

**Genetic evaluation of ewe productivity and its component traits in Katahdin and Polypay
sheep**

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by

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ABSTRACT

The objectives of this dissertation were to evaluate genetic influences on ewe productivity, its growth and reproductive components, and measures indicative of accelerated lambing performance. Genetic parameters were estimated for total weight of litter weaned per ewe lambing (TW) and its components, number of lambs born (NB), number of lambs weaned (NW) and average weight of lambs weaned (AW), measured as traits of the ewe, and lamb survival (LS) and weaning weight (WW), measured as traits of the lamb, in Katahdin sheep. Heritabilities of TW, NB, NW, and AW, were 0.12, 0.12, 0.09, and 0.13, respectively. Heritability of WW was 0.15 to 0.20. Genetic effects on LS were negligible. Genetic correlation of TW with NB, NW, and AW averaged 0.30, 0.90, and 0.74, respectively, those of NB with NW and AW averaged 0.72 and 0.01, respectively, and that between NW and AW averaged 0.50. Direct genetic effects on WW were independent of NB and NW, but correlation between maternal genetic effects on WW and animal genetic effects on NW averaged 0.35.

Ewe fertility, NB, LS, and WW were modeled using stochastic simulation and used to derive NW, AW, and TW to test alternative predictors of genetic merit for TW. A random 8% of WW observations were set to missing values and AW and TW were recalculated to evaluate the effects of data reporting inconsistencies on efficacy of different prediction strategies. Four alternative predictors of estimated breeding values (EBV) for TW involved direct univariate prediction (TW1), an index of EBV for NW and AW (TW2), indirect prediction using data for NW and AW and genetic correlations among NW, AW and TW (TW3), and indirect prediction augmenting TW3 with data and genetic correlations involving NB (TW4). To validate efficacy of predictors, daughter data sets were generated from the original ewes and their realized TW were regressed on alternative predictors. Regression coefficients from TW1, TW3, and TW4 were close to the expected value of 0.50 whereas those from TW2 were less than 0.50. Model R-square statistics were similar among predictors when there were no missing WW data but regressions involving TW1 had lowest model R-square when some WW data was missing.

Ewe lamb fertility (ELF), ages at first, second, and third lambings (AGE1 to AGE3), first and second lambing intervals (INT1 and INT2), and number of lambings by 38 mo of age (LAMB3) were evaluated for an accelerated lambing Polypay flock. Relationships among these traits and NB and WW were estimated. Heritability of ELF, AGE1, AGE2, AGE3, INT1, INT2, and LAMB3 were 0.14, 0.39, 0.28, 0.36, 0.00, 0.09, and 0.27, respectively. Heritability of AGE2 and AGE3 were negligible after accounting for variation in AGE1. Genetic correlations of ELF with AGE1 and AGE2 were -0.89, -0.91, respectively, and that with LAMB3 was 0.89. Genetic correlations of LAMB3 with AGE1 and AGE2 were -0.49 and -1.00, respectively. Genetic correlations of ELF and LAMB3 with direct genetic effects on WW were close to -0.70, but correlations with maternal genetic effects on WW were 0.88 and 0.58, respectively. Prolificacy was independent of ELF and LAMB3.

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The three main manuscripts in this dissertation were written in a manner that facilitates publication in scientific journals related to animal sciences. To that end, the manuscripts have received contributions from multiple authors which have enhanced the manuscripts' scientific quality and I would like to specifically acknowledge the other listed authors.

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Larry Kuehn was a fellow graduate student when I started work on my dissertation and has since graduated. Larry contributed to the first manuscript (Chapter 2) by providing parts of the SAS program codes used for data analyses and assisted with preliminary data analyses. He also helped by actively participating in discussions and offering suggestions which helped me understand some of the mathematics involved with the methodology and results obtained in the chapter.

DEDICATION

To Avi, my dear husband, this would not have been possible with out your love and support.
To Daddy, for all the examples you have set through your hard work and many achievements.

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INTRODUCTION

Declines in the value of wool relative to the value of lamb in the US over the past several years (USDA, 2004) have led to an emphasis on increasing lamb production to enhance overall flock profitability. Thus, the total weight of lamb weaned by a ewe (TW), or ewe productivity, is one of the most important economic traits for the sheep industry. Ewe productivity is a composite trait that is indicative of both reproductive and growth performance. It is influenced by fertility, prolificacy, and individual lamb survival to weaning (which are together indicative of the number of lambs weaned by a ewe) as well as individual lamb weaning weight and maternal performance and rearing ability of the ewe. Genetic improvement in ewe productivity could be achieved through direct selection on TW (Ercanbrack and Knight, 1998) or indirect selection on one or more of its component traits (Bradford et al., 1999; Cloete et al., 2004). Direct selection on TW may not necessarily improve all the component traits but may automatically account for any inherent antagonisms and thus result in a biologically and economically optimum balance among them. Success in direct selection programs depends on the availability of adequate genetic and phenotypic variation in the trait. Improvements in ewe productivity based on indirect selection on component traits will depend on the heritabilities of, and genetic correlations among, the component traits and the composite trait.

The greatest improvements in ewe productivity can be made by improving reproduction, expressed as the number of lambs produced by a ewe (Wang and Dickerson, 1991; Ercanbrack and Knight, 1998). In annual lambing systems, improvement in the number of lambs produced by a ewe can be achieved by improving prolificacy of the ewes and survival of the lambs. Additional improvements in this trait can be achieved by using accelerated lambing systems which allow ewes to breed more than once a year. However, seasonal fertility remains one of the biggest limitations to improving performance in accelerated lambing systems. Therefore, improvement in some measure of aseasonality or acceleration may be useful in overall improvement of TW per year.

The objectives of this dissertation were to: 1) estimate the (co)variance components of TW per ewe lambing and its component traits in an annual lambing system using field data from Katahdin flocks enrolled in the US National Sheep Improvement Program (NSIP), 2) evaluate direct and indirect genetic evaluation methods for improvement of TW using stochastic

simulation, and 3) evaluate measures of accelerated lambing in a Polypay farm flock, also enrolled in NSIP.

CHAPTER 1

LITERATURE REVIEW

Selection for improvement of total weight of lamb weaned by a ewe

Direct Selection. The goal of any selection protocol is to genetically improve the trait of interest, and success in such endeavors depends on the availability of genetic variation within the population. Specifically, the response to selection is directly proportional to the heritability, selection intensity, and phenotypic variation present in the trait under consideration (Falconer and Mackay, 1996). Generally, heritability estimates for TW have been small, which suggests that selection responses for this trait may be small. However, in spite of low heritability, there exists a large phenotypic variation in the trait, indicating that selection to improve this trait could be successful.

Snyman et al. (1997) used one Afrino and two Merino sheep flocks located at two different stations in South Africa to estimate genetic parameters for early and lifetime total weight of lamb weaned per ewe exposed to breeding (TWE). The TWE at each lambing opportunity was calculated as the sum of 120-d age-corrected, sex-adjusted weaning weights of each lamb of the litter. For ewes that failed to conceive or wean any lambs, TWE was zero. The early measure was TWE at first lambing opportunity, and the lifetime measures were TWE by third lambing opportunity. Models for the genetic analyses included random effects of the animal and fixed effects of the birth year and season of the ewe. Heritability estimates for early TWE were similar for the three flocks, at 0.06 ± 0.04 , 0.08 ± 0.03 , and 0.09 ± 0.03 for the Afrino, and two Merino flocks, respectively. Heritability of lifetime TWE was more variable among flocks and was 0.17 ± 0.07 , 0.13 ± 0.05 , and 0.22 ± 0.04 for the Afrino and the two Merino flocks, respectively. Heritability of TWE by the fourth lambing opportunity was also measured in the Merino flocks and was similar to the heritability of TWE by third lambing opportunity with estimates of 0.10 ± 0.05 and 0.26 ± 0.05 in the two flocks. Heritability estimates for lifetime TWE were higher than the heritability of early TWE as expected from using repeated records on the same animal to obtain the lifetime TWE. The higher heritabilities for lifetime TWE obtained in the second Merino flock compared to the other two flocks were attributed to the lack of any form of selection based on reproductive or growth performance in this flock, whereas in the other two flocks, culling was based on below average reproductive

performance and lifetime TWE after second parity (second Merino flock) or was based on low 120-d adjusted weaning weight and failure to conceive in two consecutive years (first Merino flock). Selection reduces genetic variation and may lead to a reduction of heritability over a period of time (Bulmer, 1971). Indeed, effects of selection on heritability of lifetime TWE were perhaps largest in the first Merino flock due to a more intensive culling based on failure to conceive twice in a row, as opposed to culling after two parities in the second flock. Overall, the authors concluded that direct selection based on lifetime TWE would lead to genetic improvement in the trait, and based on the genetic correlations among the early TWE and lifetime TWE, which ranged from 0.80 to 0.91, the authors recommended selection based on early TWE in order to reduce generation interval (Snyman et al., 1997). The use of early TWE, either by itself or with lifetime TWE in a multi-trait analysis, would also avoid selection bias that can occur for later or lifetime TWE measures due to culling based on early reproductive or TWE data (Pollak and Quaas, 1981).

In the U. S., Bromley et al. (2001) studied total weight of lamb weaned per ewe lambing (TWL) for four breeds of sheep, the Columbia, Targhee, Polypay, and Rambouillet. The TWL was calculated as the sum of weights of naturally reared lambs for each year; only lambs reared by their birth dam were included in the litter weight weaned from a ewe. For genetic analysis of TWL, they used a model that included fixed effects of ewe age, lambing year, and a fostering code (categorized as 1 for ewes that did not rear any lambs other than their own and 2 for ewes that raised a lamb other than their own), and random effects of additive direct, permanent environment, mating sire, and temporary environmental. They estimated heritabilities of 0.02, 0.10, 0.11, and 0.08 for TWL in Columbia, Polypay, Rambouillet, and Targhee sheep, respectively. The permanent environmental components were small, ranging from 0.00 to 0.10, and resulted in repeatabilities ranging from 0.10 to 0.16 among breeds. Mating sire components were negligible, ranging from 0.00 to 0.03. The heritabilities of TWL obtained in this study were lower than those obtained in some other studies. From the calculation of TWL described by the authors, it is not clear whether individual lamb weights were corrected for age and sex of the lamb before calculating TWL. Failure to correct for these known causes of variation prior to calculation of TWL, and failure to account for these effects in the genetic analyses could have resulted in the low heritabilities for TWL observed by Bromley et al. (2001).

Ap Dewi et al. (2002) estimated the heritability of total weight of lamb weaned per ewe per year in Welsh Mountain Sheep in the UK. The TW was calculated as the sum of individual 12-wk weights of lambs naturally reared by the birth ewe. It was not clear whether TW was calculated per ewe lambing or per ewe weaning at least one lamb; the range of TW was reported as 7.5 to 66.0 kg and did not include any 'zero' values, which are possible if a ewe lambs but loses her entire litter. It is possible that none of the ewes that lambed lost the entire litter although it seems unlikely in data collected from 3,445 ewes over a period of 20 yr, from 1977 to 1998. No adjustments to individual lamb weights were made for sex of the lamb, and the data consisted of only single and twin-born lambs. The genetic analysis model included fixed effects of ewe age, lambing year, and litter code (five categories combining effects of lamb sex and type of rearing), and random direct additive, permanent environment, and temporary environment effects. Heritability was estimated as 0.20 ± 0.03 , and is on the higher end of reported estimates for TW. This is perhaps the only study reported that adjusts TW for type of rearing. A ewe which weans two lambs (which are each probably lighter than a lamb born and raised as a single) could easily have higher TW than a ewe which weans a single lamb and thus should be credited as being "better" in terms of ewe productivity, but adjusting for type of rearing in the genetic model does not credit such a ewe as superior in ewe productivity as defined earlier in this review. Also, after adjusting for type of rearing and not including data from all dead litters, the estimate of heritability for TW is potentially indicative of growth potential alone rather than the combined effects of reproduction and growth, which may explain the higher heritability obtained by Ap Dewi et al. (2002).

Although the heritability of TW appears to be small to moderate, genetic improvement is still possible because of the large phenotypic variation present in the trait. However, there are few studies actually documenting the expected improvement. Ercanbrack and Knight (1998) conducted a study in Idaho to compare the effectiveness of four different selection protocols to improve TWE using 11 different lines of sheep representing four breeds and raised in a range environment over a period 12 yr. They found that direct selection, with ewes selected annually based on current lifetime average TWE and rams selected based on their dam's current lifetime average TWE, was the most effective method of genetically improving TWE. When selection was additionally accompanied by independent culling of rams based on their own adjusted 15-mo body weight, genetic improvement was only 85% of that observed in direct selection without

culling on body weight of rams. Selection based on early puberty in ewe lambs and 130-d scrotal circumference in rams, and selection based on body weight alone in both rams and ewes, were only 59% and 67% as effective as direct selection, respectively. Gains in TWE were most attributable to prolificacy (37%) and percentage of lambs weaned (27%). They also suggested that selection for TWE, instead of prolificacy or percentage of lambs weaned alone, would automatically tend to keep reproductive rates within the bounds of optimum fitness levels since ewes with high reproductive rates but low ewe or lamb fitness, expressed as low TWE, would be penalized. Based on these results, Ercanbrack and Knight (1998) suggest direct selection as an optimum means of genetic improvement in TWE.

One of the limitations to direct selection for TW arises because of its unusual distribution (Rosati et al., 2002). Estimated breeding values are usually derived using linear model theory under the assumptions that data are normally distributed (Henderson, 1984). However, TW data are not normally distributed. The distribution of TWE is conditioned by the distributions of its component traits: binomial for fertility, categorical for NW, and continuous for weaning weight, and the distribution of TWL is conditioned by distributions of NW and weaning weight. Thus, the distributions of TWE and TWL have a stack of zeros for ewes that fail to conceive or lose their whole litter, and a multimodal normal distribution for ewes that raise singles, twins, or triplets. This problem could be avoided in part by using average lifetime production records (Snyman et al., 1997; Olivier et al., 2001), which would also increase the heritability of the trait, but could reduce genetic gain by increasing generation interval. Some researchers have also suggested multi-trait selection indices involving the component traits for genetic improvement of TW (Bromley et al., 2001; Rosati et al., 2002).

Indirect selection. Selection on one or more of the component traits can also result in an increase in the total weight of lamb weaned by a ewe. Bradford et al. (1999) reported results of a long term selection experiment involving three different lines of Targhee sheep raised in a range environment. Over the last 6 yr period of the selection experiment, lines selected for increased 120-d weaning weight (HW1 and HW2) or litter size (HL1) averaged 22%, 17%, and 12%, respectively, above the control line for estimated breeding values for 120-d TWL. Although the general consensus is that improvements in reproductive performance are more important for overall improvement in ewe productivity, the results obtained in this study indicate that selection based on weaning weight led to greater improvements in TWL. In fact, the higher response of

the HW1 line was attributed to direct improvements in weaning weight as well as correlated improvements in litter size, whereas improvements in the HW2 and HL1 lines were attributed to improvements solely in weaning weight and litter size, respectively. Moreover, the improvements in litter size in the HL1 line over the entire 30 yr of the experiment were small (Sakul et al., 1999), which would have limited improvement in TWL. However, improvements in fertility were higher in the HL1 line compared to either of the weight lines, suggesting that in terms of improvements in 120-d TWE, the advantage of the HW1 line over the HL1 line would be reduced (Bradford et al., 1999).

In South African Merino lines selected for divergent multiple lambing abilities, phenotypic differences in numbers of lambs born, number of lambs weaned, and total weight of lamb weaned were evident; the high-line, in which ewes were selected for rearing at least twins, had higher ($P < 0.01$) **NB**, **NW**, and **TWL**, compared to the low line in which ewes were selected for rearing singles or less (Cloete et al., 2004). By the end of the experiment in 2002, high-line ewes averaged 10 kg more **TWL** and 0.5 more lambs weaned than low-line ewes. Positive genetic trends for **NB**, **NW**, and **TWL** were observed in the high line whereas negative genetic trends were observed in the low line. The average changes in estimated breeding values for **NW** and **TWL** were 1.6 ± 0.06 %/yr and 0.37 ± 0.02 kg/yr, respectively, in the high line but -1.1 ± 0.07 %/yr and -0.26 ± 0.02 kg/yr, respectively, in the low-line. No differences in greasy fleece weight or ewe body weight were observed among lines.

These studies suggest that selection on any of the component traits of ewe productivity should result in improvement in the trait itself, although there may be declines in other components traits, resulting in less than optimum increases in **TWL**. Generally, direct selection based on **TW** is thought to result in an optimum balance among all of its components within a given environment.

Correlated responses to selection for TW. Selection for **TW** can lead to correlated responses in component traits as well as other traits of economic importance. Selection for increased **TWE** in both sexes in Targhee sheep, as described by Ercanbrack and Knight (1998), led to increases in lamb birth weights, weaning weights, and ewe milk production (Head et al., 1995) but there were no differences in back fat, loin eye area, dressing percentage, or carcass weight when compared to animals from control lines (Head et al., 1996). Correlated responses to phenotypic selection based on **TWE** in both ewes and rams led to positive phenotypic and

genetic trends in fertility, prolificacy, number of lambs weaned, and weaning weight (Ercanbrack and Knight, 1998). Positive genetic correlations of TWL with body weight, ranging from 0.58 to 0.80, have been reported in South African and Western Australian Merinos (Snyman et al., 1998; Cloete et al., 2002). Bromley et al. (2001) reported small direct genetic correlations between TWL and direct genetic merit for birth weight and average daily gain ranging from -0.22 to +0.28 and -0.07 to +0.23, respectively, in four different breeds of sheep. They also reported favorable correlations between TWL and maternal genetic merit for birth weight and average daily gain ranging from 0.35 to 0.71 and 0.94 to 1.00, respectively. Correlations between wool traits and TW are generally small. Ercanbrack and Knight (1998) found small unfavorable trends in fleece weight and fiber diameter in lines of sheep selected for improved TWE, but in net economic terms, the losses in wool production were trivial compared to gains made in lamb production. Small positive correlations of TWL with greasy and clean fleece weights, ranging from 0.06 to 0.40, have been reported in South African and Australian Merinos (Snyman et al., 1998; Cloete et al., 2002), although Bromley et al. (2001) reported a negative correlation of -0.56 in Columbia sheep. Genetic correlations between fleece grade and TW are generally small and unfavorable (Snyman et al., 1998; Bromley et al., 2001; Cloete et al., 2002). These results suggest that selection based on total weight of lamb weaned by a ewe will not adversely affect other traits of economic importance in sheep production.

Genetic correlations among TW and two of its component traits, namely **NB** and **NW** are generally moderate to high and positive (Safari and Fogarty, 2003), averaging 0.60 and 0.80, respectively, per ewe exposed, and 0.57 and 0.89, respectively, per ewe lambing (Safari et al., 2005). Genetic correlation of TW with weaning weight averaged 0.75 and 0.10 per ewe exposed and per ewe lambing, respectively (Safari et al., 2005). Estimates of genetic correlations of TW with fertility and lamb survival are very limited. Fogarty et al. (1985) reported genetic correlations of 0.59 and 0.34 between TWE and fertility and lamb survival, respectively, in an accelerated lambing sheep flock. In general, correlations of TW with its component traits are positive and suggest that improvement in TW will lead to improvements in all of these traits. Correlations among **NW** and **TW** are typically very high, indicating that the most important contributor to improvements in TW is perhaps the number of lambs weaned.

Accelerated lambing systems

As mentioned earlier, the total number of lambs produced or weaned by a ewe can be increased by increasing the number of annual lambing opportunities for a ewe in accelerated lambing systems. Some of the popular accelerated lambing systems include lambing five times in 3 yr (STAR; Hogue et al., 1980) or three times in 2 yr (Notter and Copenhaver, 1980; Fogarty et al., 1984). In the STAR system, developed at the Cornell University, the year is divided into five breeding seasons starting in the months of January, March, June, August and October (Lewis et al., 1996). March and June breedings are out-of-season breedings and are characterized by low fertility whereas August, October and January matings are in-season. This system utilizes a 30-d breeding period and allows ewes to be bred at 7.2 mo intervals such that they can lamb up to five times in 3 yr, which is equivalent to 1.67 lambings/ yr. However, in this system, the average ewe only lambed once a year and produced 1.5 and 1.2 lambs at birth and rearing, respectively. Only 4% of the ewes lambed at five or more consecutive 7.2 mo intervals (Lewis et al., 1996). In accelerated lambing systems that allow three lambings in 2 yr (equivalent to 1.5 lambings/yr), there are usually three different breeding seasons, and ewes lamb on average at 8-mo intervals. Notter and Copenhaver (1980) used one out-of-season breeding in April, and two in-season breedings in August and November, such that ewes were bred to lamb every 7 to 9 mo. This system was designed to allow more time to rebreed for ewes that lambed in April than for ewes lambing in September. In that study, the average ewe lambed 1.3 times per year and produced 2.8 and 2.3 lambs at birth and weaning, respectively. Fogarty et al. (1984) presented a variation of this scheme with breedings in April, August, and December. The 50% Finnsheep crosses in that study averaged 1.03 lambings and 1.46 lambs weaned per year. The lower performance in the STAR system could have occurred because of shorter breeding periods and very low fertility in March and June.

Not all breeds of sheep are suitable for accelerated lambing. Breeds differ in the onset and duration of the breeding season (Hafez, 1952), and sheep with longer inherent breeding seasons are better suited to accelerated lambing systems than those with shorter inherent breeding seasons (Wang and Dickerson, 1991). Generally, crosses of sheep with Dorset, Rambouillet, and Finnsheep inheritance have been shown to be superior for accelerated lambing (Notter and Copenhaver, 1980; Fogarty et al., 1984; Fahmy, 1990) whereas breeds like Suffolk and Columbia typically have shorter breeding seasons and are inferior for accelerated lambing (Dufour, 1974; Jeffcoate et al., 1984). Hulet et al. (1984) also demonstrated that Polypay, a

composite breed of Dorset, Rambouillet, Targhee and Finnsheep inheritance, had superior performance in accelerated lambing. It is possible to extend the breeding season so that ewes may become more successful in accelerated lambing systems. Vincent et al. (2000) demonstrated an extension in the breeding season in sheep of 50% Dorset, 25% Rambouillet, and 25% Finnsheep inheritance that had been selected for improved fertility in fall lambing (Al-Shorepy and Notter, 1997).

The rest of this review will focus on some of the traits that can be used for genetic improvement of performance in accelerated lambing systems.

Factors influencing fertility and other measures of acceleration. Seasonal effects on fertility have been widely reported in the literature and spring matings generally result in lower fertility. Notter and Copenhaver (1980) studied the reproductive performance of different Finnsheep crosses over 3 yr in a system of three lambings in 2 yr and reported average fertility of 90, 80, and 53 %, respectively, in August, November, and April matings. In a system of three lambings in 2 yr system using Dorsets, Finnsheep, Rambouillet and their crosses, Dzakuma et al. (1982) reported reduced fertility (40%) from late-spring matings (mid-May to early July) compared to fertility from matings in fall (September to November) and winter (early January to February), which was greater than 85%. Fertility in spring matings increased to 62 %, when the breeding period was advanced by 10 to 20 d in fall and winter matings, respectively, to allow a longer rebreeding interval between winter lambing and spring mating. Fertility in April matings in Finnsheep, Dorsets, Rambouillet, Targhee, Suffolk, and their crosses in a system of three lambings in 2 yr was 15%, compared to fertility of about 60% in August and December matings (Fogarty et al., 1984). In the STAR system, Lewis et al. (1996) reported fertilities of 28 and 15 % in March and June matings, respectively, compared to fertilities of 46, 69, and 49 % in August, October and January matings in Dorset ewes, and Tosh et al. (2002) reported fertility of 40% in spring (April, May and June) and 85% in winter (October, November, and December) in Rideau Arcots.

Ewe age and time since previous lambing also affect fertility. Ewe lamb fertility is generally lower than fertility in adult ewes (Hulet et al., 1984; Lewis et al., 1996). Notter and Copenhaver (1980) reported that fertility increased with increasing age till about 6 yr of age and declined in older ewes. Brash et al. (1994) reported linear and quadratic effects of ewe age on fertility with maximal fertility at 3 yr of age, after which fertility declined steadily in older ewes.

Ewes lambing 2 to 4 mo earlier had lower fertility than ewes that had not lambed for at least 7 mo before exposure to rams in August or November in a system of three lambings in 2 yr (Notter and Copenhaver, 1980). Fertility of ewes lambing 2 to 4 mo earlier and more than 7 mo earlier was 73% and 90%, respectively, in August matings, and 76% and 82%, respectively, in November matings. However, in April matings, ewes that had lambed 2 to 4 mo earlier had a higher fertility than ewes that had lambed more than 7 mo earlier (65 vs. 42%). Fogarty et al. (1984) reported similar results. Fertility in August matings in ewes exposed to rams 3 mo after lambing was 62% whereas fertility in ewes exposed to rams 7 mo after lambing was 73%. However, there were no differences among different time-since-lambing classes for fertility in January and April matings. Fogarty et al. (1984) postulated that ewes exposed in August after lambing in May had a short period to recover to breeding condition during the hot summer months which may have led to lower fertility in August matings and suggested rescheduling breeding seasons so that ewes lambing in the summer months had more time to rebreed by the next fall mating. Similar observations regarding fertility in August matings have been made in the STAR system (Lewis et al., 1996). Ewes with more time since previous lambing had higher fertility in August matings than ewes that had just lambed in the previous season (0.50 compared to 0.36). Goulet and Castonguay (2002) also reported that fertility in April matings increased from 64 to 80% when mating occurred 75 d post-partum compared to 90 d post-partum in Lacaune ewes.

Age at first lambing was affected by birth season of the ewe in Dorset ewes in the STAR system (Lewis et al., 1998). Ewes born in August and October were first exposed to rams in the unfavorable March and June months; most failed to conceive at first mating opportunity and lambed at later ages. Ewes first mated in March had a higher average age at first lambing (547 d) than ewes mated in other months (453 to 499 d).

Lambing intervals were affected by season of lambing (Iniguez et al., 1986; Lewis et al., 1998). Lambings in winter were followed by longer lambing intervals than lambings in summer (Iniguez et al., 1986). Lambing intervals were reduced by about 60 d when lambing was immediately followed by mating in a favorable season (Lewis et al., 1998). Lambing interval was shortest when the first mating after lambing occurred in October and was longest when the first post-lambing mating occurred in March or June.

Genetic variation in fertility and other measures of acceleration. Reported estimates of heritability for fertility are generally low. Heritability estimates of repeated fertility records and of fertility records during favorable mating seasons range from 0 to 0.05 in different breeds of sheep (Gabina, 1989; Brash et al., 1994; Lewis, 1990; Tosh et al., 2002). Heritability estimates for fertility in seasons of low fertility are somewhat higher, ranging from 0.09 to 0.16 (Fossecco and Notter, 1995; Al-Shorepy and Notter, 1996; Tosh et al., 2002). Thus high mean fertility may preclude assessment of genetic variation in favorable seasons but underlying genetic variation may be more discernible in seasons of lower fertility. These results suggest that selection to improve fertility in out-of-season matings may be more fruitful than selection for fertility in favorable seasons. Al-Shorepy and Notter (1997) reported significant ($P < 0.10$) selection response in sheep selected for spring fertility; mean EBV for spring fertility was 0.07 ± 0.03 in sheep selected for spring fertility over five generations compared to mean EBV of 0.03 ± 0.02 in the environmental control line, indicating that selection for improvement in out-of-season fertility is feasible.

Heritability for fertility at first mating ranges from close to 0 (Fogarty et al., 1985; Lewis, 1990) to 0.10 (Fogarty et al., 1994; Fossecco and Notter, 1995). Somewhat higher heritabilities of 0.16 to 0.17 have been reported for fertility at second and third parities (Fogarty et al., 1985), and Lewis (1990) reported that heritability of first post-lambing fertility was 0.20. Notter and Cockett (2005) reported a cumulative selection response in spring fertility of 17 to 18 % in sheep over 2 yr of age but spring fertility in 7-mo-old ewe lambs exhibited little response to selection, highlighting the difficulty in evaluating out-of-season fertility in young ewes. These results suggest that selection to improve fertility would be more fruitful when based on fertility at later ages compared to early reproductive performance, although this will lead to an increase generation interval.

Heritability of age at first lambing in Rasa Aragonesa ewes in a system of three lambings in 2 yr ranged from 0.12 and 0.14 (Gabina, 1989), but heritability of age at first lambing in Dorset ewes in the STAR system was not significantly different from zero (Lewis et al., 1998). In the Cornell Alternate Month Lambing (CAMAL) system, which is a more continuous lambing system, heritability of age at first lambing was 0.31 (Iniguez et al., 1986). Thus, there appears to be some scope for improvement of this trait in continuous lambing systems but not as much in some of the other accelerated lambing systems. Heritabilities of repeated records of lambing

intervals over different parities ranges from 0 to 0.06, and repeatabilities range from 0 to 0.25 (Gabina, 1989; Iniguez et al., 1986; Lewis et al., 1998), suggesting little merit in using lambing intervals over different parities as the basis for genetic improvement in accelerated lambing. Lewis et al. (1998) reported a significant heritability of 0.30 for first lambing interval in Dorset ewes under the STAR system, but later lambing intervals had increasing environmental influences and were not heritable.

To summarize, there is potential to genetically improve total weight of lamb weaned by a ewe without major penalties in other production traits. Fertility in out-of-season matings can also be improved, which could lead to more successful accelerated lambing programs, increased numbers of lambs produced by a ewe over her life time, and improved ewe productivity.

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CHAPTER 2

Genetic (co)variance components for ewe productivity traits in Katahdin sheep¹

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ABSTRACT: The objective of this study was to estimate genetic parameters for total weight of litter weaned per ewe lambing (**TW**) and its components, number of lambs born (**NB**), number of lambs weaned (**NW**), and average weight of lambs weaned (**AW**) measured as traits of the ewe in Katahdin sheep. Weaning weights of lambs were adjusted to 60 d of age and for effects of ewe age, lamb sex, and type of birth and rearing (**WW**) and averaged over all lambs in the litter to obtain **AW**. The 60-d age-adjusted weaning weights were adjusted for ewe age and lamb sex and summed over all lambs in the litter to obtain **TW**. A total of 2,995 **NB** and **NW** records, 2,622 **AW**, and 2,714 **TW** records were available from 1,549 ewes (progeny of 235 sires) over 4 yr. Heritabilities were initially estimated for each trait from univariate REML analyses. Estimates of genetic correlations were obtained from bi- and trivariate analyses. Models for **NB**, **NW**, **AW**, and **TW** included random ewe additive and permanent environmental effects. A random service sire effect was also fit for **AW** and **TW**. Heritabilities of **TW**, **NB**, **NW**, and **AW** from univariate analyses were 0.12, 0.12, 0.09, and 0.13 (all $P < 0.01$), respectively. Permanent environmental effects were significant ($P < 0.01$) for **TW** and **AW**. Genetic correlations of **TW** with **NB**, **NW**, and **AW** ranged from 0.27 to 0.33, 0.88 to 0.91, and 0.72 to 0.76, respectively, those of **NB** with **NW** and **AW** ranged from 0.70 to 0.75 and -0.01 to 0.02, respectively, and that between **NW** and **AW** ranged from 0.40 to 0.55. Genetic parameters were also obtained for survival to weaning (**LS**) and **WW** measured as traits of the lamb and relationships between **WW** of the ewe as a lamb and her subsequent records for **NB** and **NW** were also estimated. A total of 5,107 **LS** and 5,444 **WW** records were available. Models for **WW** and **LS** included random animal and maternal genetic, maternal permanent environmental, and litter effects. Heritability of **WW** ranged from 0.15 to 0.20. There was no evidence of

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genetic effects on **LS**. Direct genetic correlations of **WW** with **NB** and **NW** were not significantly different from zero. The correlation between maternal genetic effects on **WW** and animal genetic effects on **NW** averaged 0.35. Results of this study indicate that there are no major antagonisms among **TW** and its components, so that selection for **TW** would not have adverse effects on any component traits and vice versa. Maternally superior ewes for weaning weight appear to also be somewhat superior in **NW**.

[Key words: Ewe productivity, Genetic correlations, Heritability, Katahdin, Sheep]

INTRODUCTION

In the last 10 yr, the average value of lamb has been six to 25 times greater than the average value of wool produced by ewes in the United States (USDA, 2004). Thus, ewe productivity, defined as the total weight of lamb weaned by a ewe, is one of the most important economic traits for the U.S. sheep industry and has been proposed as a biologically optimum “index” for improving overall flock productivity (Snowder, 2002). Total weight of lamb weaned per ewe exposed to breeding provides an overall indication of ewe fertility, prolificacy, maternal performance, and rearing ability as well as lamb survival and growth (Falconer and Mackay, 1996). Ewe productivity has a small genetic component (Safari and Fogarty, 2003), but selection for improvement of this trait appears possible (Ercanbrack and Knight, 1998), and ewe productivity has been identified as a target trait for genetic improvement by the U.S. National Sheep Improvement Program (Notter, 1998).

The Katahdin is a composite sheep breed developed in Maine from crosses between hair- and wool-type breeds (Wildevus, 1997). Genetic improvement in total weight of lamb weaned is important to Katahdin producers since sale of meat is the primary source of income. Estimation of genetic parameters is essential for implementation of a genetic improvement program. The objective of this study was to estimate (co)variance components for ewe productivity in Katahdin sheep, defined here as the total weight of lamb weaned per ewe lambing, and its component ewe traits, namely, number of lambs born, number of lambs weaned, and average weight of lambs weaned. Survival to weaning and weight at weaning were also analyzed as traits of the lamb, since they provide insight into the genetic control of ewe productivity. In addition, weaning weight of the ewe as a lamb was analyzed with subsequent measures of number of lambs born and weaned in bivariate analyses to ascertain relationships between early growth and later prolificacy.

MATERIALS AND METHODS

Data

Growth and prolificacy data were available from several Katahdin flocks enrolled in the U.S. National Sheep Improvement Program (NSIP) (Notter, 1998). Katahdin sheep have been evaluated by NSIP since 2000, with regular recording of birth, weaning, and postweaning weights, birth dates, management codes (e.g., creep feeding policy, location codes, etc), weigh dates, and lamb survival codes. For this study, four different ewe traits were identified for analysis: the composite trait of ewe productivity, measured as the total weight of lamb weaned per ewe lambing (**TW**); the component traits of the number of lambs weaned (**NW**) and average lamb weaning weight (**AW**); and the associated trait of number of lambs born (**NB**). Ideally ewe productivity would be measured as the total weight of lamb weaned per ewe exposed. However, with current data recording procedures in NSIP flocks, ewes that did not conceive were not always clearly identified on NSIP data sheets.

Total litter weaning weight reflects combined effects of reproduction and preweaning growth and was calculated as the sum of the weaning weights of all lambs in the litter. For calculation of **TW**, lamb weaning weights were corrected to 60 d of age and adjusted for effects of sex (to a ewe lamb basis) using multiplicative adjustment factors derived from Katahdin NSIP records (Notter and Kuehn, 2003), but the weaning weights were not adjusted for effects of type of birth and rearing, to allow expression of the anticipated negative relationship between number of lambs weaned and average lamb weaning weight. Lamb weights were likewise not adjusted for ewe age before calculation of **TW**, but ewe age effects were included in the analytical model for this trait. Ewes that lambled but lost their entire litter were given a value of zero for **TW**. Number born measures the prolificacy of the ewe whereas **NW** combines effects of prolificacy and lamb survival. Average lamb weaning weight is indicative of preweaning growth associated with both direct and maternal genetic effects. For calculation of **AW**, weaning weights were corrected to 60 d of age and adjusted for effects of lamb sex, ewe age, type of birth and rearing, and ewe age by type of birth and rearing interactions to better reflect the true genetic potential of the ewe for lamb growth. The basis for adjustment was a ewe lamb that was born and raised as a single and reared by a 3-yr-old ewe. These adjusted weaning weights were then averaged for each litter to derive **AW**. For ewes that lambled and lost their entire litter, the value of **AW** was assumed to be missing, since no weaning weights were recorded.

Ewes received no credit for lambs that were artificially reared or fostered in calculating **NW**, **AW**, and **TW**. Records of weaning weights from litters in which individual lambs did not have a valid 60-d weaning weight (i. e., a weaning weight taken between 30 and 90 d of age) nor were known to have died (i.e., did not have a survival code clearly indicating lamb death) were not used and resulted in missing values for **AW** and **TW** for the ewes. Also, for **AW** and **TW**, occasional records from ewes with lambs born in the same litter but subsequently raised in different weaning weight management groups were excluded from the analysis. Weaning weights from such litters could not be averaged or summed over the entire litter without disregarding potential lamb management differences. For analysis of ewe performance, only data from ewes lambing from 2001 through 2004 were used; older records were available but not used because of lack of confidence in information on lamb survival and therefore the actual number of lambs weaned in those data. However, all available pedigree information was used in order to utilize all genetic links between flocks.

Contemporary groups were formed for **TW**, **NB**, and **NW** based on flock, year of birth, time of birth in the lambing season (using 45-d lambing date windows), and percentage Katahdin breeding group. Only records from animals with at least 75% Katahdin breeding were used. Animals were categorized as 75 to 87.5% or greater than 87.5% Katahdin breeding, respectively. Ewes were assigned to contemporary groups for **AW** based on flock, year of birth, date of weaning of the lamb (using 7-d weaning date windows), weaning weight management code, and percentage Katahdin breeding. Lamb weaning weight contemporary groups were not used to form **TW** contemporary groups because ewes that lambled but did not wean any lambs (i.e., those with **TW** = 0) could often not be unambiguously assigned to lamb weaning weight contemporary group. Overall, data came from a total of 1,549 ewes representing 235 sires. The number of daughters per sire ranged from 1 to 19 with an average of 6.59; 50 sires had at least 10 daughters with records.

In addition to the ewe traits, 60-d weaning weight (**WW**) and survival (**LS**) were analyzed as traits of the lamb, since these traits influence ewe productivity. These analyses also allowed consideration of the relative importance of direct and maternal genetic effects on **WW** and **LS**. Lamb weaning weights were corrected to 60-d of age and adjusted for effects of lamb sex, ewe age, type of birth and rearing, and ewe age by type of birth and rearing interaction before analysis. Lambs were assigned to weaning weight contemporary groups as described for

AW. Lamb survival was measured from birth to weaning; lambs that survived to weaning were given a score of 1 and lambs that did not survive were given a score of 0. Only data from lambs whose fate was definitively known were utilized; data from lambs that did not have a valid survival code or a valid weaning weight were excluded from the analysis. Contemporary groups for lamb survival were assigned as described for **TW**, **NB**, and **NW**. The final numbers of records after editing, means and standard deviations for lamb and ewe traits, and numbers of contemporary groups are given in Table 2.1.

Statistical Analysis

Genetic analyses were carried out using multi-trait derivative-free restricted maximum likelihood (**MTDFREML**) software (Boldman et al., 1993).

Ewe traits. Initial estimates of heritability were obtained from univariate analyses. Bi- and trivariate analyses were then performed to evaluate interrelationships among traits. The model for all ewe traits included fixed contemporary group effects and random animal (ewe) and ewe permanent environmental effects. The model for **NB**, **NW**, and **TW** also included fixed effect of ewe age. The model for **AW** and **TW** also included a random service sire effect, but genetic relationships among service sires were not considered. Tests of significance for random effects in single-trait models were performed using likelihood ratio tests after deleting each random term from the model.

Lamb traits. Models for **WW** and **LS** included fixed effects of contemporary group and random additive direct, additive maternal, ewe permanent environmental, and litter effects. Weaning weight was analyzed with and without inclusion of a covariance between direct and maternal genetic effects. The model for **LS** also included effects of lamb sex, ewe age, and type of birth and was analyzed with and without inclusion of birth weight as a covariate to determine if genetic effects on lamb survival could be accounted for by differences in lamb birth weight. Tests of significance for random terms and the direct-maternal genetic covariance were performed using likelihood ratio tests after deleting each random effect or covariance from the model.

Lamb and ewe traits. Bivariate analyses to estimate relationships between **WW** of the ewe as a lamb and subsequent measures of **NB** and **NW** were also performed. Terms included in the model were as described above for each trait. Additionally, covariances were included between animal genetic effects on **NB** or **NW** and animal and maternal genetic effects on **WW**;

the resulting correlations are denoted by r_a and r_m , respectively. The **MTDFREML** software did not permit direct estimation of covariances between residual environmental effects on **WW** and subsequent ewe permanent environmental effects on **NB** or **NW**. However, environmental conditions prevalent during weaning could affect later expression of **NB** or **NW**. To accommodate such an environmental covariance, residual effects on **WW** were modeled as an animal permanent environmental effect and covariances between animal permanent environment effects on **WW** and **NB** or **NW** were included in the model (Rao and Notter, 2000); the resulting correlation is denoted by r_e . These bivariate analyses were repeated with and without inclusion of an animal-maternal genetic covariance for **WW**. Since animal permanent environment effects were fit for **WW**, which is a non-repeated trait, residual variances for **WW** in these analyses were correspondingly fixed at zero to yield an equivalent model to that used for univariate analysis of **WW**. Covariance between animal and maternal genetic effects on **WW** and animal genetic effects on **NB** or **NW** were tested for significance using likelihood ratio tests.

RESULTS AND DISCUSSION

Heritabilities and other variance proportions for ewe traits

Estimates of variance components from univariate analyses for **NB**, **NW**, **AW**, and **TW** are given in Table 2.2. All four traits had heritability estimates that were moderately low, but significantly different from zero. For **NB** and **NW**, only negligible amounts of variation were accounted for by ewe permanent environmental effects. These measures of prolificacy are expected to be under similar genetic control unless genetic differences exist in lamb survival. Effects of ewe permanent environment on **AW** were also significant, but effects of the service sire were not significant. Ewe permanent environmental effects accounted for a small amount of variation in **TW**, but the service sire of the ewe did not explain any of the phenotypic variation in **TW** and was excluded from subsequent bivariate models.

Results of bi- and trivariate analyses are given in Tables 2.3 and 2.4, respectively. Heritability estimates and proportions of variation due to ewe permanent environment and service sire effects in multivariate analyses were similar to those obtained from univariate analyses, except that the proportion of variation explained by ewe permanent environmental effects was somewhat higher for **NB** and **NW** in multivariate analyses. This result could have arisen because of the small variation in **NB** and **NW**, and was associated with large negative estimates of the ewe permanent environmental correlation.

Proportions of phenotypic variance in **NB**, **NW**, and **TW** accounted for by additive and permanent environment components in this study are in general agreement with literature estimates reviewed by Safari and Fogarty (2003) and Safari et al. (2005). The absence of service sire effects on **TW** was consistent with findings of Bromley et al. (2001) and Rosati et al. (2002) who reported that the service sire component accounted for 0 to 3% of phenotypic variance. The only heritability estimate of **AW** using an animal model that we found in the literature was 0.15 (Rosati et al., 2002). Although few literature estimates of genetic parameters are available for this trait, approximations can be made using direct and maternal variance component estimates for individual lamb weaning weight and are discussed later in this paper.

Correlations among ewe traits

Correlations among ewe traits from bivariate and trivariate analyses are given in Tables 2.3 and 2.4, respectively. Genetic correlations obtained from these analyses were similar. The genetic correlation of **TW** with **NB** averaged 0.30, whereas correlation of **TW** with **NW** and **AW** exceeded 0.88 and 0.72, respectively. Number of lambs weaned had a genetic correlation of 0.70 to 0.75 with **NB** and a genetic correlation of approximately 0.50 with **AW**. However, **NB** and **AW** were genetically independent.

Permanent environmental correlations among ewe traits varied more than genetic correlation among analyses. Permanent environmental correlations were generally negative between **NB** and **NW**, small between **NB** and **TW**, moderate to high for **AW** with **NB** and **NW**, and high for **TW** with **AW** and **NW**. The high ewe permanent environmental correlations observed between some of the traits could be artificially inflated by the small ewe permanent environment variance components associated with **NB**, **NW**, and **TW**, which make denominators of correlation terms extremely small. Residual and phenotypic correlations (Tables 2.3 and 2.4) among traits were generally moderate to high and positive except for those between **AW** and reproductive traits such as **NB** and **NW**, which were small and negative.

Genetic correlations among the component and composite ewe traits do not give any indication of antagonistic relationships. Genetic correlations among **NB**, **NW**, and **TW** from the current data are within the ranges reported by Safari and Fogarty (2003). As with heritability estimates of **AW**, few literature estimates of genetic correlations involving **AW** are available. Rosati et al. (2002) reported a genetic correlation of 0.05 between **AW** and **NB**, 0.02 between **AW** and **NW**, and -0.07 between **AW** and **TW**. Our estimates of genetic correlation between

AW and **NW** or **TW** are much higher than those of Rosati et al. (2002). A high genetic correlation between **TW** and **AW** is expected because **TW** is a product of **AW** and **NW**. However, genetic correlations between growth and reproductive traits seem to vary considerably across populations (Safari and Fogarty, 2003; Safari et al., 2005).

Heritabilities and other variance proportions for lamb traits

Estimates of variance components from univariate analyses of survival and weaning weight in lambs are given in Table 2.5. There was no evidence of direct or maternal genetic effects or ewe permanent environmental effects on lamb survival, but there were significant effects due to litter. No additive-maternal covariance was estimated for lamb survival because of the small components of variance for these genetic effects. The regression of lamb survival on birth weight was $0.031 \pm 0.003 \text{ kg}^{-1}$, indicating, as expected, that heavier lambs had a better chance of survival. However, inclusion of birth weight in the model for lamb survival had essentially no effect on estimates of genetic parameters.

Our results for lamb survival are in general agreement with literature estimates for both direct and maternal heritabilities which were generally less than 0.10 and averaged only 0.03 and 0.05, respectively (Safari and Fogarty, 2003; Safari et al., 2005). Somewhat higher estimates for direct heritability of 0.14 and maternal heritability of 0.11 for lamb survival were obtained by Everett-Hincks et al. (2005). In our study, lamb survival was analyzed as a 0/1 trait, with no transformation to either the logit or probit scales. Morris et al. (2000) reported that direct and maternal heritabilities were only slightly higher when survival data were transformed and Amer and Jopson (2003) reported that transformation of survival data using logit or probit functions did not greatly affect heritability estimates. In several studies reported by Safari and Fogarty (2003), analysis of the same data with or without transformation led to similar heritability estimates. In any case, our results suggest that there is not much genetic variation in lamb survival, although full-sib littermates appear to share a common risk of death. Selection to improve lamb survival may therefore not be fruitful in this situation, but opportunity exists for improvement by means of environmental manipulation, perhaps through more intensive management, especially in the case of triplets.

Weaning weight was moderately heritable with significant maternal, ewe permanent environmental and litter effects (Table 2.5). Direct and maternal genetic effects had a small negative correlation ($r = -0.38$; $P = 0.14$). Variance components for lamb weaning weight from

our data are in general agreement with literature estimates reviewed by Safari and Fogarty (2003) and summarized by Safari et al. (2005).

The direct genetic variance for average lamb weaning weight as a trait of the ewe can be approximated from lamb weaning weight variance components as the sum of maternal genetic variance, one-quarter of the direct genetic variance and the covariance between direct and maternal effects. The phenotypic variance for **AW** for single, twin and triplet litters can similarly be derived from the variance components for lamb weaning weight, giving a predicted weighted heritability for **AW** of 0.15, which is similar to the direct heritability estimate of 0.13 obtained for **AW**. Also, the service sire variance in **AW** is expected to be one-quarter of the direct heritability for lamb weaning weight, which is equal to 0.05 and is equal to the service sire component of **AW**. The proportion of phenotypic variance due to ewe permanent environment was similar for both individual lamb weaning weight and **AW** at 0.14. The negative correlation between direct and maternal genetic effects suggests that genetic selection to improve growth is possible but that there may be a small antagonism between direct genetic effects on growth and genetic effects on milk production. This should be taken into consideration if selection is for growth alone, as reduced milk production in ewes could reduce lamb survival. However, the magnitude of the genetic correlation between direct and maternal effects is sufficiently small that the antagonism could be easily managed by proper attention to these two components of lamb growth.

Bivariate analyses of lamb and ewe traits

Results from bivariate analyses of **WW** and **NB** or **NW** are given in Table 2.6. Heritabilities and other variance proportions for each of the traits were similar to those obtained in prior analyses. Correlations between animal and maternal genetic effects on **WW** and animal genetic effects on **NB** (r_a and r_m , respectively), as well as the phenotypic correlation (r_p), were small and not significantly different from zero, indicating that these two traits are genetically independent. Correlation (r_e) between residual environmental effects on **WW** (e_w^2), which were modeled as animal permanent environmental effects for a non-repeated trait, and animal permanent environmental effects for **NB** (c_{a-r}^2) were high and could have been artificially inflated by the small ewe permanent environment variance component associated with **NB**. Correlations between animal genetic effects on weaning weight of the ewe as a lamb and

subsequent measures of **NB** are reported to range from -0.14 to 0.38 in different breeds (Rao and Notter, 2000; Ap Dewi et al., 2002, Hanford et al., 2002). Olivier et al. (2001) reported that genetic correlation between weaning weight and lifetime **NB** over three parities in South African Merino flocks ranged from 0.32 to 0.45. Safari et al. (2005) reported an average animal genetic correlation of 0.29 between weaning weight and **NB**. Correlations between maternal genetic effects of the ewe on weaning weight and **NB** are reported to range from -0.23 to 0.40 in different breeds (Rao and Notter, 2000; Ap Dewi et al., 2002; Hanford et al., 2002).

The correlation between animal genetic effects on **WW** and **NW** was small and not significantly different from zero, but maternal genetic effects on **WW** had an average correlation of 0.35 across models with animal genetic effects on **NW**, indicating that maternally superior ewes would have somewhat higher genetic merit for **NW**. These results suggest that **WW** and **NB** or **NW** do not have major genetic antagonisms and selection for **WW** should not have an adverse effect on **NB** or **NW** and vice versa. Hanford et al. (2002) reported correlations between animal and maternal genetic effects on weaning weight of the ewe as a lamb and **NW** in Columbia sheep as 0.24 and 0.66, respectively, which are both higher than our estimates. Genetic correlation between **WW** of the ewe as a lamb and lifetime **NW** over three parities ranged from 0.34 to 0.57 (Olivier et al., 2001). Safari et al. (2005) reported an average genetic correlation of -0.05 between weaning weight at different ages and **NW**.

General discussion

The response to selection for a trait is dependent on the selection intensity, heritability and phenotypic standard deviation (Falconer and Mackay, 1996). If heritability is low, genetic progress can occur if reasonable variation is present in the trait, which is the case for **NB**, **NW**, and **TW**. Using the heritability and phenotypic standard deviation obtained in this study and assuming that 50% of females and 5% of males are selected as parents, response to selection for **TW** is expected to be 1.66 kg (5.9 %) per generation. Luxford and Beilharz (1990) reported a positive response to selection for increased litter weight at weaning in mice. Ercanbrack and Knight (1998) reported a 0.43 to 1.06 kg/generation genetic improvement in **TW** in lines of sheep selected on current lifetime average **TW**. Olivier et al. (2001) reported an estimated genetic improvement of 6.37 to 9.03 kg/generation when selection was based on the sum of individual **TW** over three parities. This prediction is considerably greater than three times the change in single parity **TW** reported by Ercanbrack and Knight (1998) or predicted from this

study, in part because of an increase in phenotypic CV for a sum of correlated measures. The heritability of **TW** in that flock was also higher, ranging from 0.19 to 0.21 in the study of Olivier et al. (2001) and from 0.13 to 0.22 in a report on the same flock by Snyman et al. (1997).

Genetic correlations among ewe traits were generally positive and moderate to high in magnitude, except for **NB** and **AW** which seem to be genetically independent. Therefore, selection on any of the component traits should result in improvement of **TW** and vice versa. Also, selection on any of the component traits should not adversely affect other component traits. High genetic correlations between **TW** and either **NW** or **AW** were expected because **TW** is a product of **AW** and **NW**. Bromley et al. (2001) indicated that direct selection for **NW** should improve ewe productivity and suggested that counting the number of lambs weaned may be more practical than weighing all the lambs, especially in extensive production systems. Improvements in total weight of litter weaned through selection on weaning weight (Bradford et al., 1999) and litter size at birth and weaning (Bradford et al., 1999; Cloete et al., 2004) have been reported. Olivier et al. (2001) also reported that selection on weaning weight, litter size at birth and litter size at weaning is expected to result in genetic improvement in total litter weight weaned.

Although selection for improved ewe productivity or total weight of lamb weaned is possible, caution must be practiced when predicting genetic merit for animals in different environments, because of the possibility of genotype by environment interactions. Caution is especially warranted for a trait like ewe productivity because of the potential for different management practices for triplet lambs and differences in average lamb survival across environments. Some researchers have also cautioned that differences in feed resources among environments or production systems must be considered as nutrition may become a limiting factor for the potentially most productive ewes (Head et al., 1995; Hatfield et al., 1996). However, selection for increased total weight of lamb weaned within a single production system or environment is likely to result in animals that are optimally adapted to that production system or environment (Snowder, 2002).

Several researchers have proposed direct selection for total litter weight at weaning (Luxford and Bielharz, 1990; Bradford, 2002; Olivier et al., 2001) and observed responses to such selection have been substantial (Luxford and Bielharz, 1990; Ercanbrack and Knight, 1998). However, direct genetic evaluation of **TW** in field data is complicated, among other reasons, because of incomplete reporting of data (for example, when weaning weights cannot be

used because they are taken outside the prescribed 30 to 90 d age window or when information on lamb survival, and thus on **NW**, is not clearly reported) and potential difficulties in forming contemporary groups. Direct genetic evaluation of **TW** is relatively straightforward if ewes that lamb together are all maintained together until weaning so that all their lambs are in the same weaning weight contemporary group but becomes difficult when lambs are divided into different weaning weight contemporary groups. This situation is common in field data and in particular creates problems in assigning ewes that do not wean any lambs to an appropriate contemporary group. Contemporary groups for **NB** can usually be assigned in a consistent manner and could also be used for **TW**, but doing so will not take into account differences in preweaning management of the lambs. It is possible to additively adjust weaning weights of lambs born within a common birth contemporary group for subsequent effects of weaning weight contemporary groups before calculating **TW** but this approach adds an additional step to the genetic analysis. In the current application, such an adjustment had little effect on variance component estimates for **TW**. The heritability estimated following adjustment for differences in lamb weaning contemporary group was 0.11 and the proportion of variance attributed to ewe permanent environment effects was 0.08, which were similar to the estimates shown in Tables 2.2 to 2.4. However, failure to account for differences in the pre-weaning environment could still bias estimates of lamb breeding values.

The direct evaluation of **TW** is further complicated by its complex distribution (Figure 2.1). As pointed out by Rosati et al. (2002), the distribution of **TW** is conditioned by the distribution of its component traits, including the categorically distributed **NW**, which can range from zero to three or four, and weaning weight (which is assumed to be normally distributed). Usually, estimated breeding values, which are used for selection of breeding animals, are derived using linear model theory under the assumptions that data are normally distributed (Henderson, 1984). Clearly, the distribution of **TW** violates this assumption.

An alternative approach to direct genetic evaluation is to indirectly predict genetic merit for **TW** using only data on its component traits of **NW**, **AW**, and **NB**, and utilizing the genetic correlations among the component traits and **TW**. This is akin to a selection index strategy which uses all available records for component traits to predict **TW**. Although **NW** and **AW** should be adequate to predict **TW**, additional information from the correlated trait of **NB** can also be used in situations where data for **NW** may not be available. By using this strategy, data

for **TW** itself are not utilized, so missing or ambiguous data on one or more of the component traits do not lead to a completely missing **TW** record and problems in forming contemporary groups can be avoided. This strategy is perhaps computationally more demanding, since it involves estimation of (co)variance components for all the component traits as well as the composite trait, but the efficacy of this indirect prediction strategy has been shown by genetic simulation to compare favorably to direct genetic evaluation for **TW** (CHAPTER 3 of Vanimisetti, 2006).

IMPLICATIONS

Heritabilities for the total weight of lamb weaned by a ewe and its components were small but significant and in spite of the low heritability, genetic improvement in total weight of litter weaned by a ewe is possible because of the large phenotypic variation present in the trait. No genetic antagonisms were observed among the component traits of number of lambs born, number of lambs weaned and average litter weaning weight, or between the component and composite traits, suggesting that selection for the composite trait should not lead to negative responses in any component traits and vice versa. Genetic merit for total weight of litter weaned could be predicted from component traits using the genetic correlations among them to avoid complications with direct evaluation of ewe productivity in field data.

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Table 2.1. Numbers of records and contemporary groups (**CG**) and means, standard deviations, and ranges for each of the ewe and lamb traits.

Item ^a	Number of:			Mean	S.D.	Range
	Records	Animals	CG			
NB	2995	1549	192	1.83	0.68	1 to 4
NW	2995	1549	192	1.59	0.64	0 to 3
AW , kg	2622	1426	335	21.78	4.22	6.7 to 39.3
TW , kg	2714	1475	134	27.84	11.72	0 to 66.4
LS	5107	5107	187	0.91	0.28	0 to 1
WW , kg	5444	5444	420	22.09	4.40	5.0 to 48.6

^a For ewe traits, **NB** = number born; **NW** = number weaned; **AW** = average weaning weight, and **TW** = total weaning weight of the litter. For lamb traits, **LS** = survival to weaning and **WW** = weaning weight.

Table 2.2. Estimates of variance components from single-trait REML analyses for number of lambs born (**NB**), number of lambs weaned (**NW**), average lamb weaning weight (**AW**, kg), and total litter weight weaned (**TW**, kg) as traits of the ewes.

Item ^a	NB	NW	AW	TW
h^2	0.12 **	0.09 **	0.13 **	0.12 **
c^2	0.004	0.009	0.14 **	0.06 **
s^2	--	--	0.05	0.00
σ_p^2	0.329	0.339	9.43	92.88

^a h^2 , c^2 , and s^2 are animal genetic, animal permanent environmental, and service sire proportions of σ_p^2 ; σ_p^2 = phenotypic variance.

** $P < 0.01$.

Table 2.3. Estimates of (co)variance components from two-trait REML analyses for number of lambs born (**NB**), number of lambs weaned (**NW**), average lamb weaning weight (**AW**, kg), and total litter weight weaned (**TW**, kg) as traits of the ewes.

Item ^a	Trait 1/Trait 2					
	TW		NB		NW	
	NB	NW	AW	NW	AW	AW
h_1^2	0.12	0.13	0.13	0.12	0.12	0.10
h_2^2	0.12	0.09	0.13	0.09	0.13	0.14
r_g	0.27	0.88	0.72	0.70	-0.01	0.40
c_1^2	0.07	0.05	0.08	0.02	0.01	0.01
c_2^2	0.004	0.02	0.16	0.03	0.14	0.13
r_c	-0.15	0.99	0.94	-0.99	0.99	0.63
s_2^2	-	-	0.03	-	0.05	0.04
r_e	0.38	0.77	0.36	0.62	-0.08	-0.13
σ_{p1}^2	92.94	92.31	93.83	0.33	0.33	0.34
σ_{p2}^2	0.33	0.34	9.99	0.34	9.47	9.48
r_p	0.35	0.79	0.47	0.60	-0.02	-0.04

^a h_i^2 , c_i^2 , s_i^2 are proportions of phenotypic variance associated with additive genetic, permanent environmental, and service sire effects, respectively, for trait i ; σ_{pi}^2 = phenotypic variance for trait i ; r_g , r_c , r_e , r_p are genetic, permanent environmental, residual, and phenotypic correlations, respectively, between traits 1 and 2.

Table 2.4. Estimates of (co)variance components from three different three-trait (Tri-1, Tri-2, Tri-3) REML analyses for number of lambs born (**NB**), number of lambs weaned (**NW**), average lamb weaning weight (**AW**, kg), and total litter weight weaned (**TW**, kg) as traits of the ewes. ^a

Tri-1	σ_p^2	$h^2, r_g, \text{ and } r_e$			$s^2, c^2, \text{ and } r_c$				
		NB	NW	AW	NB_c	NW_c	AW_c	AW_s	
NB	0.33	0.11	0.75	0.02	NB_c	0.03	-0.72	0.58	-
NW	0.34	0.62	0.10	0.55	NW_c		0.02	0.13	-
AW	9.48	-0.07	-0.13	0.13	AW_c			0.14	-
					AW_s				0.04
Tri-2		NW	AW	TW		NW_c	AW_c	TW_c	AW_s
NW	0.34	0.10	0.53	0.91	NW_c	0.02	0.31	0.84	-
AW	47.87	-0.03	0.14	0.76	AW_c		0.14	0.77	-
TW	93.17	0.77	0.36	0.15	TW_c			0.06	-
					AW_s				0.02
Tri-3		NB	NW	TW		NB_c	NW_c	TW_c	
NB	0.33	0.11	0.71	0.33	NB_c	0.03	-0.37	0.04	
NW	0.34	0.62	0.09	0.90	NW_c		0.02	0.91	
TW	92.22	0.38	0.78	0.13	TW_c			0.05	

^a Proportions of phenotypic variances are on the diagonals, genetic or and permanent environmental correlations are above the diagonals, and residual correlations are below the diagonals; σ_p^2 = phenotypic variance; h^2 , c^2 , and s^2 are additive genetic, permanent environmental, and service sire proportions of total phenotypic variance, respectively; r_g, r_c , and r_e are genetic, permanent environmental, and residual correlations, respectively.

Table 2.5. Estimates of variance components for weaning weight (**WW**, kg), both with (1) and without (2) inclusion of animal-maternal genetic covariance, and lamb survival (**LS**) from single-trait REML analyses.

Item ^a	WW ₍₁₎	WW ₍₂₎	LS
h^2	0.20 **	0.15 **	0.01
m^2	0.12 **	0.08 **	0.00
r_{a-m}	- 0.38	-	-
c^2	0.14 **	0.14 **	0.02
l^2	0.06 **	0.06 **	0.09 **
σ_p^2	12.08	11.77	0.07

^a h^2 , m^2 , c^2 , and l^2 are animal genetic, maternal genetic, ewe permanent environmental, and litter proportions of σ_p^2 ; r_{a-m} = animal - maternal genetic correlation; σ_p^2 = phenotypic variance.

** $P < 0.01$.

Table 2.6. Estimates of co-variance components from bivariate analyses of weaning weight, modeled both with (1) and without (2) direct-maternal additive genetic covariance, and subsequent numbers of lambs born (**NB**) or numbers of lambs weaned (**NW**)^a.

Item ^b	Ewe trait			
	NB (1)	NB (2)	NW (1)	NW (2)
h_w^2	0.18	0.15	0.19	0.15
h_r^2	0.12	0.13	0.10	0.10
r_a	-0.15	0.13	0.10	0.06
m_w^2	0.11	0.08	0.11	0.08
r_{am}	-0.31	-	-0.33	-
r_m	0.17	0.04	0.31 *	0.39 *
c_{m-w}^2	0.14	0.13	0.14	0.14
c_{l-w}^2	0.06	0.06	0.06	0.06
c_{a-r}^2	0.02	0.001	0.01	0.01
e_w^2	0.56	0.57	0.55	0.57
e_r^2	0.87	0.87	0.90	0.90
r_e	0.74	0.94	-0.07	0.12
σ_{p-w}^2	11.99	11.97	12.01	11.95
σ_{p-r}^2	0.33	0.33	0.34	0.34
r_p	0.06	0.05	0.02	0.03

^a Tests of significance were only performed for r_a and r_m .

^b Subscripts w and r denote weaning weight and reproductive traits, respectively. h^2 , m^2 , c_m^2 , c_l^2 , c_a^2 , and e^2 are direct genetic, maternal genetic, maternal permanent environmental, litter, animal permanent environmental, and residual proportions of σ_p^2 ; r_a = animal additive genetic correlation between weaning weight and reproductive traits; r_{am} = direct-maternal additive

genetic correlation (weaning weight only); Γ_m = correlation between maternal additive effects on weaning weight and animal additive effects on reproductive traits; Γ_e = correlation between animal permanent environmental effects on reproductive traits and residual effects on weaning weight; Γ_p = phenotypic correlation; σ_p^2 = phenotypic variance.

* $P < 0.05$.

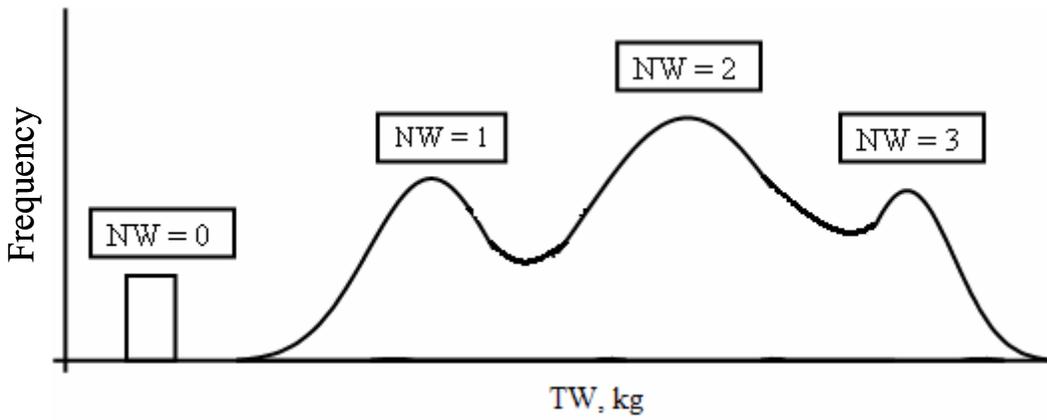


Figure 2.1. Depiction of the distribution of total weight of litter weaned (TW), which is conditioned by distributions of number of lambs weaned (NW) and the weaning weight of lambs.

CHAPTER 3

Alternative methods of predicting genetic merit for total weight of litter weaned by a ewe⁴

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ABSTRACT: Ewe fertility, litter size (**NB**), lamb survival, and lamb weaning weight (**WW**) were modeled by stochastic simulation for 5,000 ewes and their progeny for 5 yr in an annual lambing system. These traits were then used to derive ewe productivity traits including number of lambs weaned (**NW**), average weight of lambs weaned (**AW**), and total weight of lambs weaned per ewe lambing (**TWL**) in order to evaluate alternate predictors of genetic merit for **TWL**. To simulate incomplete reporting of **WW**, which is common in field data, a random 8% of **WW** records were set to missing and traits involving **WW** were recalculated. Three replicate sets of data were generated. Univariate and bivariate genetic analyses were used to estimate variance components and correlations among **NB**, **NW**, **AW**, and **TWL**. Heritabilities for **NB**, **NW**, **AW**, and **TWL** ranged from 0.08 to 0.10, 0.06 to 0.09, 0.15 to 0.22, and 0.06 to 0.10, respectively, among replicates and were reduced by 1 to 2% in the presence of missing **WW** records. Genetic correlations of **NB** with **NW**, **AW**, and **TWL** ranged from 0.29 to 0.55, -0.30 to 0.04, and 0.10 to 0.52, respectively, those of **NW** with **AW** and **TWL** ranged from -0.42 to 0.19 and 0.70 to 0.87, respectively, and that between **AW** and **TWL** ranged from 0.63 to 0.72. Genetic correlations among traits were similar in the presence of missing **WW** records. Four alternative predictors of **EBV** for **TWL** were considered: a direct univariate predictor (**TWL-1**), an index of **EBV** for **NW** and **AW** (**TWL-2**), an indirect predictor using data for **NW** and **AW** and genetic correlations among **NW**, **AW** and **TWL** (**TWL-3**), and an indirect predictor using data for **NB**, **NW**, and **AW** and genetic correlations among **NB**, **NW**, **AW**, and **TWL** (**TWL-4**). To validate efficacy of predictors, two daughter data sets were generated from each of the three original sets of ewe data, and daughter's realized **TWL** were regressed on alternative predictors of ewe **EBV**. Regression coefficients for **TWL-1**, **TWL-3**, and **TWL-4** were close to the

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expected value of 0.50 whereas those from **TWL-2** were less than 0.50. This study did not clearly identify a single superior method for predicting genetic merit for **TWL**, although multivariate linear predictors would be more robust in the presence of missing **WW** data; model R-square statistics for all four predictors were similar when there were no missing **WW** data but regressions involving **TWL-1** had lowest model R-square values in the presence of missing **WW** data.

[Key words: Ewe Productivity, Genetic Prediction, Heritability, Reproduction, Sheep]

INTRODUCTION

The total weight of lamb weaned provides an overall indication of the combined effects of ewe fertility, prolificacy, maternal performance and rearing ability, as well as lamb survival and growth (Falconer and Mackay, 1996) and is one of the most important economic traits for the U. S. sheep industry (Snowder, 2002). It is lowly heritable (Safari et al., 2005), but selection for improvement is possible due to the large variation present in the trait (Ercanbrack and Knight, 1998).

There has been an increasing interest in estimation of genetic merit for total weight of litter weaned (**TW**) by a ewe. The **TW** is a product of average weight of the lambs weaned in the litter (**AW**) and number of lambs weaned (**NW**). The **AW** is a function of individual lamb weaning weights (**WW**), and **NW** is a function of ewe fertility, number of lambs born, and survival to weaning of individual lambs within the litter. Direct estimation of genetic merit for **TW** in field data is not straightforward, because of incomplete reporting of data, potential difficulties in forming contemporary groups, and distributional complexities (Rosati et al., 2002; Vanimisetti et al., 2006). Alternatively, genetic merit for **TW** could be predicted indirectly from information on component traits and the genetic correlations among them and **TW** using selection index methodology (Vanimisetti et al., 2006) or an index formulated to predict breeding values for a multiplicative trait from **EBV** for component traits (Smith, 1967). The objective of this study was to develop a stochastic simulation model to generate phenotypes for **TW** from its component traits and use the resulting data to compare efficacy of indirect genetic prediction strategies to direct genetic evaluation for **TW** in an annual lambing system. The indirect prediction strategies considered were a multiplicative index proposed by Smith (1967) and indirect prediction by selection index using two or more of the component traits proposed by Vanimisetti et al. (2006).

MATERIALS AND METHODS

General description. A stochastic simulation model was developed using SAS software (SAS Inst. Inc., Cary, NC) to model ewe fertility (**EF**) and litter size (**NB**) and individual lamb survival (**LS**) and weaning weight (**WW**) for ewes and their offspring. The simulated flock consisted of 5,000 ewes which were offspring of 5,000 dams and 200 sires. The simulated ewes were randomly mated to unrelated service sires in an annual lambing system over a period of 5 yr. Each service sire was mated to 25 ewes. Each year, before mating occurred, 1,000 ewes were randomly culled so that 5,000 ewes were mated in the first year, 1,000 ewes were mated in the fifth year, and a total of 15,000 ewe mating records were generated. For ewes that were not culled, a 0/1 phenotypic expression was simulated for **EF**. Ewes that conceived were further simulated to have litters of 1, 2, or 3 lambs. Lambs were randomly assigned to either of the sexes (50% male and 50% female). Individual lambs were then assigned simulated values of 0 or 1 for **LS** and a **WW** was simulated for surviving lambs. Finally, several composite traits were calculated for the ewes from these simulated component traits. The simulation was replicated three times using procedures described below and input parameters given in Tables 3.1 and 3.2. The input parameters used in this study were approximated from literature estimates (Safari and Fogarty, 2003) and those obtained for Katahdin sheep by Vanimisetti et al. (2006).

Simulation models. Ewe fertility and lamb survival were expressed as all or none traits, number born was expressed as a categorical trait with three classes, and weaning weight had a continuous distribution. All four traits were assumed to have an underlying continuous normal phenotypic distribution (Falconer and Mackay, 1996). Additive breeding values for founder animals (i. e., the parents of the simulated ewe flock) were randomly generated for all traits from normal distributions with means of 0 and variances corresponding to the additive genetic effects, and breeding values for ewes were calculated as the sum of the average parent breeding values and a random Mendelian sampling term. Realized phenotypes for **EF** were then simulated using procedures described by Johnson and Notter (1987) for conception rate of beef cows. Briefly, phenotypes for **EF** on the underlying scale were calculated as the sum of normally distributed independent additive genetic and random temporary environmental effects with means of 0 and variances of $h^2 (=0.07)$ and $1-h^2$, respectively (Table 3.1). Phenotypic values on the underlying scale thus had a mean of 0 and variance of 1. Observed values for **EF** were derived by truncating the normal phenotypic distribution at a threshold corresponding to the mean fertility

for ewes of different ages (Table 3.2). Individuals above the threshold were assumed to conceive (**EF** = 1), and those below the threshold did not conceive (**EF** = 0). No effects of service sire on conception of ewes were considered in this simulation.

Number of lambs born was assumed to be affected by additive genetic, ewe permanent environmental, and temporary environmental effects (Table 3.1). Ewe permanent and temporary environmental effects were assumed to be normally distributed with means of 0 and variances of c^2 and $1-h^2-c^2$, respectively. Phenotypic values for **NB** for each successful mating were calculated as the sum of constant ewe breeding values and permanent environmental effects and a random temporary environmental effect. Observed phenotypes for **NB** of 1, 2 or 3 were generated by truncating the phenotypic normal distribution at points corresponding to the assumed litter size distributions for ewes of different ages (Table 3.2).

Based on a preliminary analysis of Katahdin data from the U. S. National Sheep Improvement Program (NSIP) flocks, survival of lambs to weaning was derived on the underlying scale as the sum of independently and normally distributed maternal genetic, litter, and temporary environmental effects with means of 0 and variances of m^2 , l^2 , and $1-m^2-l^2$, respectively (Table 3.1). An additive direct effect of the lamb on **LS** was not observed in these analyses and subsequent analysis of the Katahdin NSIP records by Vanimiseti et al. (2006) later revealed no significant additive effect of either the lamb or the dam on **LS**. Observed phenotypes for **LS** were obtained by truncating the resulting normal phenotypic distribution at a threshold corresponding to the anticipated mean lamb survival for different dam ages and lamb birth types (Table 3.2). Individuals above the threshold survived (**LS** = 1) and those below the threshold did not survive (**LS** = 0).

Weaning weights of lambs surviving to weaning at 60-d of age were derived as a sum of independently and normally distributed additive genetic, maternal genetic, ewe permanent environmental, litter, and temporary environmental effects, each with mean 0 and variances given in Table 3.1. The phenotypic value of **WW** for each lamb also included a mean value that was dependent on the age of the dam (Table 3.2). Input parameters for **NB**, **LS**, and **WW** (Tables 3.1 and 3.2) were approximated from analyses of Katahdin data (Vanimiseti et al., 2006).

The simulated traits contributing to ewe productivity (**EF**, **NB**, **LS**, and **WW**) were considered to be genetically independent. There is little compelling evidence in the literature to

suggest strong genetic associations among ewe reproductive and lambs survival traits or between these traits and lamb growth (Rao and Notter, 2000; Safari and Fogarty, 2003). A large negative association between direct and maternal additive effects on **WW** has occasionally been reported but results have not been consistent among studies (Mandal et al., 2006). Independence across traits of ewe permanent environmental effects was also assumed. The assumption of independence among components of ewe productivity means that observed associations involving composite traits were solely a result of the process used to generate records for these traits from their components and the associated nonlinear part-whole relationships.

Composite ewe traits. The number of lambs weaned at each lambing (**NW**) was calculated as the sum of observed **LS** values of all lambs in the litter. The average weight of lambs weaned (**AW**) at each lambing was the average **WW** of all lambs weaned. If **NW**=0 then **AW** was necessarily missing. For calculation of total weight of lamb weaned (**TW**), lamb **WW** were first deadadjusted for effects of type of birth and rearing using adjustment factors specific to each ewe age derived for Katahdin sheep (Notter and Kuehn, 2003). These deadadjusted **WW** were then summed to generate **TW**. The **TW** was alternatively expressed per ewe exposed (**TWE**), per ewe lambing (**TWL**), and per ewe weaning at least one lamb (**TWW**). Records of zero were thus possible for **TWE** and **TWL** but not **TWW**. Further, to simulate effects of incomplete reporting of **WW** in field data associated with missing weaning weight records or weights recorded outside acceptable age windows, 8% (D. R. Notter, unpublished) of individual lamb **WW** records were randomly set to missing and composite ewe traits were recalculated. Missing values for **WW** led to missing values for **AW**, **TWE**, **TWL**, and **TWW**.

Genetic analyses. Genetic analyses were performed using multi-trait derivative-free restricted maximum likelihood software (Boldman et al., 1993). Univariate analyses were performed for each replicate to validate input parameters for **EF** and **NB** (as traits of the ewe) and **LS** and **WW** (as traits of the lamb) using models that included fixed effects of ewe age and random effects shown in Table 3.1, and to estimate variance components for **NW**, **AW**, **TWE**, **TWL**, and **TWW** (all as traits of the ewe). Bivariate analyses were performed for all combinations of **NB**, **NW**, **AW**, and **TWL** to obtain preliminary estimates of genetic correlations among these traits. Fixed effects of ewe age and random additive genetic and ewe permanent environmental effects were included in the model for **NB**, **NW**, **AW**, and **TWL**. The model for

AW and **TWL** also included random service sire effects. All analyses were repeated with and without missing **WW** records.

Four strategies were considered for predicting genetic merit for **TWL**. Predictions of **EBV** for **TWE** and **TWW** were not determined because data on fertility of ewes are often not available from field data and because **TWW** data does not account for and penalize ewes that lamb but fail to wean any of their lambs. All analyses were again repeated with and without missing **WW** records. The methods considered were:

(1) a univariate genetic analysis of **TWL** was performed to directly obtain estimated breeding values (**EBV**) for **TWL** (henceforth referred to as **TWL-1**);

(2) bivariate BLUP analyses were performed to obtain **EBV** for **NW** and **AW**. Since **TWL** is the product of **NW** and **AW**, **EBV** for **NW** and **AW** can be combined into an additive index for prediction of genetic merit for **TWL** where **EBV** for each trait are weighted by the population mean of the other trait (Smith, 1967). Genetic merit for **TWL** was thus calculated as:

$$\mathbf{TWL-2} = \mu_{\mathbf{AW}} * \mathbf{EBV NW} + \mu_{\mathbf{NW}} * \mathbf{EBV AW}, \text{ where } \mu \text{ is the population mean;}$$

(3) **EBV** for **TWL** were indirectly predicted in a trivariate BLUP analysis using data for **NW** and **AW** and genetic correlations among **NW**, **AW**, and **TWL**. Data for **TWL** itself were not used in this prediction; **EBV** for **TWL** generated using these procedures are denoted as **TWL-3**;

(4) a four-variate BLUP analysis was performed in a manner similar to the previous method with addition that data of **NB** to predict genetic merit for **TWL**; **EBV** generated from this method are denoted as **TWL-4**.

Validation of prediction methods. For validation of prediction methods, the original 5,000 ewes were assumed mated to a new set of 200 unrelated service sires to generate 5,000 daughters. These 5,000 daughters then went through a production cycle of 5 yr as described above for their dams. For each of the three sets of ewes, two daughter data sets were generated, giving a total of six daughter datasets. The effectiveness of the four prediction methods were compared by regressing realized **TWL** values for daughters on alternative **TWL EBV** of their dams in models that also included effects of age of the daughter ewe and comparing the different regression models based on regression coefficients and R-square statistics. Quadratic effects of ewe **EBV** and interaction effects of ewe **EBV** with daughter age were also tested in separate regression analyses.

RESULTS AND DISCUSSION

Means and standard deviations for output ewe and lamb traits over the three replicates are given in Table 3.3. Means for all traits differed by less than 0.01 % among replicates and were similar to those reported by Vanimisetti et al. (2006) for **NB**, **NW**, **TWL**, **LS**, and **WW**.

Heritabilities and other variance proportions

Variance components for simulated ewe traits from univariate REML analyses of each replicate were expressed as proportions of phenotypic variance (Table 3.4). Heritability of **EF** on the observed scale ranged from 0.02 to 0.03. Heritability on the underlying continuous scale is expected to be $[p(1-p)/z^2]$ times heritability on the observed scale where p is the mean and z is the height of the standard normal curve at the threshold (Dempster and Lerner, 1950). Thus, given an input heritability on the continuous scale of 0.07 and a mean **EF** of 0.84, the expected heritability of **EF** on the observed scale was 0.03. This estimate is in accordance with literature estimates reviewed by Safari and Fogarty (2003). The heritability and ewe permanent environmental proportion of variance for **NB** ranged from 0.06 to 0.10 and 0.06 to 0.08, respectively, showing the anticipated small reduction relative to input values of 0.10 associated with translation from a continuous to a categorical scale. The heritability of **NW** ranged from 0.05 to 0.09 which is similar to the estimate obtained by Vanimisetti et al. (2006) and other literature estimates (Safari and Fogarty, 2003), and is expected to be similar to that of **NB** when genetic effects on lamb survival are small.

The input maternal heritability for **LS** on the underlying continuous scale was 0.10 and the mean for **LS** was 0.81. The expected heritability on the observed scale was thus predicted to be 0.05 and corresponded closely to realized estimates of 0.04 to 0.06 for maternal heritability and 0.07 to 0.09 for the litter proportion of phenotypic variance. The maternal heritability of **LS** was consistent with estimates reviewed by Safari and Fogarty (2003) where both direct and maternal heritabilities were generally below 0.10. Vanimisetti et al. (2006) likewise found no significant additive direct or maternal effects on **LS**.

The heritability and litter proportions of phenotypic variance for **WW** from univariate REML analyses were consistent with input values for all three replicates. However, maternal genetic and maternal permanent environmental proportions varied among replicates from 0.07 to 0.12 and 0.08 to 0.14, respectively, but their sum was consistently close to 0.20. Difficulty in partitioning these maternal effects in spite of relatively large amount of data has been observed

in other studies (e. g., Notter, 1998) and may have been accentuated in the current study by the lack of a deep pedigree and the absence of grand-dams with records, which can make the data structure inadequate for accurate partitioning of direct genetic, maternal genetic, and maternal permanent environment effects (Maniatis and Pollot, 2003).

The heritability of **AW** as a trait of the ewe (Table 3.4) ranged from 0.15 to 0.22. The additive genetic variance for **AW** is expected to equal the sum of the additive maternal variance plus one quarter of the additive direct variance for **WW**. Similarly, the phenotypic variance for **AW** for single, twin, and triplet litters can be calculated from the variance components for **WW** giving an expected heritability for **AW** as 0.20, which is similar to the estimated heritability. The service sire proportion of variance is expected to equal one quarter of the heritability of **WW** and was estimated to be 0.06 to 0.07. The ewe permanent environment component ranged from 0.09 to 0.19. Although the heritability and ewe permanent environment proportions varied somewhat, the repeatability of ewe performance was similar among replicates, again indicating difficulty in clearly identifying sources of observed ewe effects. Variance proportions for **AW** obtained in this simulation were similar to those estimated by Vanimisetti et al. (2006) and Rosati et al. (2002) who reported a heritability of 0.15 for mean litter weight at weaning in a composite sheep population.

The heritability of **TWE** ranged from 0.04 to 0.07 (Table 3.4). Service sire and ewe permanent environment effects were negligible, mainly as a result of the assumption of no ewe permanent environmental effect on **EF**. These results are consistent with the heritability estimate of 0.04 and non-significant service sire effect on **TWE** reported by Cloete et al. (2004), although in their study ewe permanent environmental effects were higher at 0.11. Rosati et al. (2002) reported a slightly higher heritability of 0.11 and a negligible service sire component for **TWE**. The heritability of **TWL** ranged from 0.06 to 0.10. Heritability and ewe permanent environmental effects on **TWL** were slightly higher than those for **TWE**, but service sire effects were still negligible. An increase in heritability of **TWL** compared to **TWE** is expected because ewe fertility, which is largely influenced by temporary environmental effects, does not affect **TWL**. Results from this simulation are consistent with estimates of heritability ranging from 0.02 to 0.11, permanent environmental effects ranging from 0.00 to 0.07, and negligible service sire effects on **TWL** reported by Bromley et al. (2001). Vanimisetti et al. (2006) likewise reported a heritability of 0.12, ewe permanent environmental component of 0.06, and negligible

service sire effects. Surprisingly, the heritability of **TWW** did not increase compared to **TWL**. An increase would have been expected because **TWW** is not affected by ewes that lose an entire litter and thus lacks values of zero. However, lamb survival still forms a component of **TWW** due to partial mortality in twin and triplet litters, and this could be the reason why heritabilities of **TWL** and **TWW** did not differ. No literature estimates for variance components of **TWW** were available. Heritabilities of **TWE**, **TWL**, and **TWW** were reduced by 1 to 2% when missing **WW** records were incorporated into the data.

In general, estimated means and variance components were consistent with input parameters and literature estimates for both the four basic simulated ewe and lamb traits (**EF**, **NB**, **LS**, and **WW**) and the associated composite ewe traits, which served to build confidence in the simulation model.

Correlations among ewe traits

Correlations among component ewe traits and **TWL** from bivariate analyses for each replicate are given in Table 3.5. Genetic and ewe permanent environmental correlations were variable across replications. This result in part reflects scaling effects associated with low values of heritability and permanent environmental proportions of variance for these traits, so that small differences in (co)variance component estimates in numerator and denominator can lead to sizeable differences in their ratio. Thus, estimates of genetic correlation between **AW** and **TWL** (the two traits with the highest average estimated heritabilities) were most stable across replicates. Environmental and phenotypic correlations were similar across replicates, reflecting larger residual and phenotypic (co)variance components. Correlations among traits did not change much due to presence of random missing **WW** values, although some ewe permanent environmental correlations tended to vary more. Genetic correlations between **NB** and **NW** ranged between 0.29 to 0.55, those between **NB** and **AW** ranged from -0.30 to 0.04, and those between **NB** and **TWL** ranged from 0.10 to 0.52. Genetic correlation between **NW** and **AW** ranged from -0.42 to 0.19, those between **NW** and **TWL** ranged from 0.70 to 0.87, and those between **AW** and **TWL** ranged from 0.63 to 0.72. Ewe permanent environmental correlations were moderate to high between **NB** and **NW**, **NB** and **TWL**, **NW** and **TWL**, and **AW** and **TWL**, ranging from a low of 0.42 between **NB** and **NW** to a high of 0.94 between **AW** and **TWL**. Ewe permanent environmental correlation between **NB** and **AW** and **NW** and **AW** ranged from -0.06 to 0.49 and -0.32 to 0.64, respectively. Phenotypic and temporary environmental correlations

were similar across replicates. At a phenotypic level, **NB** and **AW** and **NW** and **AW** were independent, **NB** and **NW**, **NB** and **TWL**, and **AW** and **TWL** were moderately correlated, and **NW** and **TWL** had a high correlation. Thus, reproduction (**NB** and **NW**) and growth (**AW**) traits were genetically lowly correlated, in agreement with input parameters, whereas **TWL** was highly correlated with **NW** and **AW**, as expected from the multiplicative part-whole relationship that exists among these traits.

Genetic correlations among **NB**, **NW**, and **TWL** obtained in this study are generally within the ranges reported by Safari and Fogarty (2003) and provide further evidence of the variability of correlations among reproductive and growth traits reported by Safari et al. (2005). The estimates obtained by Vanimisetti et al. (2006) are within the ranges obtained over different replicates in this study for all trait combinations except between **NB** and **NW** and **NW** and **AW**, for which correlations were higher than those obtained in this study, although the variance component estimates for **NB**, **LS** and **WW**, which are components of **NW** and **AW**, were similar in both studies. Independence among **NB**, **LS**, and **WW** on the underlying scale was assumed in the simulation but the higher genetic correlations among **NB** and **NW** and **NW** and **AW** reported by Vanimisetti et al. (2006) suggests that some additional positive associations among **NB**, **LS**, and **WW** may exist in Katahdin ewes. These associations may be genetic but could also reflect preferential use of fostering and artificial rearing in ewes that are judged less capable of rearing triplets.

Validation of prediction models

In a pooled analysis of daughter performance across six sets of daughters produced by three sets of ewes, prediction of daughter **TWL** from alternative dam **EBV** (Table 3.6) yielded regression coefficients that were close to their expected value of 0.50 for ewe **EBV** derived from direct univariate analysis of dam **TWL** (**TWL-1**) or from multivariate linear prediction of **EBV** for **TWL** from component traits (**TWL-3** and **TWL-4**). However, use of the multiplicative bivariate model of Smith (1967) (**TWL-2**) yielded regression coefficients of daughter **TWL** on dam **EBV** of less than 0.50. Genetic correlations for **NW** and **AW** with **TWL** are not considered in estimation of **TWL-2**, so **TWL-2** is not necessarily an optimal predictor of **BV** for **TWL**. Among the six replicates, estimates of regression coefficients were quite close to the mean

values in five of the six replicates, but considerably larger for a single replicate (see ranges in Table 3.6).

Accuracies of prediction of **EBV** for **TWL-1**, **TWL-3**, and **TWL-4** for individual dams were low, ranging from 0.05 to 0.22 across replicates. The R-square statistics for all regression models were correspondingly low, ranging from 0.148 to 0.168. Model R-squares were similar for all four prediction methods when data were complete. However, when there were missing values for **TWL** due to incomplete reporting of **WW**, regression of daughter **TWL** on ewe **EBV** from direct genetic analysis of the trait (i. e. **TWL-1**), yielded the lowest R-square value.

Among daughter sets and replicates, model R-square values involving **TWL-1** with missing **WW** records were lowest in 5 out of the 6 and second lowest in 1 out of the 6 sets of analyses. Model R-square values for regressions involving **TWL-2** and **TWL-3** were similar both in data with and without missing **WW** values. This result could be expected because both methods of **EBV** estimation use data for only **NW** and **AW**. With missing **WW** records, the four-trait predictor (**TWL-4**), which additionally utilizes data for **NB**, was not superior in R-square to either **TWL-2** or **TWL-3**, even though records on **NB** were available for all lambings.

Correlations between **NB** and **TWL** obtained from bivariate analyses were modest, ranging from 0.10 to 0.52, whereas those for **TWL** with **NW** and **AW** were high. In addition, the simulation did not consider missing observations for **NW**, so use of **NB** data did not improve the accuracy of the four-trait predictor. However in field data accurate information on lamb survival (and thus **NW**) is not always available. Among breeds in U. S. National Sheep Improvement Program records for 2004, 0.2 to 17.5 % of lambs born, with a weighted average of 7.4%, were not accounted for, with neither weaning weight records nor indications of death (D. R. Notter, unpublished). In such cases, **NB** were the only data that were unambiguously available, and the four-trait predictor would be expected to be superior to the three-trait predictor.

Literature reports document improvement of total weight of litter weaned by direct selection in sheep (Ercanbrack and Knight, 1998) and mice (Luxford and Bielharz, 1990) and indirect selection on component traits of litter size at birth in mice and sheep (Luxford and Bielharz, 1990; Bradford et al., 1999), litter size at weaning in sheep (Cloete et al., 2004), and weaning weight in sheep (Bradford et al., 1999). Direct selection for total weight at weaning per ewe exposed in females and males (based on performance of female relatives) was more effective than direct selection in females and indirect selection for body weight or early puberty

in males in the study by Ercanbrack and Knight (1998). Direct selection for total weight at weaning in mice was likewise more effective than indirect selection on litter size at birth (Luxford and Bielharz, 1990). Bradford et al. (1999) reported that when selection for improved weaning weight in sheep was accompanied by a correlated increase in litter size, improvement in total weight of litter weaned per ewe lambing was more than in other selection lines where improvement was only observed for either weaning weight or litter size.

In swine, Johnson et al. (1999) reported results of selection for increased litter size using an index of ovulation rate and embryo survival. Selection based on the index was successful in increasing litter size but was not associated with increased total weight of litter weaned because of increases in frequency of stillbirths and decreased birth weights that compromised viability of the piglets. They suggested incorporating positive selection for piglet birth weight in addition to selection for number of pigs born to improve overall productivity. Thus, it appears that maximum progress is attained by either direct selection or simultaneous consideration of all component traits. However, no literature studies were found that used true selection index methods involving all or some of the component traits to improve total weight at weaning. Perez-Enciso et al. (1995) used a simulation to compare direct and indirect methods of selection for litter size, which is also a multiplicative trait, based on an index made of ovulation rate and embryo survival. The predicted response in litter size was similar using direct selection, an index based on ovulation rate and litter size, or an index based on ovulation rate and embryo survival, but was lower when selection was based on ovulation rate alone.

Linear versus polynomial (linear and quadratic) regressions of **TWL** on **EBV** for **TWL-1**, **TWL-2**, and **TWL-4** are depicted in Figure 3.1; results were very similar for **TWL-3** and **TWL-4**. Quadratic effects of ewe **EBV** from different methods on daughter **TWL** were generally not significant, except for the regression of **TWL** on **TWL-1**. The two regression lines overlapped over most of their range and deviated only at extremes of ewe **EBV**. These results suggest that failure to account for quadratic effects of ewe **EBV** will rarely affect predictions of daughter production. Over the observed range in **EBV**, differences between linear and polynomial predictions of daughter **TWL** records based on ewe **EBV** for **TWL-1**, **TWL-2**, or **TWL-4** were at most 0.50, 0.85, and 0.32, respectively, corresponding to 2, 3, and 1%, respectively, of daughter mean **TWL**. Predictions of dam **BV** for **TWL** from **TWL-4** were least affected by nonlinearity and those from **TWL-2** were least strongly regressed (i. e., largest SD in

EBV; Table 3.6). With missing **WW** records, prediction equations were essentially unchanged but model R-squares were reduced by approximately 0.012.

Interactions of linear effects of ewe **EBV** on daughter **TWL** with daughter age were significant for all predictors ($P < 0.01$). Regression coefficients for 2-yr old and 3- to 5-yr old ewes did not differ, but coefficients for 1-yr old ewes were smaller ($P < 0.01$) than those for 3- to 5-yr old ewes. Regression coefficients for 3- to 5-yr old ewes ranged from 0.44 to 0.65 kg/kg; coefficients for 1-yr old ewes were 0.18 to 0.27 kg/kg lower than those of 3- to 5-yr old ewes, but coefficients for 2-yr old ewes were only 0.01 to 0.05 kg/kg lower than those of 3- to 5-yr old ewes. Thus, 1-yr old ewes appeared to be performing at a lower level than predicted from the **EBV** of their dams. This result likely reflects scaling effects associated with biological and physiological constraints on the performance of yearling ewes (Table 3.2).

This study did not clearly identify a single superior method for predicting genetic merit for total weight of litter weaned by a ewe, although direct prediction using **TWL-1** appeared to be least informative when some **WW** records were missing and **TWL-2** overestimated differences in daughter productivity. The most important conclusions were that multivariate linear predictors were equivalent to direct prediction in accuracy of predicting daughter performance when data were complete and would be more robust in the presence of missing data for **WW** or **LS**. Not surprisingly, use of multivariate linear methods to predict **BV** for a nonlinear composite trait yielded some level of nonlinearity between actual performance and predicted **BV** as well as some scaling effects in prediction of performance for less productive yearling ewes. However, the overall impacts of these complications were small. Explicit consideration of the nonlinear nature of **TWL** would be desirable but would also be challenging and would necessarily increase complexity of **BV** prediction systems. However, systems to predict **BV** for categorical traits are available for calving ease scores in dairy and beef cattle using threshold models (Berger, 1994; Quaas, 1996), and application of such methods to predict **BV** for **NB** and **NW** would likely improve the associated predictors of **BV** for **TWL**.

IMPLICATIONS

In the presence of missing weaning weights due to incomplete reporting of information, which is common in field data, single-trait genetic evaluation of total weight of litter weaned per ewe lambing is likely to provide breeding values of lower accuracy than multi-trait genetic evaluations that include information on some or all of the component traits and make use of

genetic correlations among component and composite traits. Nonlinear relationships among component traits are not likely to greatly impact predictions of progeny performance when EBV of the parent for the composite trait are generated using multivariate linear methods. Other methods of predicting breeding values that account for such nonlinear relationships could be developed, but would be computationally more complex and challenging.

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Table 3.1. Simulation input parameters: variance components for ewe fertility (**EF**), number of lambs born (**NB**), lamb survival to weaning (**LS**), and lamb weaning weight (**WW**, kg).

Item ^a	Trait ^b			
	EF	NB	LS	WW
h^2	0.07	0.10	-	0.20
m^2	-	-	0.10	0.10
c^2	-	0.10	-	0.10
l^2	-	-	0.10	0.05
σ_p^2	1.00	1.00	1.00	12.35

^a h^2 , m^2 , c^2 , and l^2 are additive genetic, additive maternal, ewe permanent environmental, and litter proportions of phenotypic variance (σ_p^2).

^b Variance components for **EF**, **NB**, and **LS** are on the underlying standard normal scale.

Table 3.2. Simulation input parameters by ewe age: mean ewe fertility (**EF**), mean lamb survival to weaning (**LS**) by type of birth (single, twin, or triplet), mean lamb weaning weight (**WW**), and frequency distribution of number of lambs born (**NB**).

Trait	Ewe age (yr)		
	1	2	3-5
Means			
EF , %	70	88	92
LS , %			
Single	88	88	90
Twin	82	84	85
Triplet	60	68	70
WW , kg	18.14	19.05	20.41
Frequency			
NB			
1	43	19	10
2	56	67	61
3	1	14	29

Table 3.3. Number of observations, means, and standard deviations for ewe and lamb traits over three replicates.

Trait ^a	N	Mean	SD
Ewes			
EF	45000	0.84	0.37
NB	37712	1.95	0.63
NW	37712	1.57	0.70
AW	35532	19.39	3.32
TWE	45000	21.73	13.87
TWL	37712	25.93	10.99
TWW	35532	27.53	9.19
Lambs			
LS	73508	0.81	0.39
WW	59338	19.48	3.68

^a **EF** = ewe fertility; **NB** = Number of lambs born; **NW** = Number of lambs weaned; **AW** = average weight of litter weaned, kg; **TWE** = total weight of litter weaned per ewe exposed, kg; **TWL** = total weight of litter weaned per ewe lambing, kg; **TWW** = total weight of litter weaned per ewe weaning at least one lamb, kg; **LS** = lamb survival to weaning; **WW** = 60-d weaning weight of individual lambs, kg.

Table 3.4. Estimates of variance components for ewe traits from single-trait REML analyses for each of three replicate simulations^{a,b}.

Trait ^c	Rep 1				Rep 2				Rep 3			
	h^2	s^2	c^2	σ_p^2	h^2	s^2	c^2	σ_p^2	h^2	s^2	c^2	σ_p^2
EF	0.02	-	-	0.13	0.03	-	-	0.13	0.03	-	-	0.13
NB	0.09	-	0.06	0.38	0.06	-	0.08	0.33	0.10	-	0.06	0.33
NW	0.09	-	0.02	0.47	0.05	-	0.06	0.46	0.08	-	0.03	0.47
AW	0.16	0.06	0.19	10.45	0.22	0.07	0.09	10.07	0.15	0.07	0.16	9.91
TWE	0.05	0.01	0.02	165.12	0.04	0.01	0.03	159.26	0.07	0.00	0.01	160.18
TWE-M	0.04	0.01	0.02	160.29	0.03	0.01	0.02	155.01	0.06	0.00	0.01	155.29
TWL	0.10	0.02	0.04	107.98	0.06	0.01	0.07	105.44	0.10	0.01	0.03	105.36
TWL-M	0.08	0.02	0.03	108.95	0.05	0.01	0.05	106.59	0.08	0.01	0.05	106.32
TWW	0.08	0.02	0.07	71.44	0.07	0.02	0.07	70.29	0.09	0.02	0.05	70.89
TWW-M	0.07	0.02	0.05	75.14	0.06	0.01	0.05	74.11	0.07	0.01	0.06	74.65

^a h^2 , s^2 , and c^2 are additive genetic, service sire, and permanent environmental proportions of phenotypic variance (σ_p^2).

^b For all three replicates, h^2 for all traits was significant ($P < 0.01$), s^2 was significant for **AW** ($P < 0.01$), and c^2 was significant for **NB** ($P < 0.01$), **NW** ($P < 0.10$), **AW** ($P < 0.01$), **TWL** ($P < 0.10$), and **TWW** ($P < 0.05$).

^c See Table 3 for trait definitions. The suffix ‘-M’ on **TWE**, **TWL**, and **TWW** denotes data sets with 8% missing **WW** values.

Table 3.5. Correlations among ewe traits obtained with or without missing **WW** values from bivariate analyses for each of three replicate simulations ^a.

Rep	Traits ^b	No missing WW records				8% missing WW records			
		r_g	r_c	r_e	r_p	r_g	r_c	r_e	r_p
1	NB-NW	0.29	0.42	0.50	0.47	-	-	-	-
2		0.30	0.77	0.49	0.50	-	-	-	-
3		0.55	0.85	0.49	0.50	-	-	-	-
1	NB-AW	-0.04	-0.01	0.02	0.01	-0.03	-0.01	0.00	-0.01
2		-0.30	0.49	0.01	0.01	-0.04	0.12	0.01	0.01
3		0.04	-0.06	0.02	0.02	0.05	-0.06	0.03	0.02
1	NB-TWL	0.28	0.50	0.38	0.37	0.24	0.41	0.31	0.30
2		0.10	0.60	0.37	0.37	0.23	0.50	0.31	0.32
3		0.52	0.52	0.36	0.34	0.44	0.59	0.30	0.32
1	NW-AW	-0.06	0.20	0.00	0.00	-0.02	0.12	0.00	0.00
2		-0.42	0.64	0.01	0.01	-0.25	0.20	0.01	0.01
3		0.19	-0.32	0.02	0.01	0.17	-0.23	0.02	0.02
1	NW-TWL	0.71	0.49	0.73	0.72	0.81	0.49	0.80	0.79
2		0.70	0.84	0.92	0.90	0.67	0.95	0.80	0.79
3		0.87	0.44	0.92	0.89	0.80	0.73	0.79	0.82
1	AW-TWL ^c	0.63	0.94	0.53	0.57	0.70	0.87	0.49	0.52
2		0.67	0.68	0.53	0.55	0.61	0.88	0.50	0.52
3		0.72	0.73	0.53	0.56	0.83	0.54	0.49	0.37

^a r_g , r_c , r_e , and r_p are additive genetic, permanent environmental, temporary environmental, and phenotypic correlations, respectively.

^b See Table 3 for trait definitions.

^c Service sire correlations between **AW** and **TWL** varied among replicates from 0.87 to 0.98 and from 0.87 to 0.96 with and without missing **WW** records, respectively.

Table 3.6. Regression coefficients and standard deviations ($\beta \pm \text{SD}$, kg/kg) and model R-square statistics over three replicate simulations for regression of daughter records of total weight of litter weaned per ewe lambing (**TWL**, kg) on alternative predictors of **EBV** of the dam for **TWL** with and without missing **WW** records ^a.

Ewe EBV		No missing WW records		8% missing WW records	
Predictor	SD of predictor	$\beta \pm \text{SD}$ (range)	R-square (range)	$\beta \pm \text{SD}$ (range)	R-square (range)
TWL-1	1.59	0.49±0.03 (0.40 to 0.76)	0.157 (0.149 to 0.167)	0.52±0.04 (0.40 to 0.72)	0.144 (0.134 to 0.158)
TWL-2	2.08	0.38±0.02 (0.32 to 0.76)	0.157 (0.149 to 0.168)	0.38±0.03 (0.32 to 0.62)	0.146 (0.136 to 0.168)
TWL-3	1.59	0.51±0.03 (0.43 to 0.70)	0.157 (0.149 to 0.168)	0.56±0.03 (0.49 to 0.70)	0.146 (0.136 to 0.158)
TWL-4	1.59	0.51±0.03 (0.43 to 0.70)	0.157 (0.149 to 0.168)	0.52±0.03 (0.45 to 0.68)	0.146 (0.136 to 0.158)

^a Regression coefficients and SD and R-square statistics are from a pooled analysis of all three replicates and daughter data sets within replicates. Ranges are from individual analyses of each daughter data set within each replicate.

^b See text for definitions of **EBV** predictors.

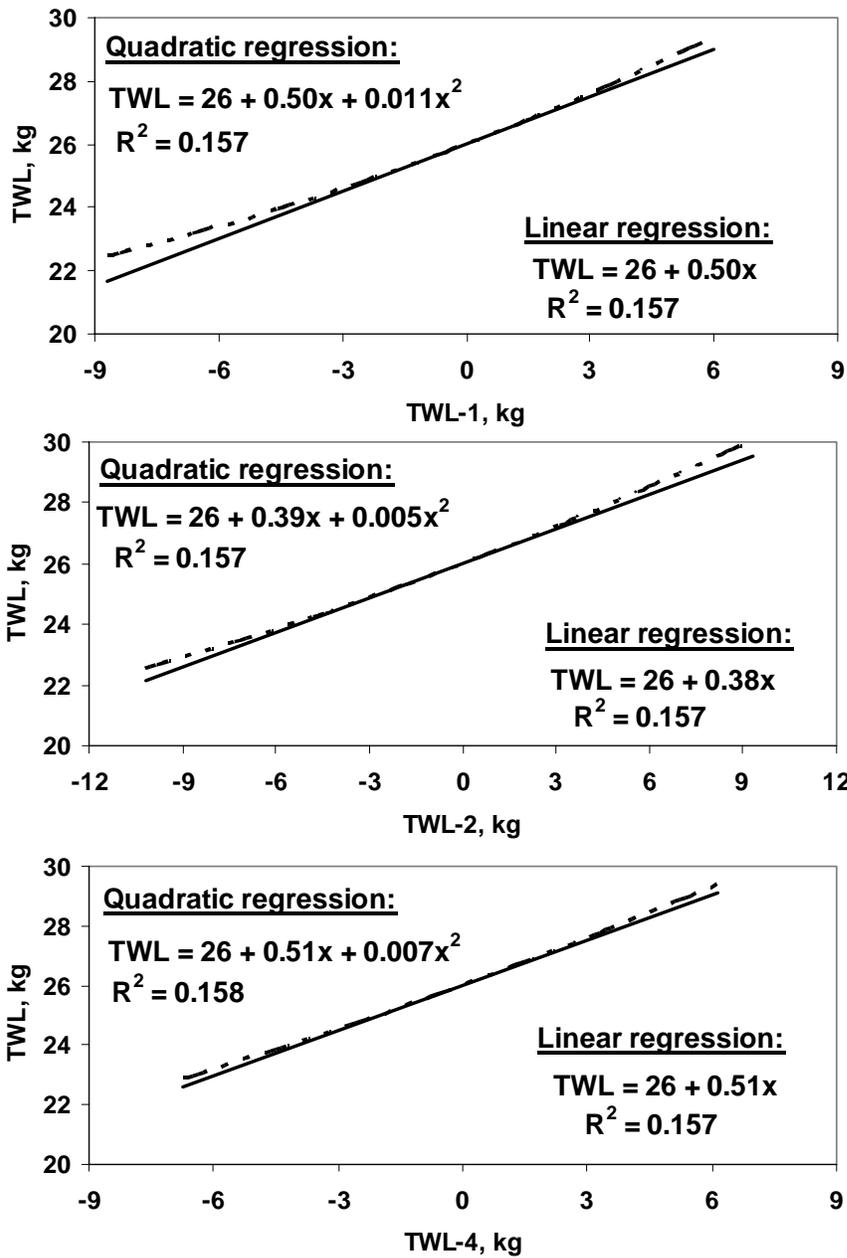


Figure 3.1. Linear and quadratic regressions of daughter total weight of litter weaned (TWL) on alternative predictors of ewe EBV for total weight of litter weaned (x). See text for definition of alternative ewe EBV. Dashed lines represent quadratic regression equations and solid lines represent linear regression. The quadratic term was significant ($P < 0.05$) only for TWL-1. Curves for TWL-3 (not shown) were essentially identical to those for TWL-4.

CHAPTER 4

Evaluation of fertility and other measures of accelerated lambing in a Polypay flock⁶

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ABSTRACT: Data from a Polypay flock practicing accelerated lambing were used to evaluate environmental effects on fertility and estimate heritabilities (h^2) for ewe lamb fertility (**ELF**), ages at first, second, and third lambings (**AGE1** to **AGE3**, mo), first and second lambing intervals (**INT1** and **INT2**, mo), and number of lambings by 38 mo of age (**LAMB3**). Genetic correlations (r_g) among these traits and prolificacy (**NB**) and 60-d weaning weights (**WW**) were also estimated. Out-of-season summer matings generally resulted in lower fertility than the in-season fall and winter matings. The h^2 of **ELF**, **AGE1**, **AGE2**, **AGE3**, **INT1**, **INT2**, and **LAMB3** were 0.14, 0.39, 0.28, 0.36, 0.00, 0.09, and 0.27 (all $P < 0.01$, except **INT2**), respectively, from univariate analyses. The h^2 and repeatability of difference between age at i^{th} lambing and i^{th} yr of age were 0.31 and 0.90, respectively. The h^2 and repeatability of deviation of the lambing intervals from 1 yr were both 0.00. The h^2 of **AGE2** and **AGE3** were not significant after accounting for variation in **AGE1**, and h^2 of **AGE1** and **AGE2** were reduced to 0.18 and 0.11, respectively, in bivariate analyses with **ELF**, indicating that culling of open ewe lambs may have resulted in downward bias in estimates of residual variances for lambing ages. The r_g of **ELF** with **AGE1**, **AGE2**, and **LAMB3** were -0.89, -0.91, and 0.89, respectively (all $P < 0.01$). The r_g of **LAMB3** with **AGE1** and **AGE2** were -0.49 and -1.00, respectively. The r_g of **ELF** and **LAMB3** with direct genetic effects on **WW** were close to -0.70, but the correlation with maternal genetic effects on **WW** were 0.88 ($P < 0.10$) and 0.58, respectively. Prolificacy was independent of **ELF** and **LAMB3** in these data. The h^2 for **ELF**, **AGE1** and **LAMB3** suggest that genetic improvement in these traits is feasible. These results suggest that **ELF** may be the best indicator of future acceleration and productivity in this system and selection for **ELF** should result in reduced ages at lambing and increased number of lambings over time. Later

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lambing ages and intervals appear to be of little value for genetic improvement of accelerated lambing performance in this flock.

[Key Words: Accelerated lambing, Fertility, Heritability, Polypay, Reproduction, Sheep]

INTRODUCTION

One of the most important traits affecting ewe productivity, or total weight of lamb weaned, is the number of lambs produced by the ewe (Ercanbrack and Knight, 1998) and in traditional sheep production systems following an annual lambing cycle, this can be increased by improving fertility and prolificacy. Further improvements in the number of lambs produced by a ewe can be attained by increasing the number of lambings. Accelerated lambing systems (**ALS**) are intensive production systems that allow ewes to breed more than once a year which leads to increases in the total number of lambs produced by the ewe. Thus, success in an **ALS** could greatly improve overall ewe productivity.

Sheep are seasonal breeders and typically have low fertility in spring and early summer months (Hafez, 1952; Rosa and Bryant, 2003) and **ALS** rely on getting ewes bred during these periods of low fertility, which tends to constrain the improvements that can be made in **ALS**. Although hormonal and light treatments can be used to make sheep cycle during these seasons (Rosa and Bryant, 2003), genetic improvement in performance in **ALS** is perhaps a more sustainable option. Genetic improvement of ewe fertility over time in **ALS** is complicated at least in part due to the different breeding patterns followed over time by ewes born in the same birth cohort, which could lead to differences in average genetic merit of different breeding groups (Notter, 2002). Traits that can be measured and potentially used to improve performance in an **ALS** are fertility at first mating, ages at different lambings, and lambing intervals. By improving ewe lamb fertility, decreasing the ages at lambing and reducing lambing intervals, ewes can potentially have more lambings over time. Thus, the number of lambings a ewe has in a given period of time is a productivity trait and gives an overall indication of acceleration over time and could be used for genetic improvement of performance in accelerated lambing systems. The objective of this study was to evaluate ewe lamb fertility, ages at different lambings, lambing intervals, and number of lambings by a specific age, and the interrelationships among them and prolificacy and growth traits in an accelerated lambing Polypay flock.

MATERIALS AND METHODS

Data for this study was obtained from a Polypay farm flock located in the western region of Nebraska which has been participating in the US National Sheep Improvement Program (NSIP) and practicing accelerated lambing since the early 1990's. The Polypays are a composite breed and were developed from a Polled Dorset-Targhee x Finnsheep-Rambouillet foundation in the early 1970's to have a high reproductive capacity, desirable growth rate and carcass quality, and superior out-of-season fertility (Hulet et al., 1984).

Breeding Plan

The general accelerated breeding plan adopted was one that allowed up to 3 lambings in 2 yr. To specifically achieve this goal, the flock was divided into two groups, A and B, and followed a general breeding pattern depicted in Figure 4.1. About 2 wk prior to breeding, a teaser ram was put in with ewes of group A. At the time of breeding these ewes were assigned to up to eight single sire groups, and the rams were left in for 6 wk. The number of ewes per sire was up to 50 or 30 in the favorable fall and the unfavorable summer seasons, respectively. About 4 mo after putting group A ewes into breeding, ewes in group B were bred in a similar manner. Also, non-pregnant ewes from group A, which were identified by visual appraisal and palpitation of udder and body cavity, were generally assigned to a single cleanup ram and transferred to group B at this time. Lambs were weaned at about 2-mo of age and ewes were dried off and rebred a month later. This basic cycle was repeated and ewes could move from one group to another based on their pregnancy status. Breeding typically occurred three times in a year, around the months of January, May, and September. The breeding around the month of May was during an unfavorable season (out-of-season) with lower fertility compared to the more favorable periods around the months of January or September. Deviations from this general pattern occurred periodically depending on the schedules of the producers. The shortest possible interval between lambings in this system was 8 mo, followed by 1 yr if ewes missed a lambing opportunity. Ewes were typically culled if they failed to lamb twice in a row; i. e. if they failed to lamb on an annual cycle. Ewes were also culled based on difficult birthing, failure to accept lambs, and poor mothering ability, all of which could lead to low numbers of lambs weaned. Ewes and rams were also culled for poor EPDs for growth and maternal traits.

General Management

At the time of lambing, ewes were moved to lambing jugs. Ewes with single and twin lambs usually remained there for a day after lambing, but ewes with triplets were left in the jugs

for a few days. Lambs were weighed and tagged at birth and common veterinary practices were followed. Afterwards, the ewes and lambs were moved to a drylot where they remained until weaning. Few lambs needed fostering as most ewes were capable of comfortably raising twins and acceptably handling triplets. Lambs were weaned at about 60-d of age and remained in drylot until about 120-d of age. About 20% of the ram lambs were retained as replacements and put on a growing diet. Ewe lambs that were judged to be of breeding quality were retained as replacements or for sale as breeding animals and kept on a growing diet. Ewe lambs were first mated at average ages of 8 to 12 mo. Ewe lambs were generally not bred for the first time in spring or summer, but were held off until the next favorable breeding season. The rest of the ram and ewe lambs were put on a finishing diet and sold at a body weight of about 65 kg. Few replacements were purchased from outside and the flock practically remained a closed flock.

During late gestation (about 6 wk prior to lambing) and lactation, ewes were fed a high grain concentrate at levels appropriate to support a 225% lamb crop. At about 1 wk prior to weaning and for 2 wk after weaning, concentrates were withheld from the ewes and they were offered straw *ad libitum* to promote drying off. Ewes remained in drylot after weaning and were provided a high energy diet through 6 wk post-breeding to replenish body condition. They were then put on pasture or crop residue till 6 wk prior to lambing.

Data

Lambing records for this flock were available in the NSIP database and information on dead lambs and ewe disposal records were available from July 1999 onwards. Mating records were obtained from the flock owners and a new data set was created using the lambing records from July 1999 onwards by incorporating the unsuccessful matings for each breeding period. Mating records were available through July 2004.

Fertility Records. Ewe lambs were not always identified on the mating records and in such cases, first ewe lamb mating date was ascertained based on the lambing dates from successful ewe lamb conceptions. For the remaining ewe lambs born in the particular year-season (birth cohort), ewe lamb fertility of '0' was assigned for that mating date. Mating sire information for these unsuccessful matings was generally not available. Similarly, cleanup matings were also not always documented on the mating records. To include potential cleanup matings, ewes with known mating records that had not lambed and had not died or been culled were assigned a '0' for fertility at the next appropriate mating date (i. e., the first available

mating date 3 mo or more after the first failure). Service sire information was not always available in such cases. This process was continued for these ewes until they either appeared on a mating sheet or were recorded as disposed in the NSIP data base files. When all potential matings had been included in the new data set in this manner, ewe records with more than three repeated failures were deleted if the ewe never lambed again or did not appear on a mating record. Ewes with lambing intervals shorter than 180 d or greater than 550 d were also removed from the analysis. Mating months were grouped together into seasons: February, March, and April as spring; May, June, and July as summer; August, September and October as fall; and November, December and January as winter. One exception was a February 1, 2001 mating which was classified as a winter 2000 mating. There were no spring matings between July 1999 and July 2004. Lambing months were grouped together into lambing seasons: January, February, and March as spring; April, May, and June as summer; July, August, and September as fall; and October, November and December as winter. Fertility data was available for 17 mating periods from 882 ewes, including ewe lambs, resulting in a total of 2679 exposures (Table 4.1) of which 8.5% were assigned as described above for unrecorded ewe lamb matings and cleanup matings.

Ewe lamb fertility (**ELF**) records were available from 676 ewes that were born between September 1998 and December 2003 and were the progeny of 32 sires. Of these 676 ewe lamb fertility records, 7.5 % were assigned as described above. Ewe lambs were typically mated for the first time in winter, and very few ewe lambs were mated out of season in summer. Numbers of records for **ELF** by birth year-season and mating year-season of ewe are given in Table 4.2. Data on 1,514 first post-lambing fertility (**FPLF**) records were available from 609 ewes; most of these were from summer and fall matings. Numbers of records for **FPLF** are given in Table 4.3.

Acceleration Records. Ages at i^{th} lambing (**AGE_i**) for first to sixth lambings, and first to fifth lambing intervals (**INT1** to **INT5**) were calculated for the ewes. Data from ewes with **AGE1** greater than 26 mo were removed from the analysis. None of the ewes born after September 1998 in the present data set had more than 6 lambings by December 2004. Also, for ewes born into birth cohorts that had an opportunity of being at least 38 mo of age, the number of lambings by 38 mo of age (**LAMB3**) was calculated. The **LAMB3** is a productivity trait and gives an indication of acceleration of lambing over a period of time. Ewes with greater number of lambings over a fixed period of time are expected to be superior for accelerated lambing than

ewes with fewer lambings, which would have potentially missed one or more lambing opportunities. Ewes should have had the opportunity to have 4 lambings by 38 mo of age in this system. However, the maximum number of lambings observed by this time was 3. The youngest age by which a ewe had 4 lambs in this system was over 40 mo. Since some ewes may leave the flock before they turn 38 mo of age and since time spent in the flock affects the number of lambings a ewe could potentially have, the time in flock by 38 mo since birth (**TIME3**) was also calculated. Similarly, for ewes born into birth cohorts that had an opportunity of being at least 48 mo of age, number of lambings and time in flock by 48 mo of age (**LAMB4** and **TIME4**, respectively) were also calculated.

Finally, the difference in months between age at the i^{th} lambing and i^{th} year of age (**AGEACCI**) were calculated, for $i = 1$ to 6, as a measure of acceleration. Similarly, interval acceleration indices (**INTACCI**) were calculated, for i equal to first to fifth lambing intervals, as the difference in months between each lambing interval and 1 yr to measure the deviation of the lambing interval from an annual cycle. These age and interval acceleration traits at each lambing age or interval are mathematically similar to age at lambing or lambing intervals with the simple subtraction of a constant. However, these traits can be considered a repeated trait when **AGEACC** and **INTACC** at all lambing opportunities are analyzed together. This allows utilization of all available data for ages at different lambing and all lambing intervals.

Growth and Prolificacy Records. Weaning weights of the ewes when she was a lamb and her subsequent **NB** records were available for the ewes in this study in the NSIP database and were utilized to study the relationships among the reproductive traits identified in this paper and growth and prolificacy. To make best use of the available data, all **WW** and **NB** records in the NSIP database for this flock were utilized in the analyses. The 60-d adjusted weaning weight (**WW**) were derived by correcting lamb weaning weights to 60-d of age and then adjusting for effects of lamb sex, ewe age, type of birth and rearing, and ewe age by type of birth and rearing interaction using multiplicative adjustment factors. The basis for adjustment was a ewe lamb that was born and raised as a single and reared by a 3-yr-old ewe. Contemporary groups for **WW** were based on year of birth, date of weaning of the lamb (using 7-d weaning date windows), and weaning weight management code. The number of lambs born (**NB**) data were adjusted using multiplicative adjustment factors to an adult ewe basis. Contemporary groups for

NB were formed based on year of birth and time of birth in the lambing season (using 45-d lambing date windows).

Numbers of observations, means, and ranges for all the traits are listed in Table 4.3.

Data Analyses

Fertility Records. Fertility data were initially analyzed for effects of mating year, mating season, ewe age at mating (categorized as < 12 mo, 12 to 24 mo, 24 to 48 mo, and > 48 mo old), time since most recent lambing (**TSL**; categorized as up to 5 mo and over 5 mo since lambing), and number of lambs reared at most recent lambing (**NLR**; categorized as 0, 1, and 2 or more). Since expression of fertility is binary (0/1), data were analyzed using generalized linear mixed models using the PROC GLIMMIX procedure (SAS Inst. Inc., Cary, NC), which allows implementation of a logistic transformation. Three different analyses were performed to describe fertility in this data set. First, for all the fertility data, since not all seasons were present in all years and not all ewe age categories were present in all mating seasons, a simple model to describe effects of mating year-season and ewe age category were fit. The model included fixed effects of mating year-season, and ewe age category nested within mating year-season, as well as random sire of ewe effects to account for random genetic effects. Random sire of ewe effects were negligible and were removed from the final model. Second, **ELF** was analyzed in a similar manner using a model that included fixed effects of birth year-season of ewe nested within mating year-season and birth and rearing type of ewe and random effects of sire of ewe. Also, to test the effects of ewe age at first mating, **ELF** was analyzed using a model that included fixed effects of birth year-season of ewe, linear and quadratic effects of ewe age at first mating in days, and random effects of the sire of the ewe to at least partially account for genetic effects. Finally, **FPLF** was analyzed separately for each mating season, using a model that included fixed effects of mating year, ewe age category, **TSL**, **NLR**, and all second order interactions among ewe age category, **TSL**, and **NLR**, as well as random sire effects. Random sire of ewe effects were negligible and were removed from the final model. Means from the linear logistic models analyses were back-transformed to the observed scale for reporting.

Acceleration Records. Data for acceleration records were initially analyzed using general linear mixed models procedures (SAS Inst. Inc., Cary, NC). Birth year-season and random sire of ewe effects were fit for all traits. For **AGE1** to **AGE3** the model included **ELF** and age at first mating. For **INT1** and **INT2**, model included **ELF**, **AGE1** or **AGE2**,

respectively, number of lambs reared at previous lambing, and previous lambing season. The models for **TIME3** and **TIME4**, and **LAMB3** and **LAMB4** included **ELF** and age at first mating. The models of **LAMB3** and **LAMB4** additionally included **TIME3** and **TIME4**, respectively. Correlations among **AGE1** to **AGE5** and **INT1** to **INT4** were estimated using multi-trait analysis of variance with models that included ewe birth-year season for both analyses. The analyses for **AGE1** to **AGE5** additionally included **ELF** and ewe age at first mating to account for the initial effects of these two factors on ages at lambing through out life.

Genetic Analyses. Genetic analyses were carried out using multi-trait derivative-free restricted maximum likelihood (**MTDFREML**) software (Boldman et al., 1993). The traits included in the genetic analyses were **ELF**, **AGE1**, **AGE2**, **AGE3**, **INT1**, **INT2**, **LAMB3**, **TIME3**, **WW**, and **NB**, as well as **AGEACC** and **INTACC** as repeated traits. Ages at lambings greater than 3 (**AGE4** to **AGE6**) and intervals greater than 2 (**INT3** to **INT5**) were not utilized in the genetic analyses because of limited numbers of observations. Also, since initial analyses did not reveal any differences among **LAMB3** and **LAMB4**, and **TIME3** and **TIME4**, and since the numbers of records for **LAMB3** and **TIME3** were greater, **LAMB4** and **TIME4** were not utilized in the genetic analyses. Initial estimates of heritabilities were obtained from univariate analyses. The models for **ELF**, **AGE1**, **AGE2**, **AGE3**, **INT1**, **INT2**, **LAMB3**, and **TIME3**, included fixed effects of birth year-season of the ewe as a contemporary group and random animal additive effects. The model for **ELF** also included ewe age at first mating as a covariate. The **TIME3** was analyzed both with and without **ELF** as a covariate. The **LAMB3** was analyzed both with and without inclusion of **ELF** and **TIME3** as covariates. Models for **AGE1** to **AGE3** included age at first mating as a covariate. Additionally, **AGE2** and **AGE3** were also analyzed with **AGE1** as a covariate to ascertain if there was any genetic variation in these after accounting for **AGE1**. The model for **INT1** included **AGE1** as a covariate. The **INT2** was analyzed with the inclusion of **AGE2** and **INT2** as covariates in two separate analyses. The models for **AGEACC** and **INTACC** included the combination of ewe birth year-season and lambing number as a contemporary group and random animal (ewe) additive and ewe permanent environmental effects, and ewe age at first mating as a covariate. Finally, summer **FPLF** was also analyzed using models that included the combination of birth year-season and mating year-season as the contemporary group, time since lambing as a covariate, and random effects of animal additive and permanent environment effects. The model for **WW** included fixed

contemporary group effect and random animal additive, and maternal additive and permanent environmental effects, and the covariance between animal and maternal additive effects. The model for **NB** included fixed contemporary group effects and random animal additive and permanent environment effects. Tests of significance for random effects in single-trait models were performed using likelihood ratio tests after deleting each random term from the model.

Bivariate genetic analyses among **ELF**, **AGE1** to **AGE3**, and **LAMB3**, and of these with **WW** and **NB** were performed. Also, bivariate genetic analyses of **TIME3** with **ELF** and **LAMB3**, and of **AGEACC** with **ELF** were performed. Direct estimation of covariances between residual environmental effects on **ELF**, **AGE1** to **AGE3**, and **LAMB3** (which are all non-repeated traits), and ewe permanent environmental effects on **NB** (which is a repeated trait), were not possible in MTDFREML software. However, environmental effects present at the time of recording of **ELF**, **AGE1** to **AGE3**, or **LAMB3** could have an effect on expression of **NB**. To accommodate such an environmental covariance, residual effects on the non-repeated traits were modeled as a ewe permanent environmental effect and covariance between animal permanent effects on the non-repeated traits and **NB** were included in the model as explained by Rao and Notter (2000). Since animal permanent environment effects were fit for the non-repeated traits, residual variances for these traits in these analyses were correspondingly fixed at zero to yield an equivalent model to that used for univariate analyses. Similar adjustments were made to the model in the bivariate analysis involving **ELF** and the repeated trait of **AGEACC**. Finally, trivariate genetic analyses for **ELF**, **LAMB3**, and **AGE1** were also performed. The bivariate analyses of **ELF** and **LAMB3** with **AGE3**, and of **NB** with **AGE1** to **AGE3** did not converge, possibly because of the limited numbers of observations available for estimation of the covariance components and only results from analyses that converged are reported in this paper. Significance of covariance terms were tested using likelihood ratio tests.

RESULTS AND DISCUSSION

Fertility Records

Mating year-season and ewe age category nested within mating year-season were significant ($P < 0.05$) in the analysis of all fertility data. Means for fertility in each mating year-season are shown in Table 4.1. Generally, summer matings had the lowest fertility and fall matings resulted in highest fertility. Fertility in winter was usually intermediate or similar to fall fertility, except in winter 2000, where fertility was lowest in winter possibly due to the late

winter mating (1 February 2001). Differences among ewe age categories varied widely among different mating year-season combinations, but generally ewes that were less than 12 mo old and ewes that were greater than 48 mo old had lower fertility than ewes that were between 12 and 48 mo of age and differences among ewe age groups greater than 12 mo old were somewhat minimized in winter and fall mating seasons with high fertility (Figure 4.2). In general, averaged across all years, summer fertility was 0.25 ± 0.04 , 0.35 ± 0.04 , 0.58 ± 0.02 , and 0.53 ± 0.04 , fall fertility was 0.76 ± 0.04 , 0.83 ± 0.02 , 0.82 ± 0.02 , and 0.64 ± 0.04 , and winter fertility was 0.59 ± 0.02 , 0.76 ± 0.04 , 0.68 ± 0.04 , and 0.65 ± 0.05 , respectively, for the less than 12 mo, 12 to 24 mo, 24 to 48 mo, and greater than 48 mo old ewes. In winter of 2000, ewes less than 12 mo old had higher fertility than older ewes (Figure 4.2) because several of the older ewes were bred late in the winter (1 February 2001). Reduced fertility in summer months has been reported for Polypay (Hulet, 1984), Dorsets (Iniguez et al., 1986; Lewis et al., 1996), and in sheep of Finnish Landrace inheritance (Notter and Copenhaver, 1980; Tosh et al., 2002). Lower conception rates in very young and old sheep have also been reported (Notter and Copenhaver, 1980; Lewis et al., 1996).

Ewe lamb fertility was affected ($P < 0.01$) by birth year-season of ewe and mating year-season, but type of birth and rearing of the ewe did not affect **ELF**. Means for birth year-season of ewe nested within mating year-season for **ELF** are shown in Figure 4.3. Spring and summer born ewes were generally mated in the winter of the same year and winter born ewes were mated in either summer or fall the next year. Average fertility of summer-born ewe lambs that were mated in the winter (in yr 2000 and 2001) did not differ across the 2 yr. Average fertility did not differ among winter-born ewe lambs that were mated in summer (in yr 1999 and 2004). Also, average fertility of winter-born ewe lambs that were mated in fall (in yr 2000, 2001, and 2003) was similar over the 3 yr. However, fall born ewe lambs mated in winter differed ($P < 0.05$) in their fertility across years because of a difference in their ages at mating; fall 1999 born ewe lambs were mated at very young age (about 5 mo; Table 4.2) in winter 1999 and had a lower fertility than fall 2001 born ewe lambs that were mated the next winter at an age of almost 15 to 16 months (Table 4.2). Spring 1999 born ewe lambs mated in winter 1999 had a higher ($P < 0.01$) fertility than spring 2001 born ewe lambs mated in winter 2001 and spring 2002 born ewe lambs mated in winter 2002, suggesting year effects on **ELF** among the spring born ewe lambs mated in winter. There were 3 mating periods where ewe lambs of different birth seasons were

mated at the same time: winters of 1999, 2001, and 2002. For these matings, it is not possible to separate effects of ewe age at mating and ewe birth season effects on **ELF**. Spring 1999 born ewe lambs had a higher ($P < 0.01$) fertility than fall 1999 born ewe lambs when mated in winter 1999, possibly because the fall 1999 born ewe lambs were very young at mating. Also, spring 2001 born ewe lambs had a higher ($P < 0.05$) fertility than summer 2001 born ewe lambs mated in winter 2001. There were no differences among fall 2001 and spring 2002 born ewe lambs mated for the first time in winter 2002. Finally, the winter born ewe lambs mated for the first time in the unfavorable summer season in 1999 and 2004 had a lower fertility ($P < 0.01$) than winter born ewe lambs that were mated at an older age and in the favorable fall season of 2000, 2001, and 2002. In general, **ELF** was higher in winter born ewe lambs mated in fall and in spring born ewe lambs mated in winter, and **ELF** was lower in summer matings. Lewis et al. (1996) also reported that ewe lamb fertility was higher in October and lowest in March or June. Linear effects of ewe age on **ELF** were significant ($\beta = 0.02 \pm 0.01$ per d; $P < 0.05$) but quadratic effects of ewe age on **ELF** were not significant when **ELF** was analyzed using a model that also included fixed effects of birth year-season of ewe and random sire of ewe effects. Sire effects on **ELF** were significant and the sire component was 0.38 ± 0.17 square units in both the analyses of **ELF** indicating preliminary evidence for some genetic variation in this trait.

For **FPLF** in summer, the final model included year ($P < 0.01$), ewe age category ($P = 0.57$), **TSL** ($P = 0.23$), and ewe age category by **TSL** interaction ($P = 0.05$). The **NLR** was not significant for summer **FPLF**. Means for the significant interaction effect are shown in Figure 4.4. There were no differences in fertility among **TSL** categories for 12 to 24 mo old ewes and 24 to 48 mo old ewes, but fertility in ewes greater than 48 mo of age that were mated less than 5 mo since previous lambing was lower than in those mated more than 5 mo after lambing ($P < 0.01$). Notter and Copenhaver (1980) found that **TSL** did not have a significant effect on post-lambing fertility in fall or winter but in summer ewes that had lambed 2 to 4 mo earlier had a higher fertility than ewes that had missed a lambing opportunity and had lambed 7 mo earlier. It is possible that the ewes that had missed the earlier mating opportunity may be of inferior fertility. In our results for **FPLF** in summer, the 48 mo and older ewes that had greater than 5 mo since lambing had previously lambed in October from a summer mating where as those with less than 5 mo since lambing had previously lambed in February from a fall mating and the former may have had a higher summer fertility. Gabina (1989a) reported that ewes that had

lambled in the season immediately preceding the mating season had higher fertility than ewes that had lambled earlier and had missed a mating opportunity. For **FPLF** in fall, the final model only included ewe age class and **NLR** effects ($P < 0.01$). Ewes older than 48 mo of age had a mean fall post-lambing fertility of 0.62 ± 0.05 which was lower ($P < 0.01$) than the mean fertility of 12 to 24 mo old ewes (0.85 ± 0.03) and 24 to 48 mo old ewes (0.81 ± 0.02). Also, ewes that did not nurse any lambs from the previous lambing had a mean fall **FPLF** of 0.69 ± 0.05 which was lower than that ewes that had raised a single (0.78 ± 0.03 ; $P < 0.10$) or twins or more (0.84 ± 0.02 ; $P < 0.01$). Thus, ewes that nurse more lambs prior to an in-season fall mating appear to have higher fertility. Lewis et al. (1996) and Gabina (1989a) reported that number of lambs reared at the previous lambing did not affect fertility. For **FPLF** in winter, the final model included year ($P < 0.01$) and ewe age category ($P < 0.05$) effects. Ewes aged 12 to 24 mo had a mean winter **FPLF** of 0.91 ± 0.05 which was higher than that of ewes aged 24 to 48 mo (0.76 ± 0.06 ; $P = 0.10$) and of ewes greater than 48 mo of age (0.65 ± 0.07 ; $P < 0.05$). The **FPLF** in the fall and winter matings decreased with increasing age. It is possible that the decline in **FPLF** with age may be due to accumulated reproductive stress due to an accelerated lambing regimen. However, Hulet (1984) reported that reproductive performance of younger ewes was superior to that of older ewes in summer matings and Lundeen and Slyter (1999) also reported that fertility increased with increasing age in spring lambings but ewes that were 4 yr and older had lower fertility than younger ewes in fall lambings.

Acceleration Records

Birth year-season of ewe was significant ($P < 0.01$) for all traits. For **AGE1** to **AGE3**, **ELF**, and ewe age at first mating (**AFM**, d) were significant ($P < 0.01$). Random sire effects were small to moderate and ranged from 5 to 25 % of the total variance. The regression coefficients for **AFM** were 1.02 ± 0.16 d/d, 1.38 ± 0.26 d/d, and 1.71 ± 0.42 d/d, respectively, for **AGE 1** to **AGE3**. Thus, among ewe lambs that had the same **ELF**, those that were older at first mating continued to be older at each successive lambing. For a unit increase in **ELF** (i. e. from **ELF** = 0 to **ELF** = 1) the decrease in **AGE1** to **AGE3** were 251 ± 4 d, 246 ± 7 d, and 247 ± 11 d, respectively. Thus, among ewe lambs that were mated at the same age for the first time, those that conceived at the first mating opportunity were approximately 8 mo younger at first and each successive lambing than ewe lambs that did not conceive at the first mating opportunity. Ewe lambs that do not conceive at first mating opportunity do not appear to catch up with their

contemporaries that conceived at first mating opportunity to lamb at similar or younger ages at later lambings. These results indicate that it is critically important for ewes to get started early and conceive at the first mating opportunity to consistently lamb at younger ages.

For both **INT1** and **INT2**, numbers of lambs reared at previous lambing, **ELF**, and **AGE1** or **AGE2** were not significant and sire effects were negligible. Gabina (1989a) reported that litter size at previous lambing did not affect lambing interval and that ewe age only affected lambing intervals in the seasons of low fertility. Previous lambing season was significant ($P < 0.01$) for both **INT1** and **INT2**. Means for **INT1**, in months, were 10.83 ± 0.17 , 10.31 ± 0.09 , 9.68 ± 1.07 , and 11.18 ± 0.30 , respectively for previous lambing seasons of spring, summer, fall, and winter. Means for **INT2**, in months, were 10.61 ± 0.16 , 10.09 ± 0.20 , and 11.58 ± 0.27 , respectively, for previous lambing seasons of spring, summer, and winter. First lambing interval was shorter ($P < 0.05$) for ewes that lambed for the first time in summer compared to spring or winter by less than a month. Second lambing interval was shortest for ewes lambing in summer and longest for ewes lambing in winter. These results are most likely due to the breeding schedule; ewes lambing in winter and spring had between 5 to 6 mo till they had a breeding opportunity where as those born in summer consistently had about 4 to 5 mo till their next breeding opportunity, usually in October. Similar effects of season on lambing intervals have reported by Iniguez et al. (1986) and Lewis et al. (1998).

Birth year-season of the ewe and **ELF** affected ($P < 0.01$) **TIME3**. However, age at first mating did not have a significant effect on **TIME3**, either in the presence or absence of **ELF**. By 38 mo after birth, ewes that conceived at first mating opportunity had been in the flock for 320 ± 22 d longer than ewes that did not conceive at the first mating opportunity. Sire component of total variance for **TIME3** was 6 % in this analysis. Birth year-season affected ($P < 0.10$) **TIME4**, but ewe age at first mating did not have a significant effect on **TIME4** either in the presence or absence of **ELF**. The **ELF** affected ($P < 0.01$) **TIME4**; by 48 mo since birth, ewes that conceived at first mating opportunity remained in the flock for 260 ± 43 d longer than ewes that did not conceive at first mating opportunity.

Birth year-season affected ($P < 0.01$) **LAMB3** but age at first mating did not affect **LAMB3** when included in the model by itself or in the presence of **TIME3** or **ELF**. The **TIME3** affected ($P < 0.01$) **LAMB3**; ewes had 0.30 ± 0.01 more lambings by 38 mo since birth for every 100 d increase in **TIME3**. The **ELF** also affected ($P < 0.01$) **LAMB3**; ewes that

conceived at the first mating opportunity had 1.59 ± 0.07 more lambings by 38 mo since birth compared to ewes that did not conceive at the first mating opportunity. Sire component for **LAMB3** ranged from 5 to 10 % of total variation when analyzed with only birth year-season in the model or additionally in the presence of **ELF** or **TIME3**. Similar results were obtained for **LAMB4**. Birth year-season affected ($P < 0.10$) and age at first mating did not affect **LAMB4** when included in the model by itself or in the presence of **TIME4** or **ELF**. Ewes that conceived at first mating opportunity had 1.49 ± 0.13 more ($P < 0.01$) lambings by 48 mo since birth than ewes that did not conceive at the first mating opportunity. Also, ewes had 0.30 ± 0.01 more ($P < 0.01$) lambings by 48 mo since birth for every 100 d increase in **TIME4**. Sire component for **LAMB4** ranged from 5 to 10 % of total variation when analyzed with only birth year-season in the model or additionally in the presence of **ELF** or **TIME4**.

Correlations from multivariate analysis of variance of **AGE1** to **AGE5** and **INT1** to **INT4** are given in Table 4.4 and 4.5, respectively. These correlations are from data from 52 ewes that had all five ages at lambing or all four lambing intervals. Correlations involving **AGE1** through **AGE5** were all significant, positive, and above 0.48. Correlations between adjacent lambing ages were higher and correlations declined with increasing distance between lambings. Thus, ewes that are younger at first lambing appear to maintain that advantage over their lifetime, although it seems to diminish somewhat over time. Correlations among **INT1** to **INT4** were small and generally not significant. A negative correlation between **INT1** and **INT2** was observed, although it was not significant. A negative correlation between **INT3** and **INT4** was also observed ($P < 0.10$). When the correlations among **INT1**, **INT2** and **INT3** were recalculated using data from ewes that had all three intervals ($N = 153$), the correlations were similar but the correlation between **INT1** and **INT2** was now significant ($r = -0.20$; $P < 0.05$). Thus, ewes that had a shorter first lambing interval had longer second lambing intervals and vice-versa. In general, these results suggest that short lambing intervals are followed by long lambing intervals in accordance to results reported by Lewis et al. (1998).

Genetic Analyses

Results from univariate genetic analyses are given in Table 4.6. Ewe lamb fertility had a small but significant heritability suggesting scope for improvement in **ELF** through selection. In our study, **ELF** was analyzed as a 0/1 trait. Other, possibly more appropriate non-linear methodologies exist for evaluation of discreet traits like fertility. However, Matos et al. (1997)

did not find any differences in predictive ability or goodness-of-fit among linear and non-linear approaches to evaluation of fertility and suggested that the incentive to using non-linear over linear approaches was little, given the complexities of the non-linear methodologies. The heritability for fertility obtained here was higher than most published estimates (Safari and Fogarty, 2003), which are typically from ewes of all ages. Complexities in appropriate partitioning of variance components for repeated fertility records, especially in **ALS**, may arise due to the accumulated environmental influences on fertility over time. Ewe lamb fertility, a relatively early life measure, is perhaps less affected by these complex environmental influences resulting in somewhat higher heritabilities. Specific reports of heritabilities for fertility at first mating range from 0.05 ± 0.07 in the STAR system (Lewis, 1990) to 0.09 in Hyfer sheep and in 7-mo-old ewe lambs bred in fall (Fogarty et al., 1994; Fossceco and Notter, 1995).

The different ages at lambing had moderate heritabilities when analyzed with age at first mating as a covariate. However, when **AGE2** and **AGE3** were analyzed with **AGE1** as a covariate instead, there was a dramatic reduction in phenotypic variation in **AGE2** and **AGE3** and there was no genetic variation in **AGE2** and the heritability of **AGE3** was reduced to a low value which was not significant (Table 4.6). This suggests that after accounting for variation in **AGE1** there may not be much variation, both at a phenotypic and genetic level, left to measure in **AGE2** and **AGE3**. Indeed, **INT1** did not have any genetic component at all and **INT2** only had a small, non-significant heritability (Table 4.6). The lambing intervals and later ages at lambing are apparently more influenced by environmental factors. Indeed, the lambing intervals will vary depending on the time till the next breeding opportunity since lambing, which may depend quite heavily on producers' decisions. It can be seen from Table 4.1 that the time between mating opportunities differed from time to time and this could have contributed to the low heritability observed here. However, when the univariate genetic analyses for **INT1** and **INT2** were performed using a combination of birth year-season and first lambing year-season or second lambing year-season, respectively, as a contemporary group effect, similar heritability estimates of 0.00 and 0.07 for **INT1** and **INT2**, respectively, were obtained suggesting that irregular mating intervals may not have been the cause for the low heritabilities observed for these traits. The results obtained here suggest that genetic improvement through selection for reduced age at first lambing is feasible, but selection to reduce the ages at later lambings (beyond that achieved as a correlated response to selection for reduced **AGE1**) or to reduce lambing

intervals may not be very effective. Our results are similar to heritabilities of 0.31 and 0.06 for age at first lambing and first lambing interval, respectively, reported by Iniguez et al. (1986), but are in contrast to heritabilities of 0.07 ± 0.05 , 0.30 ± 0.12 , and 0.14 ± 0.12 for age at first lambing, and first and second lambing intervals, respectively, reported by Lewis et al. (1998) in the STAR system.

The **LAMB3** had a moderate and significant heritability which declined slightly when **ELF** was included as a covariate. However, when both **ELF** and **TIME3** were accounted for as covariates, **LAMB3** was no longer heritable. The **TIME3** is partly indicative of performance based culling decisions made by the producers and would have a direct impact on the number of lambings a ewe will have. Therefore, it is not surprising that when **TIME3** is used a covariate, there is not much variation left in **LAMB3**, as is indicated by the reduction in phenotypic variation in **LAMB3**. The **TIME3** itself had a very similar heritability to that of **LAMB3**. The heritability of **LAMB3** obtained in this study suggests that genetic improvement in this measure of accelerated lambing performance is feasible. No reports of heritability for these two traits in sheep were found in the literature. In cattle, Morris et al. (1993) reported the heritability of the number of calvings by 12 yr of age as 0.11 ± 0.08 . Heritabilities of productive life, which was measured as the number of days a cow survived in the next N years given that she had the opportunity to stay in the herd at least N years, ranged from 0.05 to 0.15 (Martinez et al., 2004).

The **AGEACC**, which is indicative of acceleration over a period of time, was moderately heritable. The heritability was similar to that of its closely related traits, the ages at lambing. The **AGEACC** also had a very high repeatability of 0.90 suggesting that ewes that lamb early initially will continue to do so through out their life. Indeed, like the lambing intervals, when **INTACC**, which is a measure of deviation of lambing interval from the annual lambing cycle, was analyzed as a repeated trait, both heritability and repeatability were zero. Lewis et al. (1998) analyzed lambing intervals over time as a repeated trait, and reported a heritability and repeatability of 0.05, although first and second lambing intervals had low to moderate heritabilities. Somewhat higher repeatabilities of 0.10 to 0.16 for lambing intervals were reported by Gabina (1989b).

The **FPLF** in summer was not heritable but had a small repeatability (Table 4.6) suggesting that ewes that successfully lamb in the fall are more likely to continue to do so at subsequent lambings for non-genetic reasons. Our results are in contrast to reports of higher

heritability for spring fertility compared to fall fertility (Fossceco and Notter, 1995). Notter (1981) reported a repeatability of 0.19 for fertility in spring matings and suggested that selection for improving fertility may be more fruitful in the out-of-season months rather than the favorable seasons and that selection for improved spring fertility would also improve fertility in other seasons. Tosh et al. (2002) also reported higher heritability for fertility in the out-of-season exposures compared to the in-season exposures.

Weaning weight had a low but significant heritability of 0.03, suggesting that there is not much variation in growth potential in this flock. There was also a small maternal genetic component of 0.05 ($P < 0.01$) and a small negative correlation ($r = -0.30$) between additive direct and maternal effects although this correlation was not significant. Notter (1998a) reported a slightly higher heritability of 0.08 and maternal permanent environment component of 0.15, but similar maternal genetic component of 0.07, and non-significant additive-maternal genetic correlation of 0.24 using a more comprehensive Polypay dataset from the NSIP database. Number born also had a small but significant heritability and repeatability. Similar estimates of heritability of 0.09 and permanent environment component of 0.04 were reported from a more comprehensive NSIP Polypay data set by Rao and Notter (2000). These results suggest a limited scope for genetic improvement in **WW** and **NB** in this flock.

Results from the bivariate genetic analyses of **ELF** with **AGE1**, **AGE2**, **LAMB3**, and **TIME3** are given in Table 4.7. The heritabilities for **ELF**, **LAMB3** and **TIME3** were similar to those obtained in the univariate analyses, but heritability estimates for **AGE1** and **AGE2** were lower than those obtained in the univariate analyses. Ewe lambs that conceived at their first opportunity (**ELF** = 1) necessarily also had records for **AGE1**. However, open ewe lambs were not necessarily retained for later lambing and removal of some of these animals potentially introduced downward bias in estimates of residual variance for **AGE1** and **AGE2** in univariate analyses. This bias is demonstrated by increases in estimated residual variances of 94 and 75% and increases in phenotypic variances of 44 and 42% for **AGE1** and **AGE2**, respectively, when bivariate models with **ELF** were compared to univariate models (Tables 4.6 and 4.7). When univariate analyses for **AGE1** and **AGE2** were repeated after assigning high values of **AGE1** (27 mo) or **AGE2** (40 mo) for ewes that had an **ELF** observation but had missing **AGE1** or **AGE2**, similar heritability estimates to those obtained in bivariate analyses were obtained for **AGE1** and **AGE2**. Pollak and Quaas (1981) reported that multi-trait analyses incorporating records from all

animals for traits under direct selection removed the bias in evaluations of subsequently measured correlated traits on a selected subset of animals. Therefore, it may be necessary and advisable to analyze **AGE1** or **AGE2** along with **ELF** in bivariate analyses to obtain unbiased estimates of variance for **AGE1** and **AGE2**.

The **ELF** was highly negatively correlated to **AGE1** and **AGE2**, both genetically and phenotypically (Table 4.7). The high correlation of **ELF** with **AGE1** is expected, since ewes which fail to conceive at first mating opportunity will necessarily have a higher age at first lambing than ewes that conceive at the first mating opportunity. From these results, it also appears that ewes that fail to conceive as ewe lambs may not catch up with their contemporaries that did conceive as ewe lambs even at later parities. Results from the bivariate analysis of **ELF** with **AGEACC** as a repeated trait were similar; heritability of **AGEACC** was smaller, and the genetic correlation high and negative. On the other hand, **ELF** had a high positive genetic correlation with **LAMB3** and **TIME3**. Thus, ewe lambs which have a higher genetic merit for **ELF** are likely to have a higher genetic merit for **LAMB3** and **TIME3**. These results suggest that selection on **ELF** will result in improvement of performance in **ALS** measured as the number of lambings by 38 mo of age. No literature estimates for genetic correlations between **ELF** and ages at lambing or **LAMB3** or **TIME3** were found.

Results from bivariate genetic analyses of **LAMB3** with **AGE1**, **AGE2**, and **TIME3** are given in Table 4.8. The heritabilities of all the traits were similar to those obtained in the univariate analyses. The **LAMB3** was negatively correlated with **AGE1** and **AGE2**. Thus, ewes with lower genetic merit for ages at early lambings have low genetic merit for performance in **ALS** over time. The correlations between **LAMB3** and **TIME3** were close to unity. This may be more due to the mathematical nature of the relationship between these two traits rather than similar genetic control for both the traits. In any case, because of these high correlations, **TIME3** and **LAMB3** may be measuring the same thing and **TIME3** was not used in further analyses. No literature estimates for genetic correlations between **LAMB3** and different ages at lambing were found.

Results from the bivariate genetic analyses of **WW** with **ELF**, **AGE1**, **AGE2**, **AGE3**, and **LAMB3** are given in Table 4.9. Again, heritabilities for all traits were similar to those obtained from univariate analyses. The **WW** was genetically negatively correlated with **ELF** and **LAMB3**, i. e., ewes with high genetic potential for growth appear to have a tendency for

lower genetic potentials for fertility as ewe lambs and number of lambings over time, although these correlations were not significant. On the other hand, the correlations between maternal genetic effects on **WW** and direct genetic effects on **ELF** and **LAMB3** were moderate to high and approached significance for **ELF**. The ages at different lambings had an unfavorable positive direct genetic correlation with **WW**, but had a favorable negative correlation with maternal genetic effects for **WW**. Thus, ewes with higher genetic merit for growth potential had a lower genetic merit for the early fertility and later acceleration traits, but ewes with higher genetic merit for maternal performance for **WW** had a higher genetic merit for ewe lamb fertility and later acceleration traits. These results suggest that selection for increased growth potential may have an adverse effect on reproductive performance in **ALS**, whereas selection for maternal traits will have a beneficial effect. The genetic correlation between **WW** and **ELF** obtained by us are higher than other reported literature estimates of correlation between lamb weights and fertility which are generally small, negative and non-significant (Fossceco and Notter, 1995; Al Shorepy and Notter, 1996). However, maternal effects were not fit in the models for weight traits used in these studies which may have lead to the differences in results compared to our estimates. Fogarty et al. (1985) reported a genetic correlation of 0.01 between weaning weight and fertility.

Results from the bivariate genetic analyses of **NB** with **ELF** and **LAMB3** are given in Table 4.10. Prolificacy was independent of **ELF** and **LAMB3** in this dataset where prolificacy was generally high. Thus, selection for improved prolificacy will have little impact on **ELF** and **LAMB3** and vice versa in this flock, perhaps because the level of prolificacy is already high. Similar results were reported by Fogarty et al. (1994) in Hyfer sheep that are also prolific sheep. Rosati et al. (2002) reported a much higher genetic correlation of 0.71 between **NB** and fertility. Al-Shorepy and Notter (1996) reported a genetic correlation of 0.56 between spring fertility and fall litter sizes.

Correlations among **ELF** and **AGE1** and **ELF** and **LAMB3** from the trivariate analyses were similar to those obtained in the bivariate analyses (Table 4.11). Genetic correlations between **AGE1** and **LAMB3** were generally higher (more negative and unfavorable) than those obtained in the bivariate analyses. These results suggest that records from all animals for **ELF** must be included in genetic analyses involving **AGE1** to avoid biases in estimation of

correlations involving **AGE1** and other traits due to selection on **ELF** as described earlier in this paper.

General Discussion

Success in genetic improvement of fertility in **ALS** depends on availability of pertinent, reliable and accurate data, more so than in annual lambing systems, because ewes are constantly being rebred and therefore reliable mating records need to be maintained and there are more traits to record. Some guidelines for data requirements for improvement of fertility have been outlined by Notter (2002). For improvement of fertility in **ALS**, data recorded should include a list of all the ewes as well as ewe lambs that are put into breeding pastures along with service sire information and the date of introduction and removal of service sires as well as lambing information for ewes that lamb for every mating period in a given year. This will help identify ewe lambs that are put into breeding, which was not always available in the present dataset. Mating lists will also help avoid assigning an unsuccessful fertility record to ewes that are available in the flock at the time of breeding but were not bred for some reason, for example, some ewes that lamb late in the previous season and are not in good condition may be deliberately held back from breeding by the producer, or some ewes may simply be held back from breeding to control the number of lambs being born to suit market demands or facility and labor capacities. Having the entire list of ewes that are exposed to breeding along with culling, death or disposal information will also help identify ewes that go into cleanup matings at the next breeding opportunity. Ewes that are culled at the time of breeding or ewes that die after mating but before lambing should also be clearly identified so that such animals are not penalized for failure to lamb for the given mating opportunity. The NSIP data recording forms are designed to collect mating, lambing, growth and other performance records as well as animal disposal information (Notter, 1998b). However, most producers report lambing and performance information but data on ewes that fail to lamb are not always reported.

Although we did not find any genetic variation in fertility at each exposure or out-of-season fertility in this study, heritabilities for the other traits obtained in this study indicate that selection for improvement in performance in **ALS** is possible and most promising for **ELF**, **AGE1**, and **LAMB3**. Improvements in **LAMB3** would likely result from cumulative effects of improvements in **ELF**, age at first lambing, as well as lambing intervals and success in out-of-season matings, although genetic influences on the latter two were not observed in this study.

Wang and Dickerson (1991) showed that for genetic selection in **ALS**, improvement in fertility was most important, followed by improvements in prolificacy. Our results suggest that the biggest contributor to improved performance in **ALS** in this flock was **ELF**. Genetic improvements in **ELF** should result in decreased **AGE1** and increased **LAMB3**. Selection for **ELF**, **AGE1**, and **LAMB3** could be performed using multi-trait analyses utilizing data as they become available over the lifetime of the ewes, and is justified by the somewhat higher heritabilities of the later measures (Table 4.11). Using the multi-trait analyses will also help in reducing the generation interval, since **ELF** is available relatively early in life and is highly correlated to **LAMB3** which is our measure of success in accelerated lambing systems. Using these traits would also avoid some of the problems associated with utilizing fertility for the genetic improvement in **ALS** due to the different breeding patterns followed over time by ewes born in the same birth cohort which result in differences in average genetic merit of different breeding groups (Notter, 2002). Also, these traits should be easy to obtain from the data presently reported by the producers participating in the US NSIP, except for **ELF**.

Our results also suggest that selection for improved **ELF** or **LAMB3** will not result in any changes in prolificacy. Therefore, selection on **ELF** and **LAMB3** will potentially result in improvements in number of lambs produced by a ewe over time and in turn lead to improvements in overall ewe productivity. Genetic correlations of fertility with total weight of lamb weaned ranging from 0.32 to 0.92 have been reported (Rosati et al., 2002; Fogarty et al., 1985, 1994). However, selection for **ELF** may result in decreased gains in growth potential, although maternally superior ewes for weaning weight appear to have an advantage of improved performance in **ALS**. These antagonistic relationships could be managed using carefully designed breeding programs. Ages at later lambings and lambing intervals appear to be of little value in genetic improvement of performance in **ALS** in this system.

It is pertinent to mention here that genetic markers serve as advantageous alternatives to traditional breeding strategies for lowly heritable reproductive traits like out-of-season fertility that are expressed later in life and only in females. Recently, the melatonin receptor gene has been shown to affect seasonality in fertility, accounting for nearly 24% of the additive genetic variance in spring fertility (Notter and Cockett, 2003). Ewes with at least one copy of the + allele for the melatonin receptor gene had 11.2 ± 5.1 % higher spring fertility as adults than ewes that were homozygous for the – allele in the Virginia Tech out-of-season flock selected for

improved fertility in May and June matings. There was evidence of substantial allelic diversity for the melatonin receptor gene; frequencies of the + and – alleles were 0.42 and 0.58, respectively, in the Virginia Tech flock and were very similar to gene frequencies of 0.47 and 0.53 for the + and – alleles in the Polypay flock used for this study (Notter et al., 2005). Identification of ewes with at least one copy of the + allele at the melatonin receptor gene locus could be beneficial in genetic improvement of out-of-season fertility in **ALS**.

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Table 4.1. Numbers of matings and lambings, and fertility by mating year and season

Mating year and season ^a	Mating date	Number of:		
		Matings	Lambings	Fertility ^b
1999_Summer	01 July 99	228	130	0.57
1999_Fall	01 Oct 99	21	20	0.95
1999_Winter	10 Dec 99	208	160	0.77
2000_Summer	06 May 00	157	72	0.46
2000_Fall	28 Oct 00	323	242	0.75
2000_Winter	02 Dec 00, 01 Feb 01	196	86	0.44
2001_Fall	05 Aug 01, 08 Oct 01	353	281	0.80
2001_Winter	01 Dec 01	191	121	0.63
2002_Summer	08 June 02	191	108	0.57
2002_Fall	24 Aug 02	109	94	0.86
2002_Winter	01 Dec 02	159	117	0.74
2003_Summer	10 May 03	100	51	0.51
2003_Fall	08 Sep 03	216	172	0.80
2003_Winter	20 Jan 03	27	21	0.78
2004_Summer	14 July 04	200	73	0.37
Total		2679	1748	0.65

^a Summer: May, June, and July; Fall: August, September, and October; Winter: November, December, January. 1st February 2001 mating was categorized as 2000_ **Winter**.

^b Proportion of successful matings.

Table 4.2. Number of records for ewe lamb fertility, and mean \pm SD and ranges for age at first mating (AFM, d) by birth year-season and first mating year-season of ewe lamb

Birth year- season	Mating year- season	No. of records	AFM	
			Mean \pm SD	Range
1998_Winter	1999_Summer	59	261 \pm 9	238 to 275
1999_Spring	1999_Winter	84	296 \pm 12	247 to 326
1999_Fall	1999_Winter	35	149 \pm 6	142 to 158
1999_Winter	2000_Fall	81	322 \pm 10	302 to 339
2000_Spring	2000_Fall	14	216 \pm 4	209 to 223
2000_Summer	2000_Winter	111	197 \pm 9	166 to 214
2000_Winter	2001_Fall	25	297 \pm 7	284 to 306
2001_Spring	2001_Winter	103	243 \pm 5	233 to 255
2001_Summer	2001_Winter	36	207 \pm 14	181 to 228
2001_Fall	2002_Winter	17	496 \pm 7	485 to 503
2002_Spring	2002_Winter	61	315 \pm 14	281 to 338
2002_Winter	2003_Fall	13	295 \pm 3	288 to 300
2003_Winter	2004_Summer	37	275 \pm 9	243 to 285
All	All	676	263 \pm 63	142 to 503

Table 4.3. Numbers of records, sires and contemporary groups (CG), means \pm SD, and ranges

Trait ¹	Records	Sires ²	CG ³	Mean \pm SD	Range
ELF	676	32 (21)	13	0.58 \pm 0.49	0 to 1
AGE1 , mo	452	27 (14)	11	15.6 \pm 3.6	10.1 to 26.0
AGE2 , mo	345	26 (10)	11	26.0 \pm 3.7	19.8 to 39.5
AGE3 , mo	260	23 (8)	11	36.1 \pm 3.8	29.5 to 51.0
AGE4 , mo	153	-	-	47.7 \pm 4.1	40.3 to 60.2
AGE5 , mo	52	-	-	59.0 \pm 3.6	51.1 to 67.7
AGE6 , mo	6	-	-	70.7 \pm 3.7	64.3 to 75.1
INT1 , mo	345	26 (10)	11	10.4 \pm 1.2	7.5 to 15.8
INT2 , mo	260	23 (8)	11	10.5 \pm 1.4	7.5 to 16.5
INT3 , mo	153	-	-	11.9 \pm 1.8	9.3 to 18.1
INT4 , mo	52	-	-	11.9 \pm 1.9	9.5 to 16.1
INT5 , mo	6	-	-	11.5 \pm 2.1	9.5 to 14.2
LAMB3	594	28 (17)	11	1.6 \pm 1.1	0 to 3
TIME3 , mo	594	28 (17)	11	27.1 \pm 10.4	7.8 to 36.0
LAMB4	407	-	-	2.3 \pm 1.4	0 to 4
TIME4 , mo	407	-	-	36.0 \pm 13.6	7.8 to 48.3
AGEACC , mo	1,268	27 (21)	50	1.8 \pm 4.1	-8.9 to 15.5
INTACC , mo	816	26 (19)	39	-1.2 \pm 1.6	-4.5 to 6.1
FPLF_Summ	671	43 (19)	66	0.56 \pm 0.50	0 to 1
FPLF_Fall	651	-	-	0.82 \pm 0.39	0 to 1
FPLF_Wint	192	-	-	0.70 \pm 0.46	0 to 1
WW , kg	4,532	60 (47)	105	17.8 \pm 4.3	2.9 to 44.2
NB	4,949	94 (48)	86	2.05 \pm 0.69	1 to 5.8

¹ **ELF** = ewe lamb fertility; **AGE_i** = age at *i*th lambing, **INT_i** = *i*th lambing interval; **LAMB3** and **LAMB4** = number of lambings by 38 and 48 mo since birth, respectively; **TIME3** and **TIME4** = time in flock by 38 and 48 mo since birth, respectively; **AGEACC** = difference between age at *i*th lambing and *i*th yr of age for first to sixth lambings; **INTACC** = deviation of lambing interval from 1 yr for first to fifth lambing intervals; **FPLF_Summ** = first post-lambing fertility in

summer; **FPLF_Fall** = first post-lambing fertility in fall; **FPLF_Wint** = first post-lambing fertility in winter; **WW** = 60-d adjusted weaning weight; **NB** = number of lambs born.

² Number of sires only listed for traits used in genetic analyses. Number in parenthesis indicates number of sires with 10 or more progeny.

³ Number of CG only listed for traits used in genetic analyses.

Table 4.4. Phenotypic correlations among ages at lambing 1 through 5 (**AGE1** to **AGE5**; mo) from multi-trait analysis of variance using data from ewes that had all of **AGE1** to **AGE5** (N = 52)¹

Trait	AGE2	AGE3	AGE4	AGE5
AGE1	0.84	0.69	0.52	0.48
AGE2		0.65	0.52	0.50
AGE3			0.80	0.63
AGE4				0.70

¹All P < 0.01.

Table 4.5. Phenotypic correlations among first to fourth lambing intervals (**INT1** to **INT4**; mo) from multi trait analysis of variance using data from ewes that had all of **INT1** to **INT4** (N = 52)

Trait	INT2	INT3	INT4
INT1	-0.20	0.00	0.06
INT2		0.02	-0.17
INT3			-0.26 †

† P < 0.10.

Table 4.6. Variance component estimates for fertility, acceleration, growth and prolificacy traits

Trait ¹	Covariate ²	Variance proportions ³			σ_p^2
		h^2	c^2	e^2	
ELF	AFM	0.14 **	-	0.86	0.22
AGE1 , mo	AFM	0.39 **	-	0.61	10.77
AGE2 , mo	AFM	0.28 **	-	0.72	10.73
AGE2 , mo	AGE1	0.00	-	1.00	1.14
AGE3 , mo	AFM	0.36 **	-	0.64	12.81
AGE3 , mo	AGE1	0.09	-	0.91	2.31
INT1 , mo	-	0.00	-	1.00	1.14
INT1 , mo	AGE1	0.00	-	1.00	1.14
INT2 , mo	-	0.09	-	0.91	1.70
INT2 , mo	AGE2	0.07	-	0.93	1.68
INT2 , mo	INT1	0.09	-	0.91	1.69
LAMB3	-	0.27 **	-	0.73	1.20
LAMB3	ELF	0.22 *	-	0.78	0.63
LAMB3	ELF, TIME3	0.03	-	0.97	0.12
TIME3 , mo	-	0.27 **	-	0.73	92.88
AGEACC , mo	AGE1	0.31 **	0.59 **	0.10	11.93
INTACC , mo	-	0.00	0.00	1.00	1.70
FPLF_Summ	TSL	0.01	0.21 †	0.78	0.21
WW ⁴ , kg	-	0.03 *	0.06 **	0.87	12.64
NB	-	0.06 **	0.07 **	0.87	0.44

¹ **ELF** = ewe lamb fertility; **AGEi** = age at i^{th} lambing, **INTi** = i^{th} lambing interval; **LAMB3** = number of lambings by 38 mo since birth; **TIME3** = time in flock by 38 mo since birth; **AGEACC** = difference between age at i^{th} lambing and i^{th} yr of age for first to sixth lambings; **INTACC** = deviation of lambing interval from 1 yr for first to fifth lambing intervals; **FPLF_Summ** = first post-lambing summer fertility in Summer; **WW** = 60-d adjusted weaning weight; **NB** = number of lambs born,

² **AFM** = age at first mating; **TSL** = time since previous lambing.

³ h^2 , c^2 , and e^2 are direct genetic, animal permanent environmental, and residual proportions of phenotypic variance (σ_p^2).

⁴ For **WW**: c^2 is maternal permanent environmental proportion of σ_p^2 ; additionally, maternal genetic proportion of σ_p^2 was 0.05 ($P < 0.01$), and the correlation between direct and maternal genetic effects was -0.30.

Table 4.7. Estimated co-variance components from bivariate genetic analyses of ewe lamb fertility (**ELF**) with ages at first and second lambing (**AGE1** and **AGE2**, respectively; mo), number of lambings by 3 yr since birth (**LAMB3**), time in flock by 3 yr since birth (**TIME3**, mo), and difference between i^{th} lambing age and i^{th} year of age measured as a repeated trait over lifetime of ewe (**AGEACC**, mo)

Item ¹	Other trait				
	AGE1	AGE2	LAMB3	TIME3	AGEACC ²
h_{elf}^2	0.14	0.17	0.16	0.17	0.15
h_{other}^2	0.18	0.11	0.27	0.27	0.13
r_g	-0.89 **	-0.91 **	0.89 **	0.70 †	-0.92 **
e_{elf}^2	0.86	0.83	0.84	0.83	0.85
e_{other}^2	0.82	0.89	0.73	0.73	0.07
r_e	-0.97 **	-0.94 **	0.66 **	0.48 **	-0.96 **
$\sigma_{\text{p-elf}}^2$	0.22	0.22	0.22	0.22	0.22
$\sigma_{\text{p-other}}^2$	15.53	15.21	1.20	92.72	17.26
r_p	-0.96	-0.93	0.70	0.52	-0.92

¹ Subscripts ‘**ELF**’ and ‘other’ refer to **ELF** and the other trait in the bivariate analysis, respectively; h^2 and e^2 are direct genetic and residual proportions of phenotypic variance (σ_p^2);

r_g = animal additive genetic correlation, r_e = residual correlation; r_p = phenotypic correlation.

Tests of significance were performed for r_g and r_e only.

²Ewe permanent environment component was 0.80. r_e is the correlation between ewe permanent environment effects on **AGEACC** and residual effects on **ELF**.

** $P < 0.01$; * $P < 0.05$; † $P < 0.10$.

Table 4.8. Estimated co-variance components from bivariate genetic analyses of number of lambings by 38 mo since birth (**LAMB3**) with ages at first and second lambing (**AGE1** and **AGE2**, respectively; mo), and time in flock by 38 mo since birth (**TIME3**, mo)

Item ¹	Other trait		
	AGE1	AGE2	TIME3
h_{lamb}^2	0.26	0.22	0.26
h_{other}^2	0.32	0.27	0.23
r_g	-0.49 †	-1.00 **	0.98 **
e_{lamb}^2	0.74	0.78	0.74
e_{other}^2	0.68	0.73	0.77
r_e	-0.40 **	-0.85 **	0.89 **
$\sigma_{p\text{-lamb}}^2$	1.20	1.18	1.20
$\sigma_{p\text{-other}}^2$	11.24	29.05	91.70
r_p	-0.42	-0.88	0.91

¹ Subscripts ‘lamb’ and ‘other’ refer to **LAMB3** and the other trait in the bivariate analysis, respectively; h^2 and e^2 are direct genetic and residual proportions of phenotypic variance (σ_p^2);

r_g = animal additive genetic correlation, r_e = residual correlation; r_p = phenotypic correlation.

Tests of significance were performed for r_g and r_e only.

** $P < 0.01$; * $P < 0.05$; † $P < 0.10$.

Table 4.9. Estimated co-variance components from bivariate genetic analyses of 60-d adjusted weaning weight (**WW**, kg) with ewe lamb fertility (**ELF**), ages at first, second, and third lambing (**AGE1**, **AGE2**, and **AGE3**, respectively; mo), and number of lambings by 38 mo since birth (**LAMB3**)

Item ¹	Other trait				
	ELF	AGE1	AGE2	AGE3	LAMB3
h_{ww}^2	0.03	0.03	0.03	0.04	0.03
h_{other}^2	0.12	0.31	0.29	0.39	0.28
r_g	-0.68	0.80 †	0.78	0.96 †	-0.70
m_{ww}^2	0.05	0.05	0.05	0.05	0.05
r_{gm}	-0.25	-0.20	-0.27	-0.28	-0.25
r_m	0.88 †	-0.75 *	-0.81*	-0.52	0.58
c_{m-ww}^2	0.06	0.06	0.06	0.06	0.06
e_{ww}^2	0.87	0.87	0.87	0.87	0.86
e_{other}^2	0.88	0.69	0.71	0.61	0.72
r_e	0.16 *	-0.09	0.00	-0.13	0.28 **
σ_{p-ww}^2	62.48	62.45	62.49	62.51	62.56
$\sigma_{p-other}^2$	0.22	10.20	10.76	12.94	1.21
r_p	0.13	0.03	0.03	-0.02	0.18

¹ Subscripts ‘**WW**’ and ‘other’ denote weaning weight and the other trait in bivariate genetic analysis, respectively. h^2 , m^2 , c_m^2 , and e^2 are direct genetic, maternal genetic, maternal permanent environmental, and residual proportions of σ_p^2 ; r_g = animal additive genetic correlation between weaning weight and other traits; r_{gm} = direct-maternal additive genetic correlation (weaning weight only); r_m = correlation between maternal additive effects on weaning weight and animal additive effects on other traits; r_e = correlation between residual

effects on weaning weight and other traits; Γ_p = phenotypic correlation; σ_p^2 = phenotypic variance. Tests of significance were performed for Γ_g , Γ_m , Γ_{gm} , and Γ_e only.

** $P < 0.01$; * $P < 0.05$; † $P < 0.10$.

Table 4.10. Estimated co-variance components from bivariate genetic analyses of number of lambs born (**NB**) with ewe lamb fertility (**ELF**) and number of lambings by 38 mo since birth (**LAMB3**)

Item ¹	ELF	LAMB3
h_{nb}^2	0.05	0.05
h_{other}^2	0.14	0.26
r_g	-0.05	-0.07
c_{nb}^2	0.07	0.07
e_{nb}^2	0.86	0.87
e_{other}^2	0.87	0.74
r_e	0.10	0.16
σ_{p-nb}^2	0.44	0.44
$\sigma_{p-other}^2$	0.22	1.20
r_p	0.02	0.03

¹ Subscripts ‘**NB**’ and ‘other’ denote number of lambs born and the other trait in bivariate genetic analysis, respectively. h^2 , c^2 , and e^2 are direct genetic, animal permanent environmental, and residual proportions of σ_p^2 ; r_g = animal additive genetic correlation between **NB** and other traits; r_e = correlation between animal permanent environmental effects on **NB** and residual effects on other traits; r_p = phenotypic correlation; σ_p^2 = phenotypic variance. Tests of significance were performed for r_g and r_e only.

Table 4.11. Estimates of co-variance components from trivariate analysis of ewe lamb fertility (**ELF**), age at first lambing (**AGE1**, mo), and number of lambings by 38 mo since birth (**LAMB3**)

Item ¹	ELF	AGE1	LAMB3
h² and Γ_g			
ELF	0.16	-0.91 **	0.93 **
AGE1		0.20	-0.63 †
LAMB3			0.31
Γ_e, Γ_p, and σ_p^2			
ELF	0.22	-0.96	0.70
AGE1	-0.97 **	16.48	-0.70
LAMB3	0.65 **	-0.92 **	1.21

¹ h^2 is direct genetic proportion of σ_p^2 ; Γ_g = animal additive genetic correlation; Γ_e = residual correlations; Γ_p = phenotypic correlation; σ_p^2 = phenotypic variance; h^2 and σ_p^2 are on diagonal, Γ_g and Γ_p are above the diagonal, and Γ_e is below diagonal. Tests of significance were performed for Γ_g and Γ_e only.

** $P < 0.01$; † $P < 0.10$.

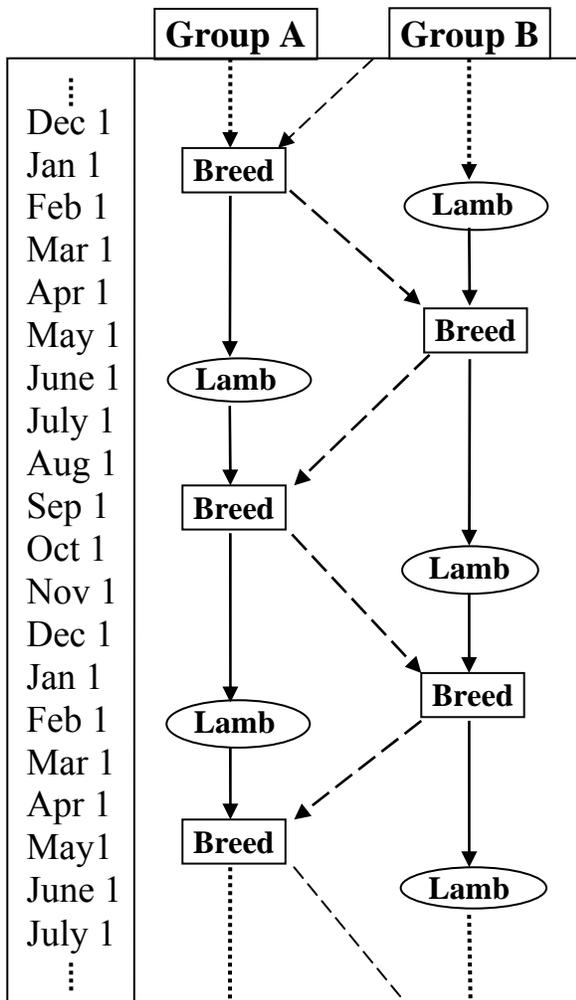


Figure 4.1. The three-lambings-in-two-years breeding plan practiced in the flock. The flock was divided into two groups A and B which were mated at different times during the year. The solid lines designate the preferred pattern of mating and lambing with three lambings every 2 yr. The dashed lines indicate movement of non-pregnant ewes from one group to another group for cleanup mating.

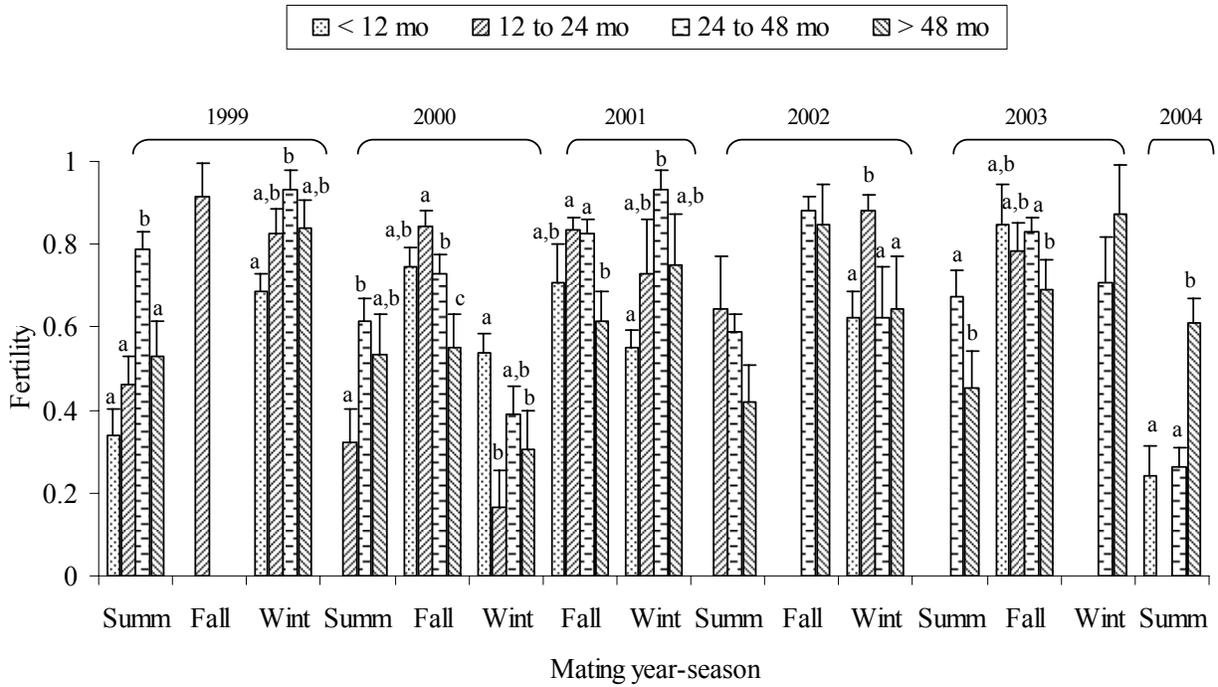


Figure 4.2. Ewe age category by mating year-season back-transformed least square means for fertility over all mating periods. Means with different letters (a, b, c) within each mating year-season are different ($P < 0.05$).

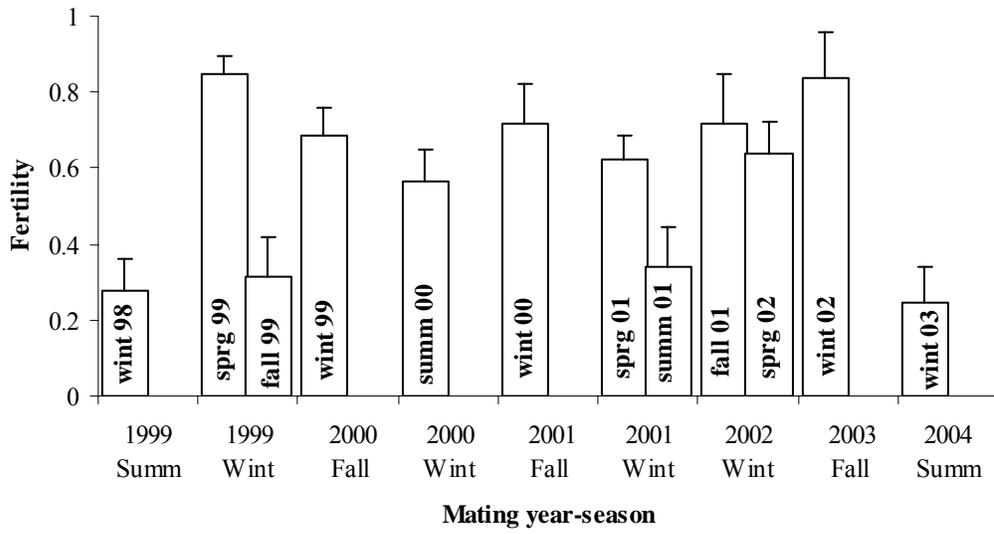


Figure 4.3. Back-transformed least square means for ewe lamb (first mating) fertility by birth year-season and mating year-season. Year-season within bar graph represents birth year-season.

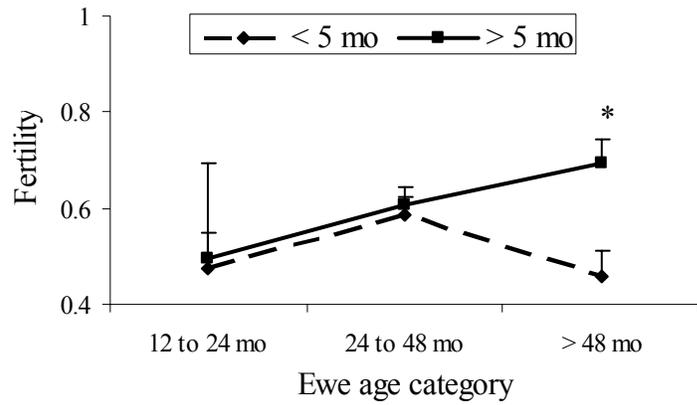


Figure 4.4. Ewe age category by time since lambing back-transformed least square means for summer post-lambing fertility. * indicates differences ($P < 0.01$) among means within each ewe age category.

CHAPTER 5

GENERAL DISCUSSION AND IMPLICATIONS

Ewe productivity or total weight of lamb weaned by a ewe is of significant economic importance for sheep producers, and genetic improvement in this trait is both highly desirable and possible. A multi-trait evaluation using data from number of lambs born, number of lambs weaned, and average weaning weight and the correlations among them and total weight of lamb weaned per ewe lambing has been implemented to generate EPDs for total weight of lamb weaned for Katahdin in the NSIP. This methodology can be extended to other breeds in NSIP such as Polypay, Targhee and Dorset, but would require more detailed data reporting than is presently in place. Selection for improvement in total weight of lamb weaned accounts for the interrelationships among its component traits and should result in an optimum biological balance between reproduction and growth and potentially maximize profitability within a given production environment. However, management decisions such as fostering and artificial rearing practices can have a big influence on the realized total weight of lamb weaned by a ewe and, since these practices generally vary among flocks, across-flock comparisons of genetic merit of candidates for selection should be made with caution. Informed decisions can be made when comparing animals across flocks but require consideration of the management systems followed in the different flocks. For example, a ram found to be superior for total weight weaned in a flock where ewes that rear triplets get extra help resulting in potentially improved lamb survival may not be superior for total weight weaned when used in a flock where ewes that rear triplets do not get any extra help and triplet survival is lower. Improving genetic connectedness between flocks by using practices such as sharing of rams will reduce, but not eliminate, the effect of these interactions.

The biggest contributor to improved total weight of lamb weaned is the number of lambs weaned by a ewe as evidenced by the high genetic correlations observed between the two traits. Selection for improved total weight of lamb weaned may thus result in increases in the proportions of triplet births. However, producers may not necessarily find this desirable because of the greater inputs that may be required for management of triplet lambs. Greater control over the improvement of individual component traits of total weight weaned can be achieved through the use of economic selection indices where genetic merit for each of the traits is weighted by their economic values such that an optimum balance among the traits which is more suitable to

the producers' needs can be attained. Furthermore, these economic selection indices can be tailored to the requirements of specific management systems.

Accelerated lambing systems can be utilized for improvement of the total weight of lamb weaned by a ewe per year by allowing ewes to breed more than once a year. Success in these programs will depend on the ability of ewes to breed out-of-season and to breed quickly after weaning their lambs. Identifying genetically superior ewes capable of breeding out-of-season requires exposure of ewes in unfavorable seasons to allow expression of variation in fertility among individuals or families, which may prove to be unprofitable in commercial production. Therefore, producers will try to avoid breeding during months of low fertility rather than challenge their animals at such times. However, a cleanup mating could be scheduled for open ewes at the very beginning of the following favorable breeding season which would minimize losses while still allowing measurement of variation in out-of-season fertility. Another alternative would be to have a co-operative nucleus breeding flock representing animals from participating flocks or co-operatives. Animals in this flock could be challenged with spring breeding in an annual lambing system and genetic improvement made in the nucleus flock could be transferred to the participating flocks by distributing sons and daughters of animals with high breeding values for out-of-season fertility. Mean genetic merit for fertility of different breeding groups in accelerated lambing systems can vary because of the different breeding histories followed by ewes over time. Genetic improvement through the nucleus breeding strategy would avoid these problems associated with genetic evaluation of fertility in accelerated lambing systems, while still leading to improvement in out-of-season fertility and accelerated lambing. Al-Shorepy and Notter (1997) have shown that selection for improved spring fertility is possible, and Notter (1981) suggested that selection for improvement in spring matings will also result in improved fertility in other seasons.

While fertility in out-of-season matings can be measured for improvement of performance in accelerated lambing systems, recording of the number of lambings by a specific age provides an attractive alternative. Although measured later in life, it is highly correlated to ewe lamb fertility and age at first lambing, which are measured relatively early in life and can be used for improvement in number of lambings by a specific age. The number of lambings by a specific age indirectly indicates superior performance for out-of-season fertility since ewes that achieve the maximum number of lambings by that period of time must not miss any mating

opportunities. The advantage of recording the number of lambings by a specific age trait is that it has the potential to be applied across diverse accelerated lambing protocols. In contrast, across flock evaluation of measures of fertility taken at a specific time or over a specific period of time can be complicated due to the different breeding histories of individual sheep within a specific mating group and due to the specific months in which breeding is practiced. For evaluating ability to accelerate in terms of number of lambings by a specific age, the different accelerated lambing protocols followed by different flocks would form a part of the contemporary group definition such that animals within a similar system are compared to each other for number of lambings by a certain period of time. For breeds practicing accelerated lambing, a multi-trait evaluation to predict breeding values for number of lambings by a specific age can be implemented using sequentially collected data on ewe lamb fertility, age at first lambing, and eventually actual data on number of lambings. The EPD for the total weight weaned trait and the acceleration traits could be combined to identify ewes that are superior for total weight of lamb weaned and the ability to accelerate which will lead to overall improvements in ewe productivity per year.

Diligent data recording is essential for success in genetic improvement programs. For improvement of ewe productivity in annual as well as accelerated lambing systems reliable information on lamb survival is essential for accurate calculation of number of lambs weaned and total weight of lamb weaned. Also, accurate ewe disposal and mating information (including mating sire and mating dates) are essential for accurate evaluation of fertility as they help in identifying ewe lambs and open ewes put into cleanup matings. This will help avoid penalizing ewes that leave the flock or die before lambing with an unfavorable mating record.