0.20 ***	0.01	0.00
pe^2	0.09***	0.00	0.00
te^2	0.14***	0.18 **	0.00
e^2	0.42	0.81	0.99
σ^2_p	0.536	0.056	0.067

1. BWT = Birth weight, Survivability = lamb survival at 3 d of age, EC = early censoring, ED = early death
2. Significance values indicate if proportion of variance is different from zero: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.
3. h^2 = heritability, m^2 = maternal heritability, pe^2 = permanent environment effects of the dam, te^2 = temporary environment of the litter, e^2 = residual effects, σ^2_p = phenotypic variance.

Table 4.8 Correlation estimates from two-trait analysis including birth weight and lamb survival at day three [1, 2, 3].

	Survivability	
Correlation	EC	ED
r_a	-1.00	0.10 *
r_m	0.50 ***	0.81
r_{pe}	0.53	1.00
r_{te}	0.18 ***	1.00
r_e	0.31 ***	0.37 ***
r_p	0.23 ***	0.26 ***

1. See table 7 for trait abbreviations.
2. Significance values indicate if proportion of variance is different from zero: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.
3. r_a = direct additive correlation, r_m = direct maternal correlation, r_{pe} = permanent environment correlation, r_{te} = temporary environment correlation, r_e = residual correlation, r_p = phenotypic correlation.