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The effect of birth rank and age of dam on the reproductive performance of ewe replacements managed under New Zealand pastoral conditions

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Abstract

Selecting replacement ewes that are born to ewe lambs is an uncommon practice in New Zealand; however, there is the opportunity to increase ewe efficiency and increase the rate of genetic gain if the practice is adopted. Lambs born to ewe lambs may be lighter until up to four years of age, compared with lambs born to mature ewes, however there are few unbiased comparisons of performance. The objective of this study was to compare the reproductive performance of replacements born to either mature ewes or ewe lambs.

A study with 115 singletons or twins born to mature ewes or ewe lambs, found that singletons born to mature ewes were heaviest, twins born to mature ewes and singletons born to ewe lambs were intermediate, and twins born to ewe lambs were lightest for their lifetime to eight years of age. There was no difference in lifetime lamb production among these four groups, and there was no difference in the efficiency among the ewe groups, however the power of that study may have been limited by relatively low numbers of animals.

A second study utilised 1082 mature ewes and 1026 ewe lambs, bred to the same rams at the same time, producing 2701 lambs, of which, 358 lambs were selected as replacements. Lambs born to ewe lambs were lighter than lambs of the same birth rank born to mature ewes from birth until weaning and had lower rates of survival at tagging and from tagging to weaning. The relationship between the probability of survival to weaning and birth weight was quadratic, and differed for each birth-rank-by-age-of-dam cohort. Lambs born to ewe lambs, and as triplets to mature ewes have lower rates of lamb survival and growth to weaning, so farmers need to prioritise time and resources to improve these.

In the third study investigating reproductive performance of replacements born to either ewe lambs or mature ewes, 135 twins born to mature ewes, 135 singletons born to ewe lambs, and 88 twins born to ewe lambs were bred (if heavier than 39 kg at breeding) as ewe lambs. Of the ewe lambs that were heavy enough to be bred, there was no difference in the number or weight of lambs produced at weaning from the three groups, but twins born to ewe lambs were less likely to reach breeding weight targets. During their second breeding (at approximately 18 months), all ewes were bred, and there were no differences in the number or weight of lambs produced at weaning. This indicates that the offspring of ewe lambs could be selected as replacements, but that farmers need to consider selecting based on weight at weaning if they intend to breed the ewe lambs at eight months of age. Further work, including an economic analysis, and continued investigation into the lifetime production and efficiency of ewes born to ewe lambs is needed.

Genomic technologies are currently being used by scientists to increase the accuracy of selection of replacement animals for traits that are difficult to measure in the adolescent at the time of selection. Reproductive performance as a ewe lamb has an impact on the lifetime production of a ewe, and live weight at the time of breeding can heavily influence the likelihood of the ewe lamb becoming pregnant during her first breeding. Using ewe lambs from the second and third studies, and additional ewe lambs, five gene regions were found to be associated with live weight at eight months of age in ewe lambs, and two gene regions were found to be associated with the occurrence of pregnancy during their first breeding at eight months of age. Further investigation into these, and other, gene regions associated with reproductive traits in ewe lambs could allow the use of marker assisted selection to identify genetically superior animals.

In conclusion, farmers should prioritise their time and resources to improve lamb survival and lamb growth for lambs born as triplets to mature ewes, or as any birth rank to ewe lambs. Lambs born to ewe lambs could be selected as replacement ewes, if they are heavy

enough to be bred themselves at eight months of age. Lambs born to ewe lambs may be lighter than lambs born to mature ewes for their entire lifetimes,but have similar reproductive performance. There is genomic control of traits such as live weight and pregnancy occurrence in ewe lambs that needs further investigation, before genomics can be considered a practical tool for farmers when selecting their replacement ewes.

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List of abbreviations and notation

Selection intensity
 Generation interval
 Accuracy of selection

 σ_{g} Genetic standard deviation

ΔG Rate of genetic gainLH Luteinising hormone

FSH Follicle stimulating hormone

E₂ Oestradiol-17βP₄ Progesterone

BCS Body condition score

LWT Live weightBWT Birth weightWWT Weaning weight

ADG Average daily liveweight gain

h² Heritability

SNP Single nucleotide polymorphism

EBV Estimated breeding value

M1 Singletons born to mature ewes
 M2 Twins born to mature ewes
 M3 Triplets born to mature ewes
 L1 Singletons born to ewe lambs
 L2 Twins born to ewe lambs

NLB Number of lambs born per ewe presented for breedingNLW Number of lambs weaned per ewe presented for breeding

PD Pregnancy detection

MBS Maternal behaviour score IGF-1 Insulin-like growth factor 1

FDR False discovery rate

GO Gene ontology

MBP Mega base pairs (1,000,000 bp)
GWAS Genome-wide association study
gEBV Genomic estimated breeding value
Dn The nth day of the experiment

Ln The *nth* day of lactation, from the average date of lambing

General Introduction

Breeding ewe lambs can increase profitability of farms, compared with not breeding ewe lambs. This is achieved by utilising an animal that has the potential to be bred, and producing more lambs per year and per lifetime (Kenyon et al., 2014a). Lambs produced by ewe lambs are traditionally born one month later, to different sires (Edwards and Juengel, 2017), and are lighter at birth, to weaning, and up to four years of age, given the same birth rank, than lambs born to mature ewes (Quirke and Hanrahan, 1983; Annett and Carson, 2006; Kenyon, 2008; Loureiro et al., 2012; Kenyon and Blair, 2014; Kenyon et al., 2014a; Pain et al., 2015; Loureiro et al., 2016). Ewe live weight is well documented to have a large influence over reproductive performance (Corner et al., 2006a; Kenyon et al., 2010; Corner-Thomas et al., 2014; Corner-Thomas et al., 2015a; Corner-Thomas et al., 2015b; Piaggio et al., 2015; Edwards and Juengel, 2017) and, therefore, lambs born to ewe lambs are not commonly selected as replacements. The reproductive performance of ewes born to ewe lambs is not well studied, compared with traditional replacements that are born to mature ewes. Selecting replacements born to ewe lambs could utilise a pool of animals that are already present, and potentially increase the rate of genetic gain on farm. Therefore, there is a need to investigate the live weight and reproductive performance of replacements born to ewe lambs. Further genomic analysis of the attainment of puberty in adolescent ewe lambs could aid in increasing reproductive performance of ewe lambs through selection based on their genotype.

The research in this thesis examines the reproductive performance of ewes born to ewe lambs compared with ewes born to mature ewes. A population of singletons or twins born to mature ewes or ewe lambs were studied for eight years, and live weight, reproductive output, reproductive efficiency, and ewe longevity were examined (Chapter 2). In the second study, mature ewes and ewe lambs were bred at the same time, and to the same

rams, allowing comparison of reproductive performance of the two groups (Chapter 3). Lambs born to these mature ewes and ewe lambs were selected as replacements and bred for the first time at eight months of age (Chapter 4), and again at 20 months of age (Chapter 5). Genotypes from the ewe lambs in Chapter 3 and Chapter 4, were analysed to search for genetic markers of live weight and fertility at first breeding (Chapter 6). The overall aim was to provide new information to industry to allow for informed decisions to be made when deciding whether to select progeny from ewe lambs as replacement ewes. It was hypothesised that age of dam and birth rank would not affect lamb production efficiency (weight of lamb weaned per weight of ewe bred).

Foreword to thesis chapters

Some of the chapters in this thesis have been published in refereed scientific journals, resulting in overlap in the information presented in the chapter introductions, to allow them to appear standalone as published papers. Additionally, some formatting has been made post-publication, to ensure consistency among the chapters. These changes are considered typographical and make no change to any outcomes of the paper. One chapter was published with Vancouver style referencing, so has been changed to a Harvard-based style.

Chapter 1

Review of literature

1.1 Preamble

Increasing the efficiency of production on New Zealand sheep farms is important to keep up with ever-changing markets. By increasing the number, and weight of lambs produced, without increasing ewe numbers, farms can be more efficient on a per hectare basis. For this reason, there has been a significant amount of research aimed at optimising production from breeding ewe lambs at eight-months of age, instead of the traditional 19-20 months of age. This has led to increased farmer uptake of ewe lamb breeding to increase production on farm. Accordingly, this literature review focuses on the current performance of ewe lambs that are bred at eight-months of age, in comparison with performance of mature ewes. Further, factors that improve, or decrease the performance of ewe lambs are reviewed, with emphasis on the attainment of puberty in the ewe lamb. Lastly, the potential performance of replacement ewe lambs that are born to ewe lambs is reviewed. This review is specifically concentrating on New Zealand sheep breeds, however, where appropriate, other breeds not common in New Zealand, or other species and countries are referenced.

1.2 The New Zealand sheep industry

The New Zealand sheep industry utilises an outdoor pastoral-based grazing system (Ferguson et al., 2014; Morris and Hickson, 2016). Most sheep farms are integrated with beef cattle production, on extensive hill country farms (Table 1.1). Sheep and beef cattle farms are categorised into eight farm classes, based on location, topography, stocking rates, and the main products sold from the farm (Beef + Lamb New Zealand, 2018a). Romney (47%), Perendale (15%), and Coopworth (11%) breeds make up the majority of straight-bred sheep on New Zealand farms (Corner-Thomas et al., 2013). Although, there is an increase in composite breeds, with farmers incorporating Finnish Landrace, East Friesian, and Texel genetics into the Romney-based flocks (Corner-Thomas et al., 2013; Morris and Kenyon, 2014). These straight-bred and composite types are considered dual-purpose, producing meat and coarse wool (Ferguson et al., 2014). Fine wool breeds make up only 8% of the national ewe flock (Beef + Lamb New Zealand, 2018a). The main income from sheep on New Zealand farms is meat, with less than 12% of income, on average, coming from wool (Table 1.1; Beef + Lamb New Zealand, 2018a).

More than 90% of New Zealand's mutton/lamb is exported, making up 47% of world sheep meat exports (Morris, 2013; Morris and Kenyon, 2014) of which almost 50% goes to the EU, and approximately 25% into China (Ferguson et al., 2014; Morris and Kenyon, 2014). Increasing the production from the same number of ewes, and more importantly the efficiency of production, will ensure New Zealand remains competitive in the market.

Table 1.1: Selected provisional commercial sheep farm class production data for 2016-2017 (adapted from Beef + Lamb New Zealand (2018a)).

		Beef and Lamb NZ Farm Classes ¹						
	1	2	3	4	5	6	7	8
No. farms	215	810	1065	3640	1275	2505	1290	495
Area per farm (ha)	7532	1538	766	409	278	436	222	449
Total sheep (000)	8643	4789	3967	2035	1458	2491	2259	2927
Average flock size	40,200	5,912	3,725	559	1,144	994	1,751	5,913
Ewe lambing %	101.2	123.3	121.0	127.8	129.5	132.8	141.0	159.1
Ewe lamb lambs (% total lambs)	1.5	1.8	3.1	5.9	5.6	4.9	3.6	4.2
Income from sheep meat (%)	37.8	53.7	49.8	40.6	32.2	52.6	66.3	10.1
Income from wool (%)	33.8	15.1	9.7	7.1	4.7	8.3	9.7	1.5

¹Farm class types: 1=South Island high country; 2=South Island hill country; 3=North Island hard hill country; 4=North Island hill country; 5=North Island intensive finishing farms; 6=South Island intensive finishing-breeding farms; 7=South Island intensive finishing farms; 8=South Island mixed cropping and finishing farms.

Ewe numbers peaked at 60+ million in the early 1980's, but have declined to 27.39 million currently (Beef + Lamb New Zealand, 2019a). However, total industry carcass production has remained almost the same as the early 1980's even with far fewer ewes (Morris, 2013; Ferguson et al., 2014; Morris and Hickson, 2016). This is due to an increase of 36 percentage points of the lambs weaned per ewe joined (Statistics New Zealand, 2016), and an increase of 4 kg in carcass weight per lamb (Morris, 2013; Morris and Kenyon, 2014; Morris and Hickson, 2016). The increase in lamb carcass weight is predominantly driven by an increase of 50 g/d average daily liveweight gain of lambs, without changes in stocking rate or slaughter pattern (Morris, 2013; Ferguson et al., 2014; Morris and Hickson, 2016).

1.2.1 Measuring performance of ewes

The productive worth of a ewe is related to the amount of lamb produced to slaughter or sale, and her mature body weight for maintenance and growth requirements (Young et

al., 2011). A ewe producing more, and heavier lambs, that are saleable earlier is more profitable. A ewe that is lighter in live weight, but still producing the same amount of lamb is also more productive as she has a lower maintenance cost, per kilogram of lamb produced (Nicol and Brookes, 2007). A lighter ewe that produces the same amount of lamb may also be more efficient in reducing greenhouse gas production (Hegarty et al., 2010). A farmer is then able to stock more animals per hectare, increasing production further (Young et al., 2011).

To measure lifetime reproductive performance of ewes, many measurements need to be recorded. Commonly, lifetime performance is measured in terms of the number of lambs born and weaned, lamb survival, weaning weight of lambs, ewe live weight throughout her lifetime, and ewe longevity (Gunn, 1972; Hohenboken and Clarke, 1981; Abdulkhaliq et al., 1989; Lee et al., 2009). Ewe efficiency can be calculated with ewe live weight and numbers/weight of lambs produced (Abdulkhaliq et al., 1989). Productive measures are commonly converted into a form of productivity (number or weight of lambs weaned per number of ewes present at breeding), or efficiency (number or weight of lambs weaned per kg of ewe live weight; Coop, 1962; Notter and McClaugherty, 1991; Snowder and Fogarty, 2009). The live weight measurement of ewe can be the mean for the entire year, at a certain time point, such as pre-breeding, or transformed as a nutritional requirement (Snowder and Fogarty, 2009; Asmad et al., 2014). A measure of productivity or efficiency can inform the farmer about the production per animal, or per hectare (Snowder and Fogarty, 2009).

1.2.2 Increasing the performance of the sheep industry

With the current lambing percentage (number of lambs weaned, per ewe bred) being 127.1%, for mature ewes and ewe lambs combined, the possibilities of increasing production from the sheep industry has greater prospect in the ewe lamb flock (Beef +

Lamb New Zealand, 2019b). When selecting for increased lambing percentage, farmers need to be cautious that they are increasing the number of twin-bearing ewes and decreasing the number of barren ewes, rather than increasing the number of triplet- or greater-bearing ewes. Lambs born as part of a triplet or greater multiple litter are likely to have lower rates of survival than lambs born as singletons or twins (Schreurs et al., 2010a; Young et al., 2010). Breeding ewe lambs (eight months old at breeding) is a management technique to increase productivity of the ewe flock (Young et al., 2010; Kenyon et al., 2014a). This better utilises those ewe lambs, that otherwise would only produce wool, increasing lamb production on farm and per ewe in her lifetime, without increasing the number of ewes on the farm. It may even be a more efficient system for a reduction in greenhouse gas production per lamb slaughtered (Hegarty et al., 2010).

1.3 Current performance of ewe lambs bred at eight-months of age

On the majority of sheep and beef farms, mature ewes are bred during the autumn (March-May), to coincide lamb birth with pasture growth increases in spring, and to avoid severe weather in winter, which may impact lamb survival (Ferguson et al., 2014). Traditionally, in New Zealand, maiden (nulliparous) ewes are bred first at around 18-20 months of age, to lamb as two-year-olds (Ferguson et al., 2014). Currently, approximately 30-43% (Table 1.2) of maiden ewes in New Zealand are presented for breeding first at around eight months of age (ewe lambs, also called hoggets; Ferguson et al., 2014; Morris and Hickson, 2016; Beef + Lamb New Zealand, 2019b). The lamb crop from ewe lambs only makes up 5.3% of the total lamb crop (Table 1.2), while ewe lambs make up 23.0% of the entire New Zealand ewe flock (Beef + Lamb New Zealand, 2018a). The mature ewe weaning rate is 136% (Beef + Lamb New Zealand, 2019b), while the ewe lamb weaning rate is only 60-70% of those bred (Ferguson et al., 2014). While there are some limitations (see later section) to breeding ewe lambs at eight months of age, there are also many advantages. These include additional lambs produced per year on farm and increased net profits (Kenyon et al., 2014a; Edwards and Juengel, 2017). It can be assumed that if more farmers in New Zealand successfully bred their ewe lambs, there would be an increase in the total number of lambs weaned per year available for sale or selection as replacements by farmers.

Table 1.2: Number of mature ewes and ewe lambs, number of lambs docked, and percentage of lambs born to ewe lambs in New Zealand in 2008, 2017, and 2018.

-	2008	2017	2018
Total mature ewes to ram (000)	23,796	18,126	17,541
Total ewe lambs (000)	6,436	6,262	6,283
Total ewe lambs to ram (000)	1,470	1,981	2,018
Total lambs docked (000)	31,020	24,127	24,707
Total lambs docked from mature ewes (000)	29,927	22,958	23,387
Total lambs docked from ewe lambs (000)	1,093	1,170	1,320
Lambs born to ewe lambs (% of total lambs)	3.5	4.8	5.3

Source: (Beef + Lamb New Zealand, 2019a; Beef + Lamb New Zealand, 2019b).

In a survey by Kenyon et al. (2004a) farmers ranked their reasons for not breeding ewe lambs from most to least important. This indicated that the biggest deterrent for breeding ewe lambs was the perceived negative effects of breeding at eight months of age on the subsequent two-year-old performance of those ewes. This was followed by insufficient winter feed, increases in workload, the inability to get ewe lambs to breeding weight, poorer lamb performance compared with those born to mature ewes, returns not justifying costs, wool growth being compromised, lower reproductive performance from ewe lambs, increased birthing difficulty of ewe lambs, lack of maternal experience of ewe lambs, and finally extra teaser/ram requirements (Kenyon et al., 2004a).

1.3.1 Advantages of breeding ewes first at eight-months of age

There are many advantages for farmers to breed their ewe lambs at eight months of age.

The advantages of breeding ewe lambs, compared with not breeding them, include:

- Additional lambs produced per year (McCall and Hight, 1981; McMillan and McDonald, 1983; Corner et al., 2013a; Corner et al., 2013b; Corner-Thomas et al., 2014)
- Additional lambs produced per ewe over her entire lifetime (Spencer et al., 1942;
 Baker et al., 1981; McCall and Hight, 1981; McMillan and McDonald, 1983;
 Kenyon et al., 2011; Corner et al., 2013a; Corner et al., 2013b; Corner-Thomas et al., 2014)
- Better utilisation of spring pasture flush (Kenyon et al., 2004b)
- Increased flock reproductive rates (number of lambs weaned per ewe wintered; McMillan and McDonald, 1983)
- Increased net profits (Kenyon et al., 2004b)
- Possible earlier identification of potential reproductive performance (Baker et al., 1978; Moore et al., 1978; Meyer, 1981)
- Increased reproductive performance as a two-year-old (McMillan and McDonald, 1983)
- Increased selection pressure/intensity for replacements, as more ewe lambs are available for selection (Baker et al., 1978; Newton et al., 2017)
- Decreased generation intervals (Baker et al., 1978; Newton et al., 2017)
- Increased rates of genetic gain (Baker et al., 1978; Newton et al., 2017)
- Utilising animals that have the potential to breed (McCall and Hight, 1981; Moore et al., 1983)
- Decreasing greenhouse gas emissions per unit of product produced (Hegarty et al., 2010; Kenyon et al., 2014a; Morris and Hickson, 2016)
- Increased lifetime reproductive performance (Spencer et al., 1942; McCall and Hight, 1981; McMillan and McDonald, 1983; Moore et al., 1983)

If there is no decrease in lamb production during the next year (as a two-year-old), the additional lamb(s) produced as a ewe lamb is worth much more than any loss of wool clip (Kenyon, 2008; Kenyon and Blair, 2014).

1.3.1.1 Additional benefits to breeding ewe lambs

There are additional benefits to breeding ewe lambs, other than increasing the number of lambs born per year and per ewe. Farmers can identify ewe lambs that failed to conceive, even though they were a sufficient weight to attain puberty, indicating potential future fertility issues (Moore et al., 1983). If they are bred as ewe lambs, but failed to conceive, they were likely to wean fewer lambs per ewe presented for breeding as a two-year-old (Kenyon et al., 2008a; Kenyon et al., 2014a).

1.3.1.2 Selection of ewe lambs as replacements

Selecting replacements is an important decision for farmers, as the ewe lambs that are selected will influence the future productivity of the flock. Traditionally, the selection of replacement ewe lambs on commercial farms occurs at their weaning, usually based on their live weight at weaning. Heavier lambs are selected because they are more likely to attain weight targets for their first breeding, at either eight months or 20 months of age (McHugh et al., 2020). Corner-Thomas et al. (2015c) reported that only 43.9% of farmers weighed their replacement lambs, indicating that most farmers select their animals based on physical appearance or other traits. Farmers that differentiate singleton-born lambs from multiples during the lambing period are more able to select heavy twin-born lambs as replacements, increasing the incidence of ewe lambs attaining puberty prior to breeding, and increasing ovulation rate of the ewe lambs (Safari et al., 2005). Twin-born lambs are smaller at weaning, and, therefore, farmers should have a lower weight threshold to select them, compared with their singleton peers (McHugh et al., 2020). Lambs born to ewe lambs are born a month later than lambs born to mature ewes and are lighter than lambs born to mature ewes at weaning, and are, therefore, not commonly selected as replacements.

Ram breeders mostly base selection of their ewe lamb replacements on estimated breeding values (EBV), maternal worth indexes and weaning weight, while commercial farmers tend to base selection on weaning weight and, if available, birth rank. Corner-Thomas et al. (2015c) reported that 25.2% of farmers used EBVs as a management tool on their farm. Some commercial farms use them to select rams from stud breeders, based on their genetic merit, indicating fewer than 25.2% of farmers select their ewe lamb replacements based on genetic merit.

1.3.1.3 Increasing rate of genetic gain by selecting replacements born to ewe lambs

Female progeny born to ewe lambs are not commonly considered for selection as replacements on commercial farms (Kenyon et al., 2004b). If progeny born to ewe lambs were selected as replacements, the rate of genetic gain could be increased, due to greater selection intensity, and reduced generation interval (Table 1.3). By selecting replacements from lambs born to ewe lambs, either with, or without breeding older ewes to a terminal sire, greater rates of genetic gain will be seen, compared with not selecting replacements from lambs born to ewe lambs. If the same number of replacements per year are selected, the proportion that are selected is reduced by having a greater total number of lambs to select from, thereby increasing the rate of genetic gain (Rendell and Robertson, 1950). By selecting lambs that are born to ewe lambs there is a decrease in the average age of the parents, with more younger dams contributing to the next generation. This reduces the generation interval, with the superior genetics passed on to the next generation sooner, increasing the rate of genetic gain (Rendell and Robertson, 1950).

Table 1.3: Example calculations for the female half of genetic gain (using $\Delta G = 1 \ r_{TI} \ \sigma_g/L$), for selecting replacement lambs born to mature ewes only, born to mature ewes and ewe lambs, and born to mature ewes and ewe lambs when five-year-old ewes are bred to a terminal sire. All scenarios assume a weaning rate of 130% from mature ewes and 80% for ewe lambs if bred, 50% of lambs weaned are female, genetic standard deviation (σ_g) of the trait in question is 2 kg, and the accuracy of selection (r_{TI}) is 50%.

Scenario	1000 mature ewes, 2-5 years old, ewe lambs not bred	1000 mature ewes, 2-5 years old, and 320 ewe lambs bred	1000 mature ewes, 2-4 years old, and 320 ewe lambs bred. Five-year-old ewes bred to terminal sire
Age structure	2-year-old n=300	1-year-old n=320	1-year-old n=320
of dams ¹	3-year-old n=270	2-year-old n=300	2-year-old n=300
	4-year-old n=240	3-year-old n=270	3-year-old n=270
	5-year-old n=200	4-year-old n=240 5-year-old n=200	4-year-old n=240
Ewe Lambs	(1000 ewes x	(1000 ewes x 130%	(800 ewes x 130% +
available for	130%)/2 = 650	+ 320 ewe lambs x	320 ewe lambs x
selection	lambs	80%)/2 = 778 lambs	80%)/2 = 648 lambs
Proportion of lambs selected	320 / 650 = 49.2%	320 / 778 = 41.1%	320 / 648 = 49.4%
Accuracy of selection $(r_{TI})^3$	0.5	0.5	0.5
Genetic standard	2 kg	2 kg	2 kg
deviation $(\sigma_g)^3$			
Selection	0.814	0.948	0.814
intensity (ī)			
Average age of the dams (L)	3.37 years	2.79 years	2.38 years
Genetic gain (ΔG)	0.24 kg/year	0.34 kg/year	0.34 kg/year

¹Assuming 30-40 ewes culled/died per year after two years old, and 20 culled/died after one year

There is a trade-off by selecting lambs that are born to ewe lambs, in that their dams will have fewer records for a particular trait, and therefore accuracy of selection may be decreased. This depends on the trait that is being measured, and the number of other familial records that are used, to determine the EBV of the ewe lamb for the trait. Older dams have more records, and, therefore, their lambs will have increased accuracy of

selection (Rendell and Robertson, 1950). If farmers are not using EBVs for selection of their replacements, there will be no impact on the accuracy of selection.

1.3.2 Limitations of breeding ewes first at eight-months of age

While there are many advantages to breeding ewe lambs at eight months of age, there are additional limitations that farmers need to consider when deciding if they want to breed their ewe lambs. Potential limitations to breeding ewe lambs, compared with breeding mature ewes, include:

- Lower reproductive performance (Baker et al., 1978; Kenyon et al., 2004b; Mulvaney et al., 2013)
- Shorter and weaker oestrus (Allison et al., 1975; Edey et al., 1978)
- Less likely to seek out ram (Edey et al., 1978; Corner et al., 2013a; Edwards et al., 2016)
- Lower ovulation rates (Beck et al., 1996; Mulvaney et al., 2013; Edwards et al., 2016)
- Lower ovum quality (McMillan and McDonald, 1985; Edwards et al., 2016)
- Lower conception rates (McMillan and McDonald, 1985; Corner et al., 2013a; Mulvaney et al., 2013; Edwards et al., 2016)
- Lower embryo survival (Beck et al., 1996; Edwards et al., 2016)
- Fewer lambs born (Corner et al., 2013a; Mulvaney et al., 2013; Gonzalez-Garcia and Hazard, 2016)
- Lighter progeny at birth (McCall and Hight, 1981; Quirke and Hanrahan, 1983;
 Kenyon et al., 2004b; Annett and Carson, 2006; Loureiro et al., 2012; Corner et al., 2013b; Pain et al., 2015; Gonzalez-Garcia and Hazard, 2016)
- Lower lamb survival (McMillan, 1983; McMillan and McDonald, 1983; Young et al., 2010; Corner et al., 2013b; Corner-Thomas et al., 2014)
- Lower progeny growth rates to weaning (Corner et al., 2013b)
- Lighter lambs at weaning (McCall and Hight, 1981; McMillan and McDonald, 1983; Loureiro et al., 2012; Corner et al., 2013b; Pain et al., 2015)

There are also limitations to breeding ewe lambs, compared with not breeding them, such as:

- Increased animal husbandry costs (Kenyon et al., 2004b)
- Decreased wool clip volumes (Spencer et al., 1942; Baker et al., 1978; Baker et al., 1981; McMillan and McDonald, 1983; Moore et al., 1983)
- Lower live weight at two-year-old breeding (Baker et al., 1981; McMillan and McDonald, 1983; Kenyon et al., 2008a; Kenyon et al., 2011)
- Decreased two-year-old lambing performance (Kenyon et al., 2008a)
- Additional feed to attain puberty before breeding (Kenyon et al., 2004b)
- Additional rams are required (Kenyon et al., 2004b)
- Additional feed requirements for pregnant ewe lambs and lambs born (Kenyon et al., 2004b)
- Additional labour requirements during lambing time (Kenyon et al., 2004b; Morel et al., 2010)

Given the above, farmers need to decide if the potential advantages outweigh the limitations on a flock-by-flock basis to determine if breeding their ewe lambs at eight months of age is profitable. Section 1.3.3 expands on the above points in more detail, comparing the reproductive performance of mature ewes and ewe lambs.

1.3.3 Comparative reproductive performance of mature ewes and ewe lambs

There are many studies comparing the relative reproductive performance of ewe lambs and mature ewes. Ewe lambs are normally bred one month after mature ewes, to different rams, with the purpose to slaughter all progeny (Edwards and Juengel, 2017). Therefore, time of lambing, and sire-breed often confound differences in lamb production between dam ages. Few studies have compared the reproductive performance of mature ewes and ewe lambs bred at the same time, and to the same rams (Kenyon and Blair, 2014).

Mature ewes have a higher reproductive performance than ewe lambs, (Table 1.4; Kenyon et al., 2014a; Edwards and Juengel, 2017). They have higher ovulation rates, conception

rates, and embryo survival than ewe lambs, resulting in more ewes pregnant and bearing multiples than ewe lambs (Beck et al., 1996; Sargison, 1997; Corner et al., 2013a; Mulvaney et al., 2013; Kenyon et al., 2014a; Edwards et al., 2016; Edwards and Juengel, 2017). In general, ewes that have higher ovulation rates have higher rates of embryonic loss, this is especially seen in ewe lambs (Sargison, 1997; Edwards et al., 2016). It is possible that poor ovum quality may contribute to this poor reproductive performance from ewe lambs (McMillan and McDonald, 1985; Edwards et al., 2016; Edwards and Juengel, 2017).

In early ewe lamb breeding studies in New Zealand, it was reported that 30% of ewe lambs presented for breeding actually lambed (Baker et al., 1981). These ewe lambs were giving birth to 1.09 lambs per ewe lambing, indicating that conception and ovulation rates were low in these animals. More recently, conception rates appear to be 70-85% (Corner et al., 2013a; Mulvaney et al., 2013; Edwards et al., 2016). Gestation length appears to be shorter, and/or more variable in length for ewe lambs compared with mature ewes (Baker et al., 1981; Quirke and Hanrahan, 1983).

Table 1.4: Comparative ovulation rate, conception rate, number of lambs born, and number of lambs weaned from different age classes of ewes.

Experiment	Ovulation rate	Conception	Number of lambs	Number of lambs	Comparison
_		rate	born per ewe bred	weaned per ewe bred	_
Baker et al. (1978)				0.95 vs. 1.10	Lambs born to two-year-old ewes that either were not joined as ewe lambs vs. those that lambed as ewe lambs
Baker et al. (1981)	1.43 vs. 1.37 vs. 1.45	0.91 vs. 0.90 vs. 0.91		1.15 vs. 1.05 vs. 1.05	Ewes that were joined and lambed as ewe lambs vs. ewes that were joined as ewe lambs but did not lamb vs. ewes that were not joined as ewe lambs
Beck et al. (1996) Annett and Carson (2006)	1.07 vs. 1.25	0.67 vs. 0.85	0.82-1.14 vs. 1.77- 2.06	0.49-0.66 vs. 1.38-1.62	Ewe lambs vs. mature ewes Ewe lambs vs. mature ewes
Mulvaney (2011) Corner et al. (2013a)	1.14 vs. 1.82	0.47 vs. 0.97 0.73 vs. 0.98	0.66 vs. 1.59	0.52 vs. 1.42	Ewe lambs vs. mature ewes Ewe lambs vs. mature ewes
Edwards et al. (2016)	1.54 vs. 2.00		0.81 vs. 1.48	0.67 vs. 1.20	Ewes lambing first as ewe lambs vs. ewes lambing first as 2-year-olds

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In summary, ewe lambs have poorer reproductive performance compared with mature ewes, including ovulation rates, conception rates, and number of lambs born and weaned. By breeding ewe lambs, however, farmers can increase the production on farm, compared with not breeding their ewe lambs. The comparative performance of ewe lambs and mature ewes is not widely documented, as they are often bred at different times, to different sires, confounding comparisons.

1.3.3.1 Comparative management of mature ewes and ewe lambs with rams

The mature ewe will seek out the ram and respond favourably for mating, by standing to be mounted, and seeking out the ram when they are on heat (Ungerfeld, 2016). As ewe lambs are adolescents, they are inexperienced with rams, are less likely to respond favourably to the ram and have weaker oestrus activity (Edey et al., 1978; Dýrmundsson, 1981). They are less likely to seek out the ram during oestrus, and less likely to stand correctly to be mounted by the ram (Edey et al., 1978; Dýrmundsson, 1981). This can result in decreased conception rates in ewe lambs (Ungerfeld, 2016). Ewe lambs have a shorter oestrus period during their oestrous cycles compared with mature ewes (Edey et al., 1978; Kenyon et al., 2014a). The breeding season appears to be shorter for ewe lambs than mature ewes, possibly due to the start of their breeding season depending on puberty attainment, while it ceases at the same time as with the mature ewe due to photoperiod signalling (Ch'ang and Raeside, 1957). Therefore, a higher ratio of rams to the number of females is required for ewe lambs. A ratio of one ram per 100-200 ewes is sufficient when breeding mature ewes but for ewe lambs, farmers should use a ratio of one ram per 30-50 ewe lambs to achieve high conception rates (Allison et al., 1975; Kenyon et al., 2004b). Mature rams should be used when breeding with ewe lambs, as ram lambs are also inexperienced, and therefore low conception rates are achieved if ewe lambs are bred with ram lambs (Kenyon et al., 2007a; Edwards and Juengel, 2017).

Combined, this shows that farmers need greater resources for breeding their ewe lambs, with more rams required to achieve successful breeding results from ewe lambs. Farmers also need to consider using vasectomised rams for 17 days prior to breeding to increase the conception rates, especially during the first cycle of breeding, in ewe lambs.

1.3.3.2 Comparative two-year-old performance of ewes that either were or were not bred as ewe lambs

Edwards et al. (2015) reported that ovulation rates in two-year-old ewes were 20% higher for those that attained puberty as a ewe lamb, resulting in a greater number of lambs born than in two-year-olds that did not attain puberty as ewe lambs. Meanwhile Moore et al. (1978) reported that ewe lambs that displayed oestrus produced 0.15 more lambs as two-year-olds than ewe lambs that did not display oestrus. This indicates that greater fertility as a ewe lamb is associated with more lambs produced in their first breeding as a two-year-old.

There are conflicting results about whether lambing as a ewe lamb results in a decrease, increase, or no change in lamb production as a two-year-old. Baker et al. (1981) and McMillan and McDonald (1983) reported that lambing as a ewe lamb resulted in 0.10-0.13 more lambs weaned from two-year-olds, than two-year-olds that didn't lamb as ewe lambs. Further, Fogarty et al. (2007) reported that ewes that lambed as ewe lambs produced 12% more lambs per year in their second and third lambings than those that did not wean a lamb as a ewe lamb. Meanwhile, Kenyon et al. (2008a) reported that two-year-old ewes that did lamb as ewe lambs had fewer multiples than two-year-olds that did not lamb as ewe lambs. Kenyon et al. (2011) reported that there were no differences over the subsequent lifetime of ewes that either lambed or did not lamb as ewe lambs. Live weight and body condition score (BCS; 1-5 score; Jeffries, 1961) are known to affect reproductive performance (Kenyon et al., 2014a), therefore the residual effects on live

weight from lambing as a ewe lamb may impact two-year-old performance, if they are still present at the start of breeding. Kenyon et al. (2011) reported no difference in live weight or body condition score at two-year-old breeding for those that lambed as ewe lambs compared with those that did not. Meanwhile Kenyon et al. (2008a) reported that ewes that had lambed as ewe lambs were 6-7 kg lighter, and were 0.5 units of body condition score lesser at their second breeding than those that didn't, likely explaining their decreased two-year-old reproductive performance, compared with those that had not lambed. Interestingly, McMillan and McDonald (1983) also noted that the ewes that lambed as ewe lambs were 6 kg lighter than those that didn't, but didn't report if there were differences in body condition score between the groups. Differences in the live weight and body condition score combined may affect the breeding performance of two-year-old ewes that did or did not lamb as a ewe lamb. If the ewe lambs that did lamb have lower BCS at the time of weaning of their first lambs, farmers need to prioritise increasing their BCS before their next breeding.

Providing the live weight of the ewe was not compromised, lambing as a ewe lamb had no negative effect on the number of lambs produced in the next four years of their life (Morel et al., 2010). At three years of age, ewes that were bred and lambed as ewe lambs had higher rates of multiple births than ewes that were presented for breeding but did not lamb as ewe lambs (Kenyon et al., 2011). This indicates that ewes that had the opportunity to lamb, but failed, have other reasons for decreased fertility, and can be identified when they are ewe lambs. Ewes that were not presented for breeding were not different to either group, and there were no differences in the number of ewes pregnant among the three groups (Kenyon et al., 2011). The was no difference in the number of multiple-bearing ewes at four or five years of age (Kenyon et al., 2011).

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Ewes that lambed as ewe lambs had greater lifetime lamb production than ewes that did not lamb as ewe lambs, driven predominantly by adding an extra lambing year. The increase in lambs produced from breeding ewe lambs is greater than any potential decrease in production from two-year-old ewes as a consequence of lambing as ewe lambs. If farmers manage the ewe lambs so that they are still growing during the pregnancy and lactation periods, and that their body condition is not poor at the start of the next breeding period, there are minimal negative effects on their reproductive performance as a two-year-old, compared with ewes that were not given the opportunity to lamb as ewe lambs.

1.4 Potential options to improve ewe lamb reproductive performance

1.4.1 Attainment of puberty in the ewe lamb

In order to be successfully bred at eight months of age, the ewe lamb must attain puberty, either prior to or during the breeding period. One of the biggest limitation farmers faced when breeding their ewe lambs was failure to attain puberty prior to the breeding period (Kenyon et al., 2014a; Edwards and Juengel, 2017). Puberty is the event where an adolescent female becomes able to reproduce, by producing viable ova, and displaying oestrus (Foster et al., 1985).

1.4.1.1 Physiology of the reproductive cycle

The oestrous cycle is made up of two stages: the luteal phase and luteolysis, and the follicular phase and ovulation (McDonald and Cumming, 1973; Edwards and Juengel, 2017). During the luteal phase (about day 15 of a 17 day cycle in the ewe) a corpus luteum forms from the follicle that ovulated, and secretes progesterone (P₄) while the pituitary is secreting luteinising hormone (LH) and prolactin (McDonald and Cumming, 1973). During this stage, independent follicles grow, with stimulation from follicle stimulating hormone (FSH), secreting oestradiol-17β (E₂), and then regress (McDonald and Cumming, 1973). The E₂ acts on the uterus, which in turn secretes prostaglandin (PGF_{2α}), which causes a depression of P₄ secretion, regressing the corpus luteum, known as luteolysis (McDonald and Cumming, 1973). Following luteolysis, E₂ that is released from maturing follicles can cause a pre-ovulatory LH release (McDonald and Cumming, 1973). Ovulation occurs afterwards, and a corpus luteum forms, beginning the luteal phase of the cycle again (McDonald and Cumming, 1973). If fertilisation occurs the corpus luteum does not regress, and by day 55 of pregnancy, the placenta is capable of supplying sufficient P₄ for fetal survival (McDonald and Cumming, 1973). The concentrations of

LH, E₂, FSH, and progesterone, and the quantity and size of granulosa cells, in relation to ovulation are shown in Figure 1.1.

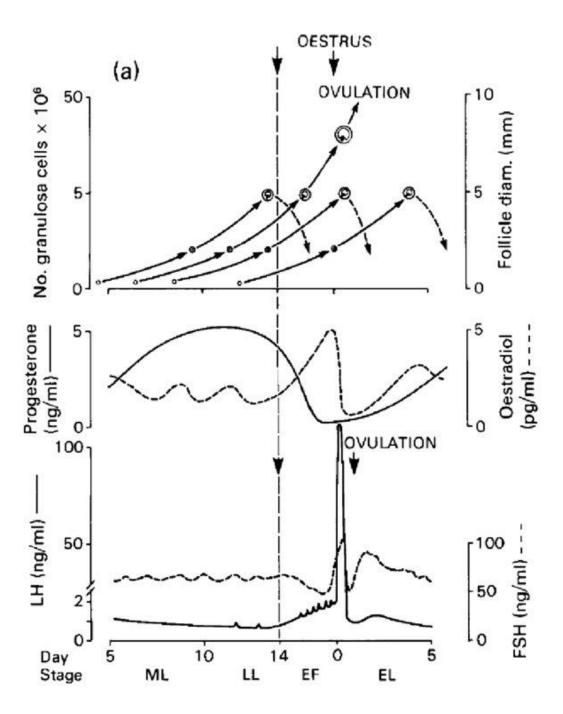


Figure 1.1: The oestrous cycle of the ewe. Follicular waves and the changes in steroid and gonadotrophic hormones are illustrated in the different stages of the oestrous cycle. ML: mid-luteal stage; LL: late-luteal stage; EF: early-follicular stage; EL: early-luteal stage (Baird, 1983).

1.4.1.2 The first reproductive cycle (puberty)

The immature female has a low frequency of LH pulses, with ovarian follicles not developing to an advanced stage (Foster et al., 1985; Edwards and Juengel, 2017). During puberty the LH pulse frequency increases, stimulating follicular development and E₂ production (Foster et al., 1985). This generates a gonadotrophin surge and ovulation occurs (Foster et al., 1985). The first ovulation at puberty or the start of the annual breeding season is usually silent, with no oestrus behaviour (Kenyon et al., 2012). The timing of first ovulation/puberty is influenced by many internal and external factors, described in Section 1.4.2 (Foster et al., 1985; Kenyon et al., 2014a; Edwards and Juengel, 2017).

1.4.2 Factors increasing the onset of puberty in ewe lambs

There are many environmental and genetic factors that influence the attainment of puberty in the ewe lamb. The timing of attainment of puberty as a ewe lamb will influence the reproductive success of that ewe lamb.

1.4.2.1 Breeding season

Most sheep breeds in temperate environments have a defined breeding season, with breeding occurring during the autumn months, controlled by photoperiod, with sheep being short-day breeders (Foster et al., 1985; Edwards and Juengel, 2017). If a ewe lamb does not attain puberty within her first breeding season, then she will not cycle until the breeding season of the next year (Edwards and Juengel, 2017), and thus will attain puberty at approximately 15-18 months of age.

1.4.2.2 Live weight and body condition score of the ewe lamb prior to and during breeding

Live weight is the largest contributor to onset of puberty in most species, including sheep (Kenyon et al., 2014a). There is a strong positive relationship between live weight at eight

months of age and puberty attainment, with ewe lambs that are heavier at eight months of age being more likely to have attained puberty (Allison et al., 1975; Meyer and French, 1979; Meyer, 1981). For each kilogram increase in live weight during the autumn there was a subsequent 1.3% increase in the chance of attaining puberty (Baker et al., 1978). Ewe lambs need to attain puberty before they can breed, which requires them to achieve ~60% (range 40-70%) of their mature live weight prior to breeding (Dýrmundsson, 1981; Corner-Thomas et al., 2015a; Piaggio et al., 2015). In the Romney, puberty was reported to occur at 30-34 kg (McCall and Hight, 1981), while Kenyon et al. (2012) stated that Romney ewe lambs were unlikely to attain puberty if they were lighter than 35 kg during their first breeding season. The mature live weight of the Romney breed has been increasing, therefore the percentage of mature live weight is a more accurate indicator than a set weight, and the higher weight reported by Kenyon et al. (2012) is a likely reflection of this.

Lamb growth over the summer period can be limited if conditions are adverse, in which case, pre-weaning growth is important for puberty attainment. Ewe lambs are traditionally joined one month later than mature ewes, to allow them an extra month of growth to achieve live weight that allows for puberty attainment (Edwards and Juengel, 2017). Live weight is not only important as a trigger for puberty, it is also important so the ewe lambs will not be disadvantaged throughout their pregnancy and lactation, as the mother draws on her own reserves to partition nutrients to the fetus or to milk in times of negative energy balance (Edwards and Juengel, 2017). Live weight also affects the rebreeding potential of the ewe lamb as a two-year-old, with ewe lambs that are heavier during their first pregnancy and lactation being closer to their re-breeding live weight target, for successful conception as a two-year-old (Edwards and Juengel, 2017).

Improved BCS has a positive effect on puberty attainment (Cave et al., 2012). Ewe lambs with BCS above 2.5 at eight months of age had greater conception rates, indicating puberty was attained, than ewe lambs with lower BCS (Cave et al., 2012; Corner-Thomas et al., 2015a). Increasing BCS above 3.0 at breeding does not appear to affect either conception rate, or puberty attainment, of ewe lambs (Corner-Thomas et al., 2015a). This indicates that there is likely a threshold BCS where further gains in body condition will not achieve greater rates of conception. There was no difference in the number of ewe lambs conceiving that had, or had not, been exposed to a vasectomised ram, that were of a BCS of 1.5 (Cave et al., 2012). This indicates that ewe lambs of a lower body condition score are less likely to attain puberty during their first breeding, regardless of their exposure to vasectomised rams.

1.4.2.3 Birth rank of the ewe lamb

At weaning, lambs born as singletons that showed oestrous during breeding at eight months of age were 3.4-4.4 kg heavier than singletons that didn't show oestrous (Hight et al., 1973). Similarly, twins that showed oestrous were 1.8-3.9 kg heavier than twins that didn't show oestrous (Hight et al., 1973). Ewe lambs that were heavier at weaning are more likely to achieve oestrous during breeding at eight-months of age, but the live weight difference between those showing oestrous and those not showing oestrous was smaller for lambs born as twins compared with lambs born as singletons. This indicates that there is a long-acting physiological mechanism, driven by birth rank and fetal growth, which affects the live weight at which singletons versus twins attain puberty. This suggests that farmers should set different live weight targets for selection of their replacements at weaning based on their birth rank, with singletons needing to be heavier than their twin counterparts.

Singleton lambs were found to attain puberty at a younger age than twin-born lambs (van der Linden et al., 2007). This may be confounded with live weight, as singleton lambs are also heavier than twin-born lambs at a given age before maturity (Edwards and Juengel, 2017). Maternal nutrition during pregnancy and dam size appear to have no effect on puberty attainment of the female offspring, however, dam size does appear to affect growth rate and live weight until 13 months of age (van der Linden et al., 2007; Paten et al., 2011).

1.4.2.4 Age of the ewe lamb

Puberty attainment usually occurs around eight months of age (Kenyon et al., 2014a; Edwards and Juengel, 2017), but age and live weight are often confounded. For each day later in the season that a lamb is born, there is a decrease in the chance of attaining puberty by 0.8% (Baker et al., 1978). Ewe lambs that displayed oestrous were older at a given weaning date in singletons and twins than those that did not display oestrous (Hight et al., 1973). Thus, farmers need to be selecting ewe lamb replacements from those that are born earlier in the spring lambing period to guarantee successful breeding at eight-months of age.

1.4.2.5 Vasectomised rams

Sheep farmers sometimes join vasectomised rams to mature ewes prior to induce an early start to the natural breeding season, to elicit an oestrous response from the ewes (Ungerfeld, 2016; Edwards and Juengel, 2017). A similar, but lesser, response occurs in adolescent females when exposed to a male just prior to naturally attaining puberty, stimulating an oestrus response earlier (Kenyon et al., 2012; Kenyon et al., 2014a). The first oestrous cycle is accompanied by a silent heat, and with the presence of the male inducing puberty onset sooner, the silent heat will commonly occur when the

vasectomised ram is present. This means the oestrous cycle(s) during the breeding period will be accompanied with oestrus activity, which provides the opportunity for conception.

Ewe lambs that were growing at 200 g/d had greater responses to vasectomised rams than ewe lambs that were maintaining live weight (Kenyon et al., 2014b). An eight-day exposure to vasectomised rams was insufficient to increase conception rates during the first breeding cycle, but a full 17-day period of exposure to vasectomised rams increased conception rates during the first breeding cycle (Kenyon et al., 2006a). Ewe lambs with BCS of 2.0 or greater had higher conception rates when previously exposed to a vasectomised ram, compared with those that were not exposed to a vasectomised ram (Cave et al., 2012). Therefore, farmers should aim to have their ewe lambs at a BCS of greater than 2.0 and gaining live weight, and to use vasectomised rams for at least one 17-day reproductive cycle prior to the start of breeding.

1.4.2.6 Genetic effects

Breed effects

There are reports that breed differences influence the age and live weight that first oestrous occurs, although this is commonly influenced by the mature live weight of the breed, with puberty attainment generally occurring at 60-65% of mature live weight (Meyer and French, 1979; Dýrmundsson, 1981; Kenyon et al., 2014a). Breed effects can alter timing of puberty, with more prolific breeds attaining puberty earlier relative to other breeds (Kenyon et al., 2014a). Finnish Landrace ewes are highly prolific, and as ewe lambs they attained puberty at younger ages than Romney ewes (Meyer and French, 1979). Crossbreed animals had greater reproductive performance compared with purebreed animals, indicating that heterosis may have an influence (Dýrmundsson, 1981; Kenyon et al., 2004a). Farmers can incorporate more-prolific breeds into their flocks to

increase the number of ewe lambs attaining puberty before or during their first breeding at eight months of age.

Heritability

The heritability of a trait indicates the proportion of that trait controlled by genetics, passed on from one generation to the next. Traits with high heritability are easily passed on to the next generation, meanwhile, traits with lower heritability take longer to make the same genetic progress. Heritabilities of some reproductive traits in ewe lambs are reported in Table 1.5. Genetic correlations indicate the level of connection, genetically, between two traits, where direct selection for one trait will have indirect selection for another trait. These can be both positive or negative. Scrotal circumference and ewe lamb fertility at eight months of age have a genetic correlation of 0.20-0.46, indicating that selection for scrotal circumference in sires could increase genetic gain for puberty attainment in ewe lambs (Fossceco and Notter, 1995; Toe et al., 2000). The genetic correlation between age at puberty and weight at puberty was estimated to be -0.65 (Alkass et al., 1994). This indicates that ewe lambs that are genetically heavier, need to attain greater live weight to get to 60% of their mature weight for puberty attainment, compared to a ewe lamb that is genetically lighter. Selecting ewe lambs from dams that conceived as ewe lambs themselves or alternatively, culling ewe lambs that do not conceive could increase the proportion of the flock attaining puberty during their first breeding, but with a relatively low heritability, the genetic progress would be slow.

Table 1.5. Heritability estimates for fertility, and age and weight at puberty for ewe lambs.

Trait	Sheep Breed	Heritability	Reference
Fertility (conceived	Dorset, Rambouillet and	0.09	Fossceco and
or not) as a ewe	Finnish Landrace		Notter (1995)
lamb	composite		
Age at puberty	Ethiopian Highland sheep	0.14	Toe et al. (2000)
Age at puberty Awassi sheep		0.35	Alkass et al. (1994)
Weight at puberty	Awassi sheep	0.26	Alkass et al. (1994)

Single Nucleotide Polymorphisms

Single nucleotide polymorphisms (SNPs) are specific locations in a genome where a particular nucleotide differs among individuals (Haldar et al., 2014; Xu et al., 2018). Where there is variation in the nucleotides at a given chromosomal location, the variation is referred to as a SNP allele. Any SNP that occurs in the coding region of the gene has the potential to change the amino acid sequence of the protein produced by the particular gene (Haldar et al., 2014). Associations between SNPs and phenotypes can be used to identify genes that influence the trait. Once SNPs are identified for specific traits, farmers can use these to select for genetically superior animals rather than relying on phenotypes alone. Estimated breeding values that are estimated using a combination of performance records and SNPs are typically referred to as genomically enhanced breeding values (gEBVs). Genomically enhanced breeding values can be more accurate than EBVs based on performance records alone, especially when the trait is not expressed before animals are selected as replacements.

Reproduction is a complex trait made up of many component traits, so it is unsurprising there are many genes controlling reproductive success. It is known that reproductive traits are heritable, with low- to-moderate heritability, depending on the trait (Safari and Fogarty, 2003). Some chromosome regions with known genetic influence over

reproductive traits are listed in Table 1.6. There is little literature available on SNPs influencing live weight at the start of the breeding season as a ewe lamb, or the pregnancy result from breeding as a ewe lamb. If farmers were able to select ewe lambs that were likely to be heavier at the start of breeding, or more likely to successfully achieve pregnancy during their first breeding, they are likely to increase the lambing performance of their ewe lambs.

Table 1.6. Genes associated with onset of puberty in sheep, cattle and pigs, from the literature.

Trait Species (Breed)		Location	Reference
Daughter's age at	Sheep	Three SNPs in the LEPR	Haldar et al.
onset of puberty	(Davisdale)	(leptin receptor gene)	(2014)
Early expression Pigs		SNPs found in the SSC5,	Tart et al.
of puberty		SSC8, and SSC12 genes	(2013)
Age at first	Cattle	32 SNPs on	Fortes et al.
corpus luteum	(Brahman)	Chromosome BTA 14	(2012)

1.4.2.7 Summary of factors affecting the onset of puberty in ewe lambs

There are many factors influencing the onset of puberty in ewe lambs, and subsequently influencing the reproductive success of the ewe lamb during her first breeding. Ewe lambs need to be ~60% of their mature live weight to attain puberty, and farmers need to ensure they are growing during the period between weaning and breeding. Body condition score should ideally be at least 2.5 for high conception rates, which indicates puberty was attained prior to breeding. Since the live weight that puberty is attained is related to mature live weight, and lambs born as twins have lighter mature live weights than singletons, their target breeding weight can reflect this, also being lighter. Lambs born earlier during the lambing period are more likely to attain puberty, by being older and more likely to be heavier at the start of the breeding season. Using a stimulus, such as contact with a vasectomised ram, can induce an oestrous response in a ewe lamb that is

close to attaining puberty. Incorporating prolific breeds, using the effects of heterosis, or selecting daughters of ewes that successfully lambed as ewe lambs can also increase the chance of attaining puberty during the breeding season. Genetic technologies may be used in future when more information on traits selected for becomes available.

1.4.3 Ewe lamb live weight

The live weight of a ewe lamb throughout her first breeding period will influence many reproductive traits, and, to a certain degree, determine the success of her first lambing and the potential for her second lambing as a two-year-old (Corner et al., 2006a; Corner-Thomas et al., 2015b).

1.4.3.1 Reproductive response in ewe lambs to nutrition prior to breeding

Nutrition of mature ewes prior to breeding can affect ovulation rates in two ways: via under-nutrition, and via nutritional supplementation (Scaramuzzi and Martin, 2008). Under-nutrition inhibits reproduction via action on the hypothalamic-ovarian axis, which prevents ovulation (Scaramuzzi and Martin, 2008). Supplementary feeding creates a flushing effect, acting on the ovary function directly, to increase ovulation rates in females that are already ovulating (Scaramuzzi and Martin, 2008). This is similarly seen in ewe lambs. Ewe lambs that are fed *ad-libitum* prior to the breeding season are less likely to be non-pregnant, and are heavier at weaning themselves than ewe lambs that are fed medium levels of herbage during breeding (Mulvaney et al., 2010a). Ewe lambs that are heavier at the start of breeding are more likely to be bred during the first cycle of breeding, and are more likely to be multiple bearing than ewe lambs that are lighter at the start of breeding (Kenyon et al., 2010; Corner-Thomas et al., 2014; Corner-Thomas et al., 2015a; Edwards and Juengel, 2017). Schreurs et al. (2010b) reported that increased ewe lamb live weight prior to breeding and during early gestation had the greatest effect on lamb birth and weaning weight, and of the ewe lamb's own live weight at weaning of her lambs.

Growth rates from weaning to breeding, and pre-breeding live weight were the most important live weight traits to determine likelihood of conceiving in ewe lambs (Piaggio et al., 2015). Ewe lambs that are heavier at breeding are more likely to conceive during the first 17-day breeding cycle, and more likely to carry twins than those that are lighter (Kenyon et al., 2005). Ewe lambs should not be bred if they are under 38 kg at the start of breeding (Kenyon et al., 2014a). Low conception rates, and increased mortality rates of the ewe lambs and their progeny are expected if ewe lambs are presented for breeding when they are lighter than 38 kg (Kenyon et al., 2014a). Ewe lambs that were heavier at breeding weaned heavier lambs, and were heavier themselves at weaning of their lambs, compared with ewe lambs that were lighter at breeding (Kenyon et al., 2006b; Mulvaney et al., 2010a; Griffiths et al., 2016).

Ewe lambs that were twin-ovulators were on average 2 kg heavier than single-ovulators at the start of breeding (Meyer, 1981). Ewe lambs that are of BCS above 2.5 at breeding had more fetuses present per ewe bred than ewe lambs of BCS 1.5 at joining (Cave et al., 2012). Ewe lambs that are heavier are more likely to have attained puberty prior to the start of breeding, are more likely to conceive, and are more likely to be multiple-bearing. Therefore, farmers need to prioritise the feeding of replacement ewe lambs during the weaning-to-breeding period to improve ovulation and conception rates. Monitoring live weight and/or BCS of the ewe lambs during this period will enable them to make more informed feed-management decisions.

1.4.3.2 Reproductive response in ewe lambs to nutrition during the breeding period Wallace et al. (1996) and Wallace (2000) reported that offering high nutrient allowances to ewe lambs, in feedlot systems to achieve growth rates above 230 g/d, during breeding resulted in lower conception rates, decreased fetal and placental growth, and lower lamb birth weights than those with medium nutrient allowances. This mechanism is due to

changes in the hierarchy of nutrient partitioning in the pregnant adolescent, with partitioning favouring the growing dam, subsequently restricting placental and fetal growth in the very well-fed ewe lambs (Wallace, 2000). Different results have been seen in New Zealand pastoral conditions. Kenyon et al. (2008b) and Morris et al. (2005) reported that ewe lambs offered high levels of nutrition (growing at 200 g/d) during breeding had similar pregnancy rates, lambing rates, or lamb birth weight (within lamb birth rank) compared with those that were offered medium levels of nutrition, indicating overfeeding was not an issue in New Zealand farming systems. For those farmers committed to breeding ewe lambs, ewe lambs should be fed to achieve growth rates between 100-200 g/d during the breeding period, and monitor the flock through regular live weight measurements.

1.4.3.3 Reproductive response of ewe lambs to nutrition during pregnancy

Lambs born to ewe lambs fed well throughout pregnancy (average daily liveweight gains of 200 g/d) were heavier at weaning than those born to ewe lambs with moderate pregnancy nutrition (average daily liveweight gains of 100 g/d before and 200 g/d after day 36 of pregnancy), and the well-fed dams were heavier at weaning compared with the moderate-nutrition dams (Morris et al., 2005; Kenyon et al., 2008b). Mulvaney et al. (2008) showed that ewe lambs offered low (maintenance) or high (*ad libitum*) feeding during pregnancy gave birth to fewer lambs than those offered medium (average daily liveweight gains of 100 g/d) feed. Lambs that were born to ewe lambs offered low nutrition during the entire pregnancy were lighter at birth, docking and weaning, and had lower survival than lambs born to ewe lambs offered medium or high nutrition during the entire pregnancy period (Mulvaney et al., 2008; Mulvaney et al., 2010b; Mulvaney et al., 2012). Using similar treatments, Corner et al. (2006b) reported that low-to-medium levels of maternal nutrition during the entire pregnancy appeared to have no effect on lamb birth

weight or survival rate of lambs born to ewe lambs. This indicates that there may be other environmental factors influencing the lamb birth weight and survival rate among these studies.

As ewe lambs are still growing themselves, farmers need to manage them carefully, to ensure that they have a sufficient nutrient supply during pregnancy and lactation in addition to their growth requirements (Kenyon et al., 2004b). Ewe lambs bearing multiples have higher nutritional requirements during pregnancy compared with ewe lambs bearing singletons (Kenyon et al., 2004b), and deficits in the level of nutrition have a more significant effect on ewe lambs that are carrying multiples (Kenyon et al., 2009a). In summary, growth of ewe lambs during pregnancy is important to increase reproductive success. Ewe lambs that have greater body condition during pregnancy have a greater ability to buffer nutritional stress than those with lower body condition. Multiple-bearing ewe lambs need to be managed carefully by farmers to ensure their nutritional needs for

ewe lambs need to be managed carefully by farmers to ensure their nutritional needs for growth and pregnancy are met, especially in late pregnancy, when their needs are highest. Ewe lambs should have average daily liveweight gains of 100-200 g/d during their pregnancy. Those that are multiple-bearing should be gaining more than 200 g/d in the last 50 days of pregnancy, to allow for the growth of the conceptus and their own growth.

1.4.3.4 Reproductive response of ewe lambs to nutrition during lactation

Separation of ewe lambs during lactation based on the birth rank of their lambs improves the survival and growth of lambs until weaning (Kenyon et al., 2004b). Since ewe lambs need to be gaining maternal weight and providing milk for lambs, preferential treatment of lactating ewe lambs, especially those with twins, is important (Kenyon et al., 2014a). Any ewe lambs that are feeding multiple lambs should have additional allowances to ensure progeny growth, progeny survival, and dam live weight gain are at an optimum

(Kenyon et al., 2014a). Ewe lambs should gain 5-10 kg during the lactation period to ensure re-breeding performance is not compromised, but gains greater than 10 kg do not have any further impact on re-breeding (Corner-Thomas et al., 2015b).

1.4.4 Increasing conception and ovulation rates with exposure to vasectomised rams Studies have shown that there is an increase in the lambing percentage of the ewe lamb flocks that are exposed to a vasectomised ram prior to breeding, compared with ewe lambs that are not exposed (Kenyon et al., 2005; Kenyon et al., 2008c; Cave et al., 2012). Kenyon et al. (2005) and Cave et al. (2012) reported that ewe lambs that were exposed to vasectomised rams prior to joining had 6-12% higher conception rates in the first 17-day cycle than those that did not have male exposure. The total conception rate over a 34-day joining period was not different between ewe lambs that either were, or were not, exposed to a vasectomised ram prior to joining (Cave et al., 2012). Kenyon et al. (2006a) reported that exposure to a vasectomised ram for eight days was insufficient to increase conception rates during the first 17-day cycle of breeding, while Kenyon et al. (2008c) reported that exposure for 2-4 days still resulted in an increase in conception rates over a two-cycle (34-day) breeding period, compared with ewe lambs that were not exposed to the male. This indicates that when ewe lambs are exposed to vasectomised rams for a whole 17day cycle there are increases in conception rates during the first cycle, but those that are exposed for shorter periods likely attain puberty within one cycle of the introduction of the presence of a male.

1.4.5 Shearing during mid- or late-pregnancy

Shearing ewe lambs during mid-pregnancy increased the birth weights of singleton lambs (Kenyon et al., 2006c). Mid-pregnancy shearing of ewe lambs that are twin-bearing does not increase the birth weight of their lambs (Kenyon et al., 2006c). Mid-pregnancy shearing ewe lambs did not appear to influence survival rates in either singletons or

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multiples (Kenyon et al., 2006c). Farmers should make the decision to mid-pregnancy shear their ewe lambs based on other management factors, such as lower rates of casting prior to lambing. If there are issues with dystocia caused by lambs being too large, farmers should consider not shearing their singleton-bearing ewe lambs.

1.5 Ways to avoid decreasing ewe lamb reproductive performance

While there are many things that a farmer can do to increase the reproductive performance of his ewe lambs, there are many factors that they also need to avoid to ensure that breeding eight-month-old ewe lambs is successful. Any factor that decreases the rate of onset of puberty will significantly decrease the reproductive rate of the ewe lambs during their first breeding.

1.5.1 Live weight and condition score

There is evidence to suggest that ewe lambs that are fed to maintenance requirements or higher during breeding have lower conception rates and embryo survival rates than ewe lambs that are offered below maintenance requirements (Annett and Carson, 2006). These low allowance ewe lambs did not produce more lambs at weaning than those offered maintenance or higher nutrition, indicating a loss of production later in the reproductive cycle (Annett and Carson, 2006). Therefore, from a welfare perspective, farmers should ensure that ewe lambs are fed maintenance or above, to reduce the losses of lamb produced to weaning.

1.5.2 Shearing pre-breeding

Shearing can have a negative effect on the age of puberty onset in the ewe lamb if done near the time of puberty onset, by causing nutritional and physical stress on the animal, thereby delaying onset (Dýrmundsson and Lees, 1972a). Shearing is a stressful time for the sheep, with a short period of no feed intake prior to being shorn, and the physical process of shearing as well. This disruption to normal growth patterns can take days or weeks to recover and disrupts the natural oestrous cycling of the female. Dýrmundsson and Lees (1972a) reported that there was a small, but insignificant, delay of 6-8 days in the onset of puberty, in ewe lambs shorn one month prior to breeding. If they are shorn too close to the start of the breeding period, this disruption may result in fewer ewe lambs

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displaying oestrus during the breeding period, especially if they were close to attaining puberty at the shearing time, so should be avoided (Kemp et al., 1991).

1.6 Performance of lambs born to ewe lambs compared with lambs born to mature ewes as either singletons or twins

1.6.1 Effects pre-weaning

1.6.1.1 Weights of lambs at birth, early lactation and weaning, born to ewe lambs or mature ewes

Lambs that are born to ewe lambs are lighter and smaller at birth than those that are born to mature ewes (Table 1.7; Quirke and Hanrahan, 1983; Annett and Carson, 2006; Kenyon, 2008; Kenyon and Blair, 2014; Kenyon et al., 2014a). Since lambs born to ewe lambs are growth-restricted by the uterine capacity of the dam, compared with those born to mature ewes, these lambs also have lower live weights until weaning (Loureiro et al., 2012; Corner et al., 2013b). In addition, lamb birth rank negatively affects lamb birth weight and growth to weaning (Kenyon and Blair, 2014). This indicates that there are maternal constraints placed on lambs based on the physiological capacity of the dam *in utero*, and via milk production (Kenyon and Blair, 2014). Multiple-born lambs are lighter than singleton-born lambs, and lambs born to ewe lambs are lighter than lambs born to mature ewes, therefore lambs born as multiples to ewe lambs are further disadvantaged in terms of live weight, compared with lambs born as singletons to mature ewes. Ewe lambs produce less milk than mature ewes, resulting in lower liveweight gain from birth to weaning in lambs born to ewe lambs, compared with those born to mature ewes, especially those born as multiples (Loureiro et al., 2012; Kenyon and Blair, 2014).

Lambs that are born to ewe lambs are normally born a month later than those born to mature ewes, and are often sired by different rams (Kenyon and Blair, 2014). This creates different environmental conditions between the two age groups, making a comparison of lamb performance difficult. While it is well documented that the lambing performance of ewe lambs is less than that of mature ewes, currently, there are few direct comparisons of

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lambing performance between the dam age groups, when the mature ewes and ewe lambs are bred at the same time, to the same rams.

4

Table 1.7: Comparative birth weight, survival rate and weaning weight of lambs born to different dam age classes, or different birth ranks when born to ewe lambs.

Experiment	Lamb birth weight (kg)	Lamb survival rate (%)	Lamb weaning weight (kg)	Comparison
Lewis (1959)	3.8 vs 3.2	-	-	Singleton vs. twin-born lambs born to ewe lambs
Purser and Young (1964)	2.99 vs. 3.43	72.9 vs. 85.9	-	Singleton lambs born to two-year-old ewes vs. singleton lambs born to three- to six-year-old ewes
Baker et al. (1978)	4.2 vs. 4.3	76.0 vs. 89.9	-	Lambs born to two-year-old ewes that either were not joined as ewe lambs vs. those that lambed as ewe lambs
Baker et al. (1981)	-	88 vs. 85 vs. 80	21.6 vs. 19.1 vs. 19.2	Ewes that were joined and lambed as ewe lambs vs. ewes that were joined as ewe lambs but did not lamb vs. ewes that were lambed first as two-year-olds
McCall and Hight (1981)	-	78 vs. 86	14.4 vs. 16.8	Lambs born to one-year-old ewes vs. two-year-old ewes and over
Annett and Carson (2006)	4.73 vs. 5.29	-	28.6 vs. 31.8	Ewe lambs vs. mature ewes
Kenyon et al. (2008d)	4.8 vs. 4.5 vs.	-	24.7 vs. 23.6 vs.	Lambs born to two-year-old ewes that are 2 nd parity vs.
	4.6		23.7	first parity but were presented for breeding vs. first parity and were not presented for breeding
Young et al. (2010)	4.6 vs. 3.6	79 vs. 67	30.6 vs. 29.1	Lambs born to ewe lambs as either singletons vs. twins
Mulvaney (2011)	-	79 vs. 89	-	Ewe lambs vs. mature ewes
Loureiro et al. (2012)	5.0 vs. 4.2	-	23.4 vs. 20.0	Singleton ewe lambs born to mature ewes vs. singleton ewe lambs born to ewe lambs
Blair (2015)	4.6 vs. 3.7	-	-	Lambs born to mature ewes vs. ewe lambs

1.6.1.2 Mortality rates of lambs born to ewe lambs or mature ewes

Lamb mortality rate from birth to weaning varies between 5% and 30% with many animal, climatic and farm factors influencing the mortality rate (Sargison, 1997; Everett-Hincks and Dodds, 2008; Everett-Hincks and Duncan, 2008). The majority of lamb mortalities occur during the first three days after birth, accounting for 80-90% of lamb mortalities from birth to weaning (Sargison, 1997). Lambs born to ewe lambs have higher mortality rates, due to being smaller and therefore having a greater risk of starvation/exposure than lambs born to mature ewes (Kenyon et al., 2014a; Edwards and Juengel, 2017). Lamb mortality rates from ewe lambs ranged from 18-35%, with 13% of all lambs born to ewe lambs dying from dystocia (McMillan, 1983). Young et al. (2010) reported that mortality of lambs born to ewe lambs during the first three days of age was 20%, and from birth to weaning was 28% (Table 1.7).

Poor maternal behaviour is thought to be a contributor to higher rates of lamb mortality, especially in lambs that are born to adolescent dams, that are inexperienced at rearing a lamb (Robertson et al., 2017). In contrast, Arnold and Morgan (1975) and de Moraes et al. (2016) reported that there was no effect of maternal behaviour on rates of lamb mortality, indicating that environmental factors may be more influential on lamb mortality than maternal behaviour during tagging. Lambing mature ewes and ewe lambs together, in an attempt to allow ewe lambs to learn behaviours from mature ewes, did not decrease the rate of lamb mortality from ewe lambs (Robertson et al., 2017).

1.6.1.3 The relationship between birth weight and lamb survival

Lamb birth weight has an effect on lamb survival at birth, such that lambs that are too heavy die from dystocia, and lambs that are too light die from starvation and/or exposure. The birth weight at which these deaths occur differs between the age of the dam, and the birth rank of the lamb(s). Lambs born as singletons, especially to ewe lambs, are much

more likely to die from dystocia due to feto-maternal disproportion than lambs born as twins, due to their heavier birth weight (Everett-Hincks and Dodds, 2008). Twin-born lambs were lighter at birth, and were more likely to die from starvation/exposure than singleton lambs (Young et al., 2010). It then follows that, regardless of dam age, higher mortality rates are seen in larger litters (triplet and above), due to lighter birth weights and the associated increased risk of starvation/exposure, and dystocia due to entanglement. Therefore, there is an optimum birth weight range, for greater survival from lambs, differing based on dam age and lamb birth rank. The differences in the rate of survival, and optimum birth weight for greater lamb survival, within different dam age and lamb birth rank while using the same sires has not been investigated.

1.6.2 Effects post-weaning

Ewes that were born to ewe lambs were lighter until at least one year of age for singletons (Loureiro et al., 2012), until at least 2.5 years of age for singletons and twins (Loureiro et al., 2016), and until at least four years of age for singletons (Pain et al., 2015), compared with ewes that were born to mature ewes (Kenyon, 2008; Pain et al., 2015; Loureiro et al., 2016). Interestingly, the age of dam did not affect their reproductive or lactation performance, to four years of age (Loureiro et al., 2012; Pain et al., 2015; Loureiro et al., 2016). Lighter live weight at puberty for lambs that were born to ewe lambs may indicate that they are more suited to being bred, compared with lambs that are born to mature ewes, because they can be bred at a lighter weight (Loureiro et al., 2011). It may also be indicative of a lighter mature weight, and that the ewe lambs born to ewe lambs are at the same, or higher proportion of their mature weight at breeding.

In summary the performance of lambs born to ewe lambs compared with lambs born to mature ewes as either singletons or twins, lambs born to ewe lambs are lighter than lambs born to mature ewes, at birth, to weaning, and to one year of age, within each birth rank.

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Lambs that are born to ewe lambs have greater mortality rates during the neonatal period and to weaning than lambs born to mature ewes. Most studies comparing the performance of lambs born to either ewe lambs or mature ewes are confounded, because they do not compare the two groups during the same lambing period, in the same climatic environment using the same sires. There is an absence of complete lifetime data sets, reporting on the longevity and stayability of ewes born to ewe lambs, total production, and efficiency of production. The few studies that are not confounded are based on small numbers of animals, resulting in only cautious recommendations to farmers.

1.7 Summary and implications

Currently, 30-43% of replacement ewe lambs are bred at eight months of age in New Zealand. By breeding ewe lambs, farmers can increase annual farm production, and ewe lifetime production. Production from ewe lambs is known to be lower than production from mature ewes; this is driven by:

- lower ovulation rate
- fewer number of lambs born and weaned
- lower weight of lambs born and weaned
- lower rate of lamb survival to weaning.

Remarkably, there are few direct comparisons between mature ewe and ewe lamb reproductive performance under the same environmental conditions, using the same service sires.

It is known that the attainment of puberty prior to first breeding is a key determinant of ewe lamb reproductive success. Identification of ewe lambs that are more likely to attain puberty prior to their selection as replacements in the flock would aid farmers in increasing ewe lamb production during their first breeding. Identification of candidate genes associated with live weight and puberty would enable the use of gEBVs.

Breeding ewe lambs and selecting their replacements can increase the rates of genetic gain by reducing the generation interval. By knowing the potential reproductive performance of replacements born to ewe lambs, farmers can make more informed decisions about their replacement selection policies, and their ewe lamb breeding policies. Commercial farmers can consider the lambs born to ewe lambs to make up numbers in the replacement selection process, while ram breeders can prioritise selecting lambs born to ewe lambs to increase the rate of genetic gain in their flock.

1.8 Thesis objectives

The aims of this thesis were to:

- Compare the lifetime ewe live weight, body condition score, and longevity of singletons or twins born to either mature ewes or ewe lambs, until eight years of age.
- Compare the lifetime reproductive performance of singletons or twins born to either mature ewes or ewe lambs.
- Compare the lifetime efficiency of singletons or twins born to either mature ewes or ewe lambs.
- Compare the lamb birth weight, growth to weaning, and survival of lambs born as singletons, twins, or triplets, to mature ewes or ewe lambs, when all dams were bred to the same sires at the same time.
- Compare the reproductive performance of ewe lambs born as singletons or twins
 to ewe lambs and twins born to mature ewes, when bred for the first time at eight
 months of age.
- Compare the reproductive performance of ewe lambs born as singletons or twins
 to ewe lambs and twins born to mature ewes, when bred for the second time at
 eighteen months of age.
- Identify genes of interest that influence live weight at the start of breeding, at eight months of age.
- Identify genes of interest that influence the chance of pregnancy occurring, when bred for the first time at eight months of age.

Chapter 2

The effects of birth rank (singleton or twin) and dam age on the lifetime productive performance of female dual-purpose sheep (*Ovis aries*) offspring in New Zealand

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2.1 Abstract

Greater rates of genetic gain can be achieved by selecting animals born to younger parents. However, little is known about the lifetime performance of dual-purpose ewes (Ovis aries) that are born to primiparous ewe lambs (eight-to-nine months old at breeding). This experiment investigated the effect of being born from either a ewe lamb or mixed age dam as either a singleton or twin on the lifetime performance of ewe progeny. Lifetime performance was measured in terms of the lifetime live weights of the ewes, the weight and number of lambs born and weaned, the efficiency of production (kilograms of lamb weaned / predicted pasture intake (kgDM) of the ewes), and ewe survival. The study followed the lifetime production of 17 singleton and 41 twin female lambs born to mature ewes (M1 and M2, respectively), and 28 singleton and 29 twin lambs born to ewe lambs (L1 and L2, respectively). Over their lifetime L2 ewes were lighter (P<0.05) but had similar body condition scores to the other three ewe groups. There was no difference in average progeny weaning weight or total progeny litter weaning weights between groups. The M1 ewes had the greatest longevity (P<0.05) of the four groups. Even though L2 ewes were lighter than the other three groups, this was insufficient to increase their lifetime efficiency of production (kg lamb weaned/predicted pasture consumption), relative to the other groups. These results suggest farmers could select replacements born to ewe lambs without sacrificing animal production.

2.2 Introduction

Currently, 30-43% of dual purpose breeding ewes (*Ovis aries*) in New Zealand are bred for the first time as ewe lambs, at eight to nine months of age (Morel et al., 2010; Cave et al., 2012; Kenyon et al., 2012; Pain et al., 2015; Beef + Lamb New Zealand, 2019a). Ewe lambs are lighter and have lower body condition scores than mature ewes (Corner et al., 2013a). Lambs born to ewe lambs are smaller and lighter at birth (Everett-Hincks and Dodds, 2008; Morel et al., 2010; Corner et al., 2013a; Kenyon et al., 2014a; Pain et al., 2015), weaning (Loureiro et al., 2011; Mulvaney, 2011; Pain et al., 2015), and to 12-months of age (Loureiro et al., 2011; Pain et al., 2015), and have lower survival rates (McMillan, 1983; Mulvaney, 2011; Kenyon et al., 2014a), compared with lambs born to mature ewes. Twin-born lambs born to mature ewes are also smaller and lighter than singleton-born lambs to weaning (Kenyon et al., 2014a). The same relationship occurs in ewe lambs (Corner et al., 2013a).

Progeny born to ewe lambs have difficulty achieving a suitable breeding live weight as a ewe lamb, compared with lambs born to mature ewes, due to slower early growth (Kenyon et al., 2014a), in addition they are born a month after lambs born to mature ewes in New Zealand (Kenyon et al., 2004a). Lambs born to ewe lambs are not commonly selected as replacements in New Zealand (Kenyon et al., 2004a), with light live weight at weaning being the primary reason (Kenyon et al., 2009b; Kenyon et al., 2010; Kenyon et al., 2014a; Kenyon et al., 2014b). Puberty is attained at 40-60% of mature live weight (Kenyon et al., 2014a), or 38-48 kg in Romney ewe lambs (Kenyon et al., 2014b). Ewe lambs must have attained this percentage of live weight to have any chance of being successfully bred, and being able to support pregnancy and lactation requirements (Kenyon et al., 2014a).

Singleton lambs born to ewe lambs have been reported to be lighter than singleton lambs born to mature ewes from birth to 12 months of age, and occasionally until four years of age (Pain et al., 2015). Despite this, they produced similar numbers and weights of lambs at birth and weaning, and had a similar production efficiency (kg lamb weaned/estimated maintenance MJME). Loureiro et al. (2011) showed that for the first year of life, lambs born as singletons to mature ewes were heaviest from birth to weaning, with twin lambs born to mature ewes and singleton lambs born to ewe lambs being intermediate and not different from each other, and twin lambs born to ewe lambs were the lightest. There was no difference in pregnancy rate, and number and weight of lambs weaned, for ewes born as either singletons or twins, to either mature ewes or ewe lambs for their first lambing at two years of age (Loureiro et al., 2016), and as singletons born to either mature ewes or ewe lambs for their first two lambings as two- and three-year-olds (Loureiro et al., 2012). There was no difference in milk production from singletons born to mature ewes or ewe lambs for their first two lactations (Loureiro et al., 2012). Dual purpose ewes in New Zealand have an average expected productive life of 4.3-5.0 years (Hohenboken and Clarke, 1981). However, little is known about the lifetime productive performance of dual-purpose ewes that were born to ewe lambs, in New Zealand. Therefore, this experiment aimed to investigate the effects of birth rank and dam age on the maternal performance of ewes over six lambings. Lifetime performance was measured as the lifetime live weights of the ewes, the weight and number of lambs born and weaned, the efficiency of production (kilograms of lamb weaned / predicted pasture intake (kgDM) of the ewes), and ewe survival.

2.3 Materials and methods

The experiment was conducted at Massey University's Riverside Farm (latitude 40°50′S, longitude 175°37′E) 11 km north of Masterton, and Keeble Farm (latitude 41°10′S, longitude 175°36′E) 5 km south of Palmerston North, New Zealand, with the approval of the Massey University Animal Ethics Committee (MUAEC12/21). The experiment ran from April 2009 until January 2017. Animals were managed at Riverside Farm from September 2009 (birth) to January 2010 (weaning), then moved to Keeble Farm for the remainder of the experiment.

2.3.1 Experimental design

The study used Romney nulliparous ewe lambs (L; eight-to-nine months of age) and multiparous mature Romney ewes (M; three-to-five years of age) as the parents of the experimental ewes. They were naturally bred with Romney composite rams (at a ram to ewe ratio of 1:40) as one cohort for a 34-day mating interval in April 2009 (Loureiro et al., 2011; Corner et al., 2013a; Loureiro et al., 2016). The ewes were grazed under commercial New Zealand grazing conditions, with post-grazing covers at a minimum of 1000 kg DM/ha during breeding and gestation and of 1200 kg DM/ha during lactation (Corner et al., 2013a). At weaning all female lambs were selected from resulting progeny to create four groups based on dam age (mature ewe or ewe lamb; M and L, respectively) and birth rank (singleton or twin; 1 or 2, respectively; Loureiro et al., 2011; Loureiro et al., 2016). No triplet-born ewe lambs were selected from either dam age group. At the initiation of the main experiment, the progeny groups included singleton progeny born to mature ewes (M1, n=17), twin progeny born to mature ewes (M2, n=41), singleton progeny born to ewe lambs (L1, n=28), and twin progeny born to ewe lambs (L2, n=29). The four groups were managed as one mob (n=115), from selection onwards (Loureiro et

al., 2011; Loureiro et al., 2016), and were followed for the following eight years across six lambing periods.

Ewes were first bred in 2011, at 18 months of age (Loureiro et al., 2016). Rebreeding subsequently occurred once yearly from 2011 to 2016, between the 24th of March and 24th of April for different years. The ewes were treated with progesterone using CIDRs (controlled internal drug release; Pfizer Inc., New York, NY 10017) to achieve synchronised oestrus prior to joining with rams each year.

2.3.2 Measurements

At birth, the ewe progeny had their live weight, thoracic girth, and crown-rump length measured within 12 hours of birth. The midpoint of the lambing period was defined as day one (D1). Further live weights (LWT) were recorded at day 41, weaning (D99), and monthly until their first breeding (D552; Loureiro et al., 2011). In later years live weights were recorded pre-breeding, at pregnancy detection in mid-pregnancy, one week prior to lambing, and at weaning. Body condition scores (BCS; 1=emaciated, 5=obese; (Jefferies, 1961)) were measured twice prior to the ewes' first breeding (D369 and D412), and at each subsequent live weight.

Pregnancy diagnosis via transabdominal ultrasonography to count the number of fetuses present occurred each year between 72 and 86 days after ram introduction. Ewes were checked twice daily during the lambing period, beginning seven days before the planned start of lambing, and the birth weight, crown-rump length, and girth of their progeny were measured. Lambs had additional live weights measured at day 40 of lactation and weaning (average age of 99 days). No culling of ewes occurred unless on welfare grounds. Ewe deaths were recorded.

2.3.3 Data handling

Live weight of ewes during pregnancy were adjusted via Gompertz equation (Freer, 2007) to calculate a conceptus-free live weight, based on birth weight of the litter and lambing dates. A transformational regression was used to fit a spline polynomial (order 2) curve to the adjusted live weights of each individual ewe. Spline knots were placed at D0, D99, D188, D337, and D432 prior to first breeding, then at breeding, pre-lambing, and at weaning each year, until the end of the experiment. A daily live weight prediction was generated for each ewe from their weaning as a lamb, until their death, or the end of the experiment (D2623).

Progeny weights were added together to form a total litter weight per ewe per year for birth, day 40 of lactation, and weaning weights. Total litter weight of lambs at weaning divided by the weight of the ewe at breeding, for each year to determine a ratio of progeny weaning weight to ewe breeding weight. If the ewe was present at breeding, but did not wean a lamb, a litter weaning weight of zero was given.

Predicted daily live weights from the spline models were used to determine the daily nutritional requirements for each ewe for their maintenance and growth/loss (Nicol and Brookes, 2007). Litter birth weights and birth dates were used to determine daily nutrient requirements for gestation (Freer, 2007). Lactation requirements were modelled from Peart et al. (1975) based on week of lactation, and number of lambs reared. Lamb nutritional requirements were modelled based on birth date and weight, weaning date and weight, and average daily gain (Nicol and Brookes, 2007). Equations for daily energy requirements are presented Appendix 9.2. Total lifetime number of lambs weaned was calculated by adding yearly number of lambs weaned for each ewe. Similarly, the total lifetime weaning weight of lambs was calculated by adding yearly weaning weight of lambs weaned for each ewe. A total estimated lifetime feed requirement was calculated

for all ewes, along with their lifetime litter weaning weight, the values were utilised to generate an estimated feed efficiency value for each ewe.

As the ewes were only culled based on welfare grounds, hypothetical culling was imposed retrospectively on ewes, if a particular ewe was barren at pregnancy diagnosis, day 40 of lactation, or weaning, as per commercial farming conditions. This allowed survival analysis to be carried out for actual survival of the ewes, and the expected survival of the ewes if they were managed under commercial farming conditions. All ewes alive for actual survival or imposed-culling survival at the end of the experiment (D2623) were censored at that date for survival analysis.

2.3.4 Statistical analysis

Statistical analysis was carried out using SAS version 9.4 software (SAS Institute, Cary, NC, USA). The aim of this study was to classify production consequences of retaining singleton or twin ewes born to either a ewe lamb or a mature ewe. Thus, in all models, even if the interaction between dam age and birth rank was non-significant (P>0.05), the two-way interaction remained in the model, to allow for testing of the experimental question. Ewe live weights and some production traits up to 2.5 years of age have been previously reported by Loureiro et al. (2016) and Loureiro (2014).

Ewe weight at birth, 41 days of age, and weaning, crown rump length, thoracic girth, progeny litter birth weight, progeny weight of the litter at 40 days of age, progeny litter weaning weight, ratio of progeny weaning weight to ewe breeding weight, total lifetime progeny weaning weight, total lifetime pasture consumed, and efficiency were analysed using a mixed linear model. The model included the fixed effects of age of dam (mature ewe vs ewe lamb) and ewe birth rank (singleton vs twin), and their interaction. Date of birth was included as a covariate in the model for the analysis of ewe weight at birth, 41

days of age, and weaning, crown rump length and thoracic girth. The model to analyse progeny litter weights at birth, 40 days of lactation, and weaning, and the ratio of progeny weaning weight to ewe breeding weight considered the fixed effect of year, and the random effect of ewe.

Least squares means for predicted ewe live weights every 50 days during their productive life were obtained with a linear model that included the fixed effects of day, age of dam, ewe birth rank, interaction between age of dam and ewe birth rank, and the interaction of day, age of dam and ewe birth rank.

Least squares means for predicted ewe live weight at breeding were obtained with a linear model that included the fixed effects of age of dam, ewe birth rank and year, and the interaction of age of dam and ewe birth rank.

Body condition score at breeding, number of lambs born per year, number of lambs weaned per year, and total lifetime number of lambs weaned were analysed using a generalised linear model, assuming a Poisson distribution and logit transformation. The model included the fixed effects of age of dam, ewe birth rank, and their interaction. Body condition score at breeding, number of lambs born per year, and number of lambs weaned per year also included the fixed effect of year, and the random effect of animal to account for repeated measures.

Lamb survival was analysed using a generalised linear model, assuming a binomial distribution and logit transformation. It included the fixed effects of age of dam, ewe birth rank, year, sex of lamb, and lamb birth rank, and the interaction of age of dam and ewe birth rank.

Ewe survival analysis was carried out using exit data of all ewes that died or were removed prior to the end of the experiment (D2623). All ewes alive at the weaning of their 6th lamb (D2623) were censored at that date for the survival analysis. In addition, hypothetical culling was imposed, retrospectively, if a particular ewe was barren at pregnancy detection, day 40 of lactation, or weaning, as per commercial farming conditions. All ewes that were alive, and not culled at the end of the experiment were censored on D2623 for the survival analysis.

2.4 Results

2.4.1 Measurements on the ewes

There was no significant interaction (P>0.05) between age of their dam and their birth rank for birth weight, crown rump length, or thoracic girth for the ewes at their own birth (Table 2.1). The ewes that were born to mature ewe dams were heavier (P<0.0001), and had greater (P<0.0001) crown rump length and thoracic girth than the ewes born to ewe lambs. The ewes that were born as singletons were heavier (P<0.0001), and had greater (P<0.0001) crown rump length and thoracic girth than the ewes born as twins.

The M1 ewes were consistently heaviest (P<0.05) throughout the experimental period, while M2 and L1 ewes were not significantly different (P>0.05) from each other, but were heavier (P<0.05) than L2 ewes (Figure 2.1).

Table 2.1: Least-squares means (± S.E.M) for weight, crown-rump length, and thoracic girth at birth, and weight at day 41 of life and weaning of ewes born as singletons or twins to mature ewes or ewe lambs.

	n ⁴	Birth weight (kg)	Crown- rump	Thoracic Girth	Day 41 of life weight	Weaning weight
			length (cm)	(cm)	(kg)	(kg)
Age of dam	1					
M	58	4.60 ± 0.12^{b}	51.9 ± 0.5^{b}	41.2 ± 0.4^{b}	18.5 ± 0.4^{b}	33.0 ± 0.6^{b}
L	57	3.77 ± 0.10^{a}	47.6 ± 0.5^{a}	37.6 ± 0.4^{a}	14.4 ± 0.3^{a}	27.0 ± 0.5^{a}
P Value		< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Birth rank ²						
1	45	4.55 ± 0.12^{b}	51.9 ± 0.6^{b}	40.6 ± 0.4^{b}	18.3 ± 0.4^{b}	32.7 ± 0.6^{b}
2	70	3.82 ± 0.10^{a}	47.6 ± 0.4^{a}	38.1 ± 0.3^{a}	14.5 ± 0.3^{a}	27.2 ± 0.5^{a}
P Value		< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Interaction ³						
M1	17	4.94 ± 0.20	54.2 ± 0.9	42.6 ± 0.7	20.3 ± 0.7	35.2 ± 1.0
M2	41	4.27 ± 0.12	49.6 ± 0.6	39.7 ± 0.4	16.6 ± 0.4	30.8 ± 0.6
L1	28	4.16 ± 0.15	49.7 ± 0.7	38.6 ± 0.5	16.3 ± 0.5	30.3 ± 0.8
L2	29	3.37 ± 0.15	45.5 ± 0.7	36.5 ± 0.5	12.5 ± 0.5	23.6 ± 0.7
P Value		0.6947	0.7896	0.4525	0.9423	0.1617

¹Dam age group: M=mature ewe, L=ewe lamb; ²dam birth rank: 1=singleton, 2=twin; ³interaction of dam age group and dam birth rank: M1=singleton born to a mature ewe, M2=twin born to a mature ewe, L1=singleton born to a ewe lamb, and L2=twin born to a ewe lamb; ⁴number of ewes.

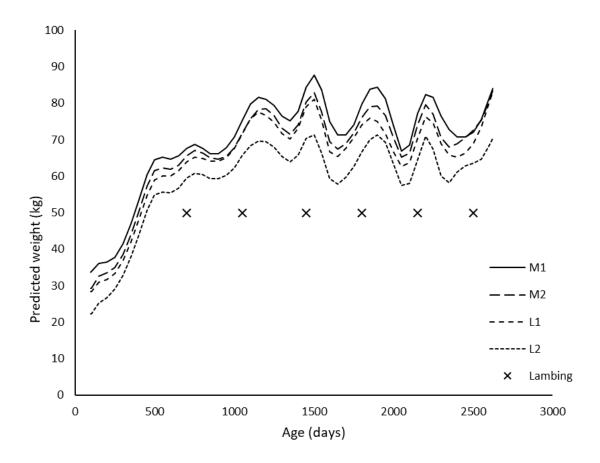


Figure 2.1: Spline fit (knots at breeding, lambing and weaning each year) predictions of daily live weight of ewes from their weaning (D99) to the weaning of their last lambs (D2623) for the interaction of dam age group and birth rank.

M1=singleton born to a mature ewe, M2=twin born to a mature ewe, L1=singleton born to a ewe lamb, and L2=twin born to a ewe lamb. Times marked with an x indicate lambing dates each year (D692, D1057, D1442, D1790, D2146, and D2507).

The interaction of dam age group and birth rank was not significant (P>0.05) for live weight or body condition score at joining (Table 2.2). Ewes born to mature ewe dams were heavier (P<0.001) and had greater (P<0.01) body condition score at breeding than ewes born to ewe lambs. Ewes born as singletons were heavier (P<0.002) at breeding than ewes born as twins. There was no difference (P>0.05) in body condition score for ewes of different birth ranks.

Table 2.2: Least-squares means (± S.E.M.) for ewe live weight and body condition score at breeding over their lifetime based on age of their dam, and their birth rank, and the interaction of dam age group and ewe birth rank.

	n ⁴	Live weight (kg)	Body condition score
Age of dam ¹			
M	348	69.0 ± 0.5^{b}	2.91 (2.80-3.02) ^b
L	342	62.7 ± 0.5^{a}	2.69 (2.61-2.77) ^a
P Value		< 0.0001	0.0014
Birth rank ²			
1	270	68.0 ± 0.5^{b}	2.83 (2.73-2.93)
2	420	63.8 ± 0.4^{a}	2.77 (2.68-2.86)
P Value		< 0.0001	0.3087
Interaction ³			
M1	102	70.6 ± 0.8	2.98 (2.83-3.13)
M2	246	67.5 ± 0.5	2.84 (2.70-2.99)
L1	168	65.3 ± 0.7	2.69 (2.58-2.82)
L2	174	60.1 ± 0.7	2.69 (2.60-2.79)
P Value		0.1155	0.3177

¹Dam age group: M=mature ewe, L=ewe lamb; ²dam birth rank: 1=singleton, 2=twin; ³interaction of dam age group and dam birth rank: M1=singleton born to a mature ewe, M2=twin born to a mature ewe, L1=singleton born to an ewe lamb, and L2=twin born to an ewe lamb; ⁴number of ewe records.

2.4.2 Lamb production

Number of lambs born, number of lambs weaned, and lamb survival did not differ (P>0.05) among ewe groups (Table 2.3). There was no significant interaction (P>0.05) of dam age group and ewe birth rank on the total litter weight at birth and day 40 of lactation (Table 2.4). Ewes born to mature ewes had lighter (P<0.05) litters at birth, but litter weights did not differ (P>0.05) at 40 days of age. There was no interaction (P>0.05) of dam age group and ewe birth rank on the total litter weight at weaning. Ewes that were born to mature ewes as either singletons or twins were not different (P>0.05).

Table 2.3: Least-squares means (95% confidence interval) for the mean number of lambs born (NLB) and weaned (NLW) per year, and lamb survival (%) for dam age group, ewe birth rank, and the interaction of dam age group and ewe birth rank.

	n ⁴	NLB /ewe	NLW/ewe	Lamb survival (%)
Dam age group ¹				
M	348	1.51 (1.42-1.62)	1.48 (1.38-1.58)	85.2 (80.5-88.8)
L	342	1.51 (1.42-1.61)	1.42 (1.33-1.53)	80.9 (75.6-85.2)
P Value		0.9880	0.4513	0.1342
Birth rank ²				
1	270	1.49 (1.39-1.59)	1.47 (1.37-1.58)	84.4 (79.3-88.4)
2	420	1.54 (1.46-1.63)	1.43 (1.34-1.53)	81.8 (77.1-85.7)
P Value		0.4166	0.5528	0.3679
Interaction ³				
M1	102	1.47 (1.32-1.63)	1.46 (1.30-1.64)	84.9 (77.0-90.5)
M2	246	1.51 (1.38-1.65)	1.48 (1.36-1.62)	85.4 (80.4-89.2)
L1	168	1.56 (1.45-1.69)	1.49 (1.40-1.59)	83.8 (77.4-88.6)
L2	174	1.52 (1.40-1.65)	1.37 (1.23-1.53)	77.6 (69.8-83.8)
P Value		0.5232	0.2910	0.2942

¹Dam age group: M=mature ewe, L=ewe lamb; ²dam birth rank: 1=singleton, 2=twin; ³interaction of dam age group and dam birth rank: M1=singleton born to a mature ewe, M2=twin born to a mature ewe, L1=singleton born to a ewe lamb, and L2=twin born to a ewe lamb; ¹number of ewe records.

Table 2.4: The effect of dam age group and ewe birth rank on total litter weight (kg) per year at birth, day 40 of lactation, and weaning, and ratio of progeny weaning weight to ewe breeding weight. Data presented are least squares means (± S.E.M).

	n ⁴	Litter birth weight (kg)	Litter day 40 of lactation weight (kg)	Litter weaning weight (kg)	Ratio of progeny weaning weight to ewe breeding weight
Dam age grou	$ \mathbf{i}\mathbf{p}^{1}$				
M	314	8.51 ± 0.15^{a}	21.0 ± 0.6	48.8 ± 1.2	0.713 ± 0.019
L	286	8.92 ± 0.15^{b}	19.9 ± 0.6	46.3 ± 1.2	0.745 ± 0.019
P Value		0.0476	0.1672	0.1434	0.2235
Birth rank ²					
1	241	8.58 ± 0.16	20.4 ± 0.6	47.7 ± 1.3	0.709 ± 0.021
2	359	8.85 ± 0.13	20.5 ± 0.5	47.4 ± 1.1	0.749 ± 0.017
P Value		0.2001	0.9303	0.8241	0.1396
Interaction ³					
M1	96	8.29 ± 0.25	20.8 ± 0.9	47.5 ± 2.0	0.675 ± 0.032
M2	218	8.73 ± 0.16	21.2 ± 0.6	50.1 ± 1.4	0.750 ± 0.021
L1	145	8.87 ± 0.20	20.1 ± 0.8	48.0 ± 1.7	0.743 ± 0.026
L2	141	8.97 ± 0.20	19.8 ± 0.8	44.6 ± 1.7	0.747 ± 0.027
P Value		0.4063	0.6230	0.0745	0.1786

¹Dam age group: M=mature ewe, L=ewe lamb; ²dam birth rank: 1=singleton, 2=twin; ³interaction of dam age group and dam birth rank: M1=singleton born to a mature ewe, M2=twin born to a mature ewe, L1=singleton born to a ewe lamb, and L2=twin born to a ewe lamb; ⁴n number of ewe records.

2.4.3 Ewe Efficiency

There was no significant interaction (P>0.05) between dam age group and ewe birth rank on estimated total volume of pasture eaten, weight of lamb weaned, and efficiency of conversion of pasture to lamb growth over the eight years (Table 2.5). Calculated feed intake of ewes born to mature ewes was greater (P<0.05) in their lifetime than ewes that were born to ewe lambs. Calculated feed intake of ewes born as singletons was greater (P<0.05) in their lifetime than ewes that were born as twins. There was no effect (P>0.05) of dam age group or ewe birth rank on lifetime total progeny weaning weight or the efficiency of lamb production for estimated lifetime ewe intake. The total number of lambs weaned was similar (P>0.05) among all ewe groups.

Table 2.5: The effect of dam age group and ewe birth rank on the lifetime total predicted pasture consumption (kgDM), total lifetime progeny weaning weight (kg), total lifetime number of lambs weaned and efficiency of lamb production (total lamb weaning weight divided by predicted pasture eaten). Data presented are least squares means (± S.E.M) for pasture, weaning weight and efficiency, and least squares means (95% confidence intervals) for number of lambs weaned.

	n ⁴	Total lifetime predicted pasture eaten (kgDM)	Total lifetime weaning weight (kg)	Total number of lambs weaned	Efficiency (%)
Dam age group ¹					
M	58	4620 ± 180^{b}	232 ± 14	7.12 (6.41-7.92)	4.88 ± 0.21
L	57	4000 ± 170^{a}	203 ± 13	6.26 (5.64-6.94)	4.64 ± 0.19
P Value		0.0140	0.1257	0.0859	0.3992
Birth rank ²					
1	45	4490 ± 190	222 ± 15	6.94 (6.19-7.78)	4.75 ± 0.22
2	70	4140 ± 150	213 ± 12	6.42 (5.84-7.06)	4.76 ± 0.17
P Value		0.1677	0.6273	0.3032	0.9738
Interaction ³					
M 1	17	4690 ± 310	230 ± 24	7.18 (6.01-8.57)	4.80 ± 0.35
M2	41	4560 ± 200	235 ± 15	7.07 (6.30-7.94)	4.96 ± 0.22
L1	28	4280 ± 240	215 ± 19	6.71 (5.82-7.75)	4.71 ± 0.27
L2	29	3720 ± 240	191 ± 18	5.83 (5.01-6.78)	4.57 ± 0.27
P Value		0.3925	0.4325	0.3995	0.6022

¹Dam age group: M=mature ewe, L=ewe lamb; ²dam birth rank: 1=singleton, 2=twin; ³interaction of dam age group and dam birth rank: M1=singleton born to a mature ewe, M2=twin born to a mature ewe, L1=singleton born to a ewe lamb, and L2=twin born to a ewe lamb; ⁴number of ewes.

2.4.4 Ewe longevity

When no culling occurred, the L2 ewes had the lowest (P<0.05) proportion of survival of all the ewes (Figure 2.2a). The M1 ewes had no deaths until their third set of lambs, at four years of age. However, with culling retrospectively imposed, survival proportions were much lower (P<0.05) than the actual survival of the ewes (Figure 2.2b), for all dam ages and birth ranks. If culling was imposed, M1 ewes were initially culled at weaning of their first lambs, as two-year olds, rather than as four-year-olds, after the weaning of their third lambs.

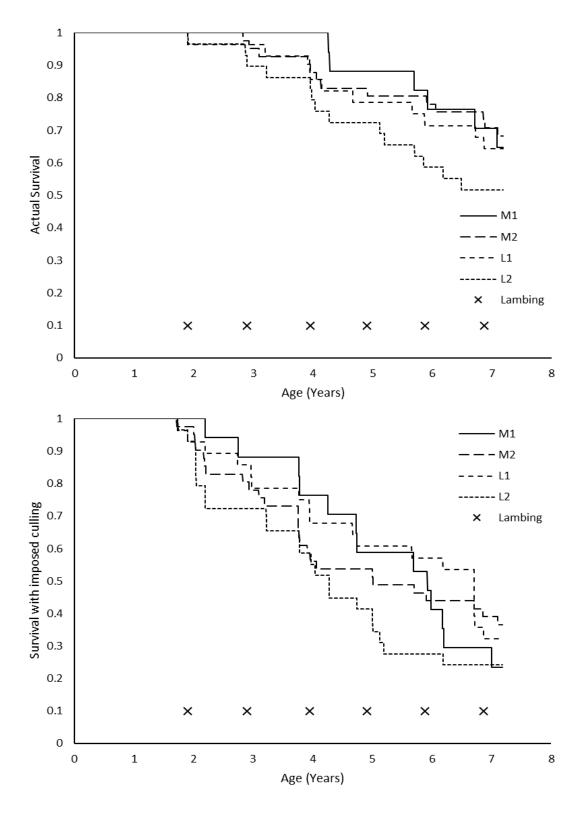


Figure 2.2: The actual (Figure 2.2a) and imposed-culling (Figure 2.2b) survival curves of ewes based on the interaction of dam age group and birth rank for eight years of the experimental period.

M1=singleton born to a mature ewe, M2=twin born to a mature ewe, L1=singleton born to a ewe lamb, and L2=twin born to a ewe lamb. Times marked with an x indicate lambing dates each year (D692, D1057, D1442, D1790, D2146, and D2507).

2.5 Discussion

The aims of this experiment were to determine the effects of dam age and birth rank on the lifetime performance of female offspring and to extend the data of Loureiro et al. (2012) which only followed these ewes to 2.5 years of age. Ewes that were born as twins to ewe lambs were lighter at birth, and throughout their lifetime compared with ewes born as singletons to ewe lambs or as singletons or twins born to mature ewes. This supports previous studies that show lambs born as twins are smaller at birth than singletons (Schreurs et al., 2010a; Young et al., 2010), and lambs born to ewe lambs are smaller than lambs that are born to mature ewes (Dýrmundsson, 1981; Annett and Carson, 2006; Gootwine et al., 2007; Young et al., 2010). However, it adds that there is an interaction of age of dam and birth rank on the ewe's live weights, with twins born to ewe lambs having additive effects on their live weight. Lambs born to ewe lambs are lighter than lambs born to mature ewes, due to the maternal constraint of body size of the ewe lambs. This is a result of the maturity of the ewe lamb, who is still growing to mature size while pregnant, and has different nutrient partitioning than a mature ewe, who is no longer growing (Gardner et al., 2007). Combined with the effect of being born as a twin, the L2 ewes are smaller at birth than the M2 ewes, and from the results of this study, these effects appear to persist for their lifetime. Body condition scores (Jefferies, 1961) did not differ during the experimental period, indicating that the lighter live weight is not due to poorer condition. This suggests that the 10 kg difference in live weight might be explained by differences in their mature frame size, and warrants investigation in future studies.

Previous studies have shown that ewe reproductive traits, such as ovulation rate (Ducker and Boyd, 1977), reproductive rate (fetuses/100 ewes bred; Corner-Thomas et al., 2015a), and lamb birth and weaning weights (Kenyon et al., 2009a) are affected by live weight of the ewe, with heavier ewes having more lambs, which are heavier at birth and weaning.

Therefore, it was expected that the L2 ewes would be disadvantaged in their reproductive performance, because they were 10 kg lighter than the M1 ewes. However, there was no difference in reproductive rates between the L2 and M1 ewes. The L2 ewes had heavier litter birth weights, but lighter litter weaning weights than the M1 ewes. This is possibly due to the lower rates of lamb survival among the L2 ewes and the other three groups. The L2 ewes had a similar number of lambs born, but weaned 0.1 less lambs than the other three groups, leading to lighter litter weaning weights than the other ewe groups.

Even though the L2 ewes were 10 kg lighter than the M1 ewes at breeding, this was not enough to significantly increase the ratio of litter weaning weight to ewe weight at breeding. The L2 ewes also had a lower predicted pasture consumption, but weaned fewer lambs for their lifetime, resulting in a similar efficiency to the M1 ewes. While the L2 ewes were not more efficient, there was no loss of production from having lighter live weights. However, because of the small group sizes further investigation, with larger group sizes, is warranted, to increase the statistical power, especially with binomial traits. Given the results in this study, a sample size of 189 per group would be required to show a statistically significant difference in efficiency among the groups.

The lighter live weights of L2 ewes with similarity in production indicates farmers could have more of these types of ewes on their farm for a given total feed availability, and subsequently produce greater weight of lamb per hectare. However, a more powerful study, with an economic evaluation would be warranted to determine the economic benefits for farmers. In New Zealand, the Sheep Improvement Limited (SIL) dual purpose index indicates ewe live weight for feed to have a value of \$-0.14/kg, indicating lighter ewes are more economical to feed (Amer, 2000). Additionally, selecting replacements that are born to ewe lambs can increase the rate of genetic gain, with a shorter generation

interval (younger parents) and greater selection intensity (more animals to select from; Rendell and Robertson, 1950). While it is not practical to select all lambs from ewe lambs, this result gives some incentive for farmers to breed their ewe lambs, and select some of their replacements from the lambs produced, especially those that are born as singletons.

Ewe survival tended to be lowest in L2 ewes compared with the other ewe groups, with losses occurring earlier in these ewes than in the other groups. This may have decreased their lifetime number and weaning weight of lambs produced, but it will also decrease their lifetime estimated pasture consumption. With sharp decreases in ewe numbers associated with lambing time, there are many ewes being fed from the weaning of their previous lamb until lambing, without any lambs being weaned, which may decrease efficiency of the L2 ewes.

Previous studies have shown that the average longevity of ewes under commercial conditions is 4.3-5.0 years of age, with the average rate of loss within flock being between 4.6-4.9% per year (Norman and Hohenboken, 1979; Hohenboken and Clarke, 1981; Brash et al., 1994). The M1 ewes had lower rates of reproductive performance compared with the other ewe groups, which is more apparent when looking at the survival curve when culling was imposed. This indicates that these ewes are producing fewer lambs, with high rates of barrenness. Ewe lambs that were detected to be showing oestrous prior to breeding, but were not bred, were heavier at their next breeding than ewe lambs that showed oestrous, were bred, and did rear a lamb (Baker et al., 1978). Therefore, barrenness in the M1 ewes may be a cause for their larger live weights throughout their lifetime, as they were not disadvantaged by pregnancy and lactation.

2.6 Conclusions

Ewes that are born to ewe lambs as twins are lighter than ewes born to ewe lambs as singletons and ewes that are born to mature ewes as twins, which are lighter than ewes born to mature ewes as singletons, for their lifetime to 6.5 years of age. The L2 ewes have the fastest rate of mortality, and M1 ewes have the slowest rate of mortality. The live weights of L2 ewes may not affect litter weight at weaning, producing similar weights of lambs weaned as the M1 ewes. However, this is insufficient to increase the efficiency of the L2 ewes compared with the other ewe groups, but consequently may not impair their production. Therefore, farmers could reasonably select lambs born to ewe lambs as replacements for their flock, without compromising their production. Further investigation is warranted, with a larger dataset and greater statistical power, to confirm the effects of selecting lambs born to ewe lambs, on their production and survival. An economic analysis is now required to determine whether there is sufficient financial benefit to farmers to warrant them implementing a policy of mating ewe lambs.

Chapter 3

Lambing performance of mature ewes and ewe lambs bred to the same rams at the same time

Previously published in part as the following:

Pettigrew EJ, Hickson RE, Blair HT, Griffiths KJ, Ridler AL, Morris ST, and Kenyon PR 2018. Differences in birth weight and neonatal survival rate of lambs born to ewe hoggets or mature ewes. New Zealand Journal of Animal Science and Production 78: 16-20.

Pettigrew EJ, Hickson RE, Blair HT, Griffiths KJ, Ridler AL, Morris ST, and Kenyon PR 2020. Differences in lamb production between ewe lambs and mature ewes. New Zealand Journal of Agricultural Research, DOI: 10.1080/00288233.2020.1713177.

Foreword to Chapter 3

The previous chapter (Chapter 2), demonstrated that there were significant differences in ewe mature weights based on their birth rank and the age of their dam, but produced similar numbers and weights of lambs over their lifetime. This suggests that ewes born to ewe lambs may be more efficient than ewes born to mature ewes. This study was a pilot study, and, therefore, had relatively small populations in each cohort, especially singletons born to mature ewes, and singletons and twins born to ewe lambs. To build on these findings and extend the knowledge of breeding ewe lambs, another experiment, with more animals, was undertaken (Chapters 3-5). The experiment included ewe lambs and mature ewes, bred at the same time, and to the same rams, lambed in the same environmental conditions, to produce the replacement ewes. This breeding, comparing all lambs born to a cohort of mature ewes and a cohort of ewe lambs, is presented in Chapter 3. This was followed by another study (Chapter 4) investigating breeding female progeny born in Chapter 3 as replacement ewe lambs themselves and comparing their lambing performance. The second breeding and lambing of the replacements is presented in Chapter 5. The intention is for these animals to be followed for their lifetime; however, this is out of the time limit scope of this PhD project.

Chapter 3 has been published in two parts in the New Zealand Journal of Animal Science and Production based on a presentation at the 78th Conference of the New Zealand Society of Animal Production, and in the New Zealand Journal of Agricultural Research.

The first publication describes the ewes and presents their breeding and lambing performance. Lamb survival is briefly examined. The second publication examines lamb performance from birth to weaning and includes a more extensive examination of lamb survival. As these are both stand-alone publications, there is necessarily some repetition

between them. Due to low numbers of triplets born to ewe lambs, and even lower survival of these lambs, they were excluded from the second paper, which required a change from analysing the data with a lamb birth rank by dam age group interaction to a contemporary group analysis. Due to the different analyses (using an interaction or a contemporary group), and the removal of triplets born to ewe lambs and lambs that were identified as born prematurely (via post-mortem examination) after publishing the initial paper, the means and their variations differ between published papers. Additionally, 95% confidence intervals are presented in Chapter 3.1, and S.E.M. are presented in Chapter 3.2 for lamb birth weights, for consistent formatting with other data presented in their respective tables.

3.1 Differences in birth weight and neonatal survival rate of lambs born to ewe lambs or mature ewes

3.1.1 Abstract

This experiment investigated differences in birth weights and survival in lambs born to ewe lambs or mature ewes. It included 1082 mature ewes with a scanning rate of 1.87 fetuses per ewe joined and 1026 ewe lambs with a scanning rate of 0.80 fetuses per ewe lamb joined, that were bred together, and lambed separately, under commercial farming conditions. At lambing, birth weight, lamb vigour score, and ewe maternal behaviour score were recorded. Lambs born to ewe lambs were lighter and less vigorous than lambs born to mature ewes (P<0.05). Singleton-born lambs were heavier at birth (P<0.05), and had greater survival at birth (P<0.05) than did twin-born lambs. Twin-born lambs were heavier (P<0.05) at birth, and had greater survival at birth (P<0.05) than triplets. There was an interaction of dam age and birth rank on lamb survival to weaning (P<0.01). At all birth ranks lambs born to ewe lambs had lower survival to weaning than lambs born to mature ewes, and the difference in survival increased with increasing birth rank. Lambs that had a vigour score of one had lower survival (83.5%; P<0.05) than lambs that had a vigour score of either two or three (88.6- and 91.4%, respectively). Maternal behaviour score did not affect lamb survival (P>0.05). Lambs born to ewe lambs are at greater risk of mortality, so farmers need to prioritise their time and resources towards ewe lambs at lambing time.

3.1.2 Introduction

Only 30-43% of farmers in New Zealand breed their ewe lambs at eight to nine months of age (Beef + Lamb New Zealand, 2019b). Breeding ewe lambs can have benefits, including increased lamb output per year and per lifetime, and better pasture utilisation during the spring (Kenyon et al., 2004a). However, lamb outputs from ewe lambs are lower, compared with that of mature ewes, weaning fewer lambs that are lighter at birth and at weaning (Kenyon et al., 2004a; Kenyon et al., 2014a; Pain et al., 2015).

Ewe lambs are commonly joined one month later than mature ewes in New Zealand (Kenyon, et al., 2004b). This allows the ewe lambs more time to attain puberty and maximises the chance that they become pregnant (Corner, et al., 2013a), but also confounds results of experiments that compare ewe lamb and mature ewe reproductive performance. Corner, et al. (2013a) joined ewe lambs and mature ewes to the ram at the same time, and reported lower pregnancy rates in ewe lambs, which gave birth to fewer lambs, that had lower birth and weaning weights and survival rates to weaning. However, that study had relatively low numbers, using 400 ewe lambs, and 399 mature ewes.

The majority of lamb deaths between birth and weaning occur during the first three days after birth (McMillan, 1983). Mortality rates have been reported between 5-30% in different farming systems (Kerslake, et al., 2005; Stevens, 2010), and the main causes of lamb mortality are dystocia and starvation and/or exposure (Everett-Hincks and Duncan, 2008; Stevens, 2010). Lamb mortality is largely associated with lamb birth weight (McMillan, 1983; Everett-Hincks and Dodds, 2008). There are few reports comparing causes of death and survival rate of lambs born to ewe lambs and mature ewes. This experiment was part of a larger experiment examining the effects of birth rank and dam age on replacement ewe performance. This experiment compared birth weight, vigour

Chapter 3

score and survival rate, in lambs born to either ewe lambs or mature ewes. It was hypothesised that twin-born lambs from ewe lambs would display lower rates of survival compared with lambs born to mature ewes of any birth rank, or with singletons born to ewe lambs.

3.1.3 Materials and methods

All animal procedures were carried out with the approval of the Massey University Animal Ethics Committee (MUAEC 17/16 and MUAEC 17/12).

3.1.3.1 Experimental design

The experiment was undertaken at Riverside Farm, Massey University, 11 km north of Masterton, New Zealand, between April 2017, and January 2018. It included 1082 multiparous three- and four-year-old mature Romney ewes, and 1026 nulliparous eightmonth-old Romney ewe lambs (minimum 38 kg) that were randomly allocated to one of two management mobs, each containing 541 mature ewes, and 513 ewe lambs. Pregrazing pasture measures prior to breeding were 2000 kg DM/ha for each mob. Ewe lambs were run with vasectomised rams for 68 days prior to the start of breeding. Mature ewes joined the ewe lambs and vasectomised rams 17 days before the start of breeding. Each mob was joined with 18 mixed-age Romney rams on 7th May 2017, for 34 days (two 17day reproductive cycles). After 34 days, mature ewes were removed and ewe lambs were run as a singleton group for a further ten days of breeding. Mature ewes and ewe lambs were maintained as separate mobs throughout pregnancy, under commercial farming conditions. Unfasted live weights and body condition scores of mature ewes and ewe lambs were recorded at breeding, pregnancy detection, and eight days prior to the start of lambing. Pre-grazing pasture measures during pregnancy were 1300 kg DM/ha for ewe lambs, and 1200 kg DM/ha for mature ewes, with supplemented baleage. All mature ewes and ewe lambs were shorn during late pregnancy (26 days prior to the start of lambing). Eight days prior to the planned start of lambing, mature ewes and ewe lambs were allocated to lambing paddocks based on dam age, pregnancy rank, and cycle pregnant. Pre-grazing pasture measures were 800 kg DM/ha for all classes. Mature ewes that were diagnosed pregnant in the second cycle were grouped together, as were ewe lambs that were diagnosed pregnant in the third cycle, regardless of pregnancy rank. Mature ewes and ewe lambs were checked twice daily until three days after the expected end of lambing. Lambs were tagged within 20 hours of birth, their birth rank, sex, and dam were identified, and birth weights were recorded. Dam maternal behaviour score (MBS; 1-5 score; 1= ewe flees and does not return during tagging, 5= ewe touches recorder during tagging; O'Connor, et al., 1985), and lamb vigour (adapted from Plush (2013), where 1= no- 2= moderate- and 3= regular struggle/movement during catching and restraint) were also recorded at this time for live lambs. Behavioural observations were made by one of three trained operators. Trained operators were sometimes accompanied by an additional person, who was present during scoring, but did not assign a score. The presence of the additional person was recorded in case ewes retreated further from two people than one. Two sets of quadruplet lambs were removed from the dataset.

3.1.3.2 Statistical analysis

Statistical analysis was carried out using SAS v9.4 (SAS, 2014). Live weight of ewes at breeding, pregnancy detection, and pre-lambing was analysed using a linear mixed model allowing for repeated measures. It included the fixed effects of mating mob, pregnancy rank, pregnancy cycle, ewe age, day of measurement, a two-way interaction of ewe age and day of measurement, and the random effect of ewe. Body condition score of ewes at breeding, pregnancy detection, and pre-lambing was analysed using a generalised linear model allowing for repeated measures, assuming a Poisson distribution and a logit transformation. It included the fixed effects of mating mob, pregnancy rank, pregnancy cycle, ewe age, day of measurement, a two-way interaction of ewe age and day of measurement, and the random effect of ewe. Pregnancy cycle and pregnancy rate were analysed using a generalised linear model, assuming a binomial distribution and a logit

transformation. The model included the fixed effect of ewe age, with a Bonferroni adjustment to allow for multiple comparisons.

Lamb birth weights were analysed using a general linear model that included the fixed effects of sex of lamb, birth rank, and age of dam, a covariate of date of birth, and a twoway interaction of age of dam and birth rank. Lamb vigour at birth was analysed using a generalised linear model using a logit transformation, assuming a Poisson distribution, with fixed effects of sex of lamb, birth rank, person scoring, and age of dam, a covariate of date of birth, and a two-way interaction of age of dam and birth rank. Maternal behaviour score of the ewe was analysed using a generalised linear model using a logit transformation, assuming a Poisson distribution, with fixed effects of litter size, person scoring, number of people present, and age of dam, a covariate of date of birth, and a twoway interaction of age of dam and litter size. For all models two-way interactions of age of dam and sex of lamb, and birth rank and sex of lamb, and a three-way interaction of age of dam, sex of lamb and birth rank were considered in initial models, but removed from all models as they were not significant (P>0.05). Analysis of variance for lamb survival to weaning and birth weight was analysed using a generalised linear model, assuming a binomial distribution and a logit transformation. The model included fixed effects of sex of lamb, birth rank, and age of dam, a covariate of date of birth, and a twoway interaction of age of dam and birth rank. This was used to create an equation of probability of death, based on birth weight for lambs born as singletons to either mature ewe or ewe lamb dams.

Lambs were recorded as alive or dead at tagging (as a proxy for survival at birth) and at weaning (lambs not present at weaning were assumed dead). Survival at tagging and weaning was analysed using a generalised linear model, assuming a binomial distribution

and using a logit transformation. The model included fixed effects of sex of lamb, birth rank, and age of dam, a covariate of date of birth, and a two-way interaction of age of dam and birth rank. In a second analysis, for lambs born alive, vigour score was added to the model predicting survival to weaning. A third analysis was conducted in which birth weight was added to the model to generate a prediction equation for survival to weaning for all singleton lambs born based on birth weight. The effect of birth weight on survival was modelled for singleton born lambs from mature dams, and ewe lamb dams.

3.1.4 Results

Mature ewes were heavier (P<0.0001) and had greater BCS (P<0.0001) than ewe lambs at breeding, and pregnancy detection (Table 3.1.1). Pregnancy results are shown in Table 3.1.1, for mature ewes and ewe lambs. Ewe lambs had a lower (P<0.0001) conception rate during the first cycle (19.8% versus 94.3%), lower (P<0.0001) overall pregnancy rate than mature ewes (80% versus 187%) and gave birth to fewer (P<0.0001) lambs per ewe bred (70% versus 183%).

Table 3.1.1: Number of mature ewes and ewe lambs present at breeding, pregnancy detection (PD), and pre-lambing, least-squares means (± S.E.M.) of live weights, and body condition scores at these dates, along with pregnancy-detection results (percent per birth rank, cycle, and pregnancy rate; (95% CI)), number of lambs tagged from mature ewes and ewe lambs and number of lambs born per ewe bred (NLB).

	Ewe lambs	Mature ewes	P value
n			
Breeding	1026	1082	
Pregnancy detection	1013	1079	
Pre-lambing	604	1050	
Live weight (kg)			
Breeding	49.5 ± 0.4	71.2 ± 0.4	< 0.0001
Pregnancy detection	52.2 ± 0.4	70.5 ± 0.4	< 0.0001
Pre-lambing	59.8 ± 0.4	74.2 ± 0.4	< 0.0001
Body condition score			
Breeding	2.85 ± 0.05	3.36 ± 0.06	< 0.0001
Pregnancy detection	2.74 ± 0.05	3.11 ± 0.05	< 0.0001
Pre-lambing	3.03 ± 0.05	2.93 ± 0.05	< 0.0001
Cycle pregnant (%)			
1^{st}	19.8 (17.1-22.0)	94.3 (93.8-96.4)	< 0.0001
$2^{ m nd}$	26.9 (23.8-29.2)	4.1 (2.9-5.3)	< 0.0001
3^{rd}	15.7*	-	
Pregnancy detection			
Pregnancy rate (number of	80	187	
fetuses per 100 ewes joined)			
Pregnancy rank (%)			
0	37.2 (34.3-40.2)	1.4 (0.8-2.3)	< 0.0001
1	44.3 (41.3-47.4)	18.9 (16.7-21.4)	< 0.0001
2	17.0 (14.8-19.5)	69.9 (67.1-72.6)	< 0.0001
3	0.2 (0.04-0.8)	9.1 (7.6-11.0)	< 0.0001
Number of lambs tagged	722	1979	
NLB (%)	70	183	

^{*}Means for animals pregnant in the third cycle were not analysed, as only ewe lambs were presented for breeding during this time.

There were no significant interactions between dam age and lamb birth rank (P>0.05) for lamb birth weight, lamb vigour, MBS, and lamb survival at birth (Table 3.1.2). Lambs that were born to mature ewes were heavier (P<0.001) at birth, and had greater survival (P<0.001) and vigour scores (P<0.01) at birth than lambs born to ewe lambs. There was no difference (P>0.05) in MBS between mature ewes and ewe lambs. At all birth ranks

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lambs born to ewe lambs had lower (P<0.05) survival to weaning than lambs born to mature ewes, and the difference in survival increased with increasing birth rank.

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Table 3.1.2 Least-squares means \pm S.E.M. for birth weight of lambs (BWT), least-squares means (95% CI) for lamb vigour (Vigour) and maternal behaviour score (MBS), and survival (95% CI) of lambs at tagging and to weaning, by dam age (mature ewe (M) vs. ewe lamb (L)), birth rank (singleton (1) vs twin (2) vs triplet (3)), sex of lamb (male vs female) and the interaction of dam age and lamb birth rank.

	n	BWT (kg)	Lamb survival at tagging (%)	n	Vigour	n	MBS	Lamb survival to weaning (%)
Dam age								
Mature ewe	1967	$5.14^{b}(5.09-5.19)$	96.1 ^b (94.6-97.1)	1877	2.38 ^b (2.23-2.54)	985	2.69 (2.49-2.91)	83.1 ^b (80.4-85.5)
Ewe lamb	717	3.47 ^a (3.27-3.66)	82.2 ^a (72.1-89.2)	624	1.85 ^a (1.56-2.19)	499	2.66 (2.09-3.39)	74.3 ^a (30.5-64.8)
P value		< 0.0001	0.0002		0.0027		0.9263	< 0.0001
Birth rank								
Singleton	622	5.31° (5.24-5.38)	94.4 (91.5-96.3)	570	2.23 (2.08-2.40)	554	2.61 (2.43-2.80)	85.5° (82.0-88.4)
Twin	1763	4.34 ^b (4.28-4.39)	94.0 (92.5-95.2)	1667	2.17 (2.03-2.31)	839	2.64 (2.46-2.86)	76.3 ^b (73.7-78.8)
Triplet	299	3.27 ^a (2.99-3.55)	82.1 (66.6-91.3)	264	1.91 (1.50-2.43)	91	2.78 (1.94-3.97)	32.8 ^a (14.5-58.4)
P value		< 0.0001	0.0627		0.4050		0.9258	< 0.0001
Sex								
Male	1288	4.44 ^b (4.34-4.55)	90.6 (87.1-93.3)	1197	2.07 (1.87-2.28)	-	-	64.1 ^a (55.0-72.3)
Female	1389	4.16 ^a (4.06-4.27)	92.1 (90.0-94.4)	1306	2.14 (1.94-2.35)	-	-	71.2 ^b (62.9-78.4)
P value		< 0.0001	0.2583		0.2102	-	-	0.0009
Dam age * birth r	ank							
M1	216	6.14 (6.03-6.25)	97.4 (94.3-98.8)	209	2.48 (2.25-2.74)	201	2.60 (2.35-2.87)	90.5 ^e (85.9-93.7)
M2	1461	5.18 (5.13-5.22)	97.4 (96.5-98.1)	1411	2.39 (2.25-2.55)	696	2.70 (2.51-2.92)	84.1 ^d (82.1-85.9)
M3	290	4.11 (4.01-4.20)	91.1 (87.3-93.9)	257	2.27 (2.07-2.50)	88	2.78 (2.43-3.18)	70.3° (64.7-75.3)
L1	406	4.48 (4.39-4.56)	88.3 (84.4-91.4)	361	2.01 (1.85-2.19)	353	2.63 (2.42-2.85)	78.6 ^b (73.9-82.6)
L2	302	3.49 (3.40-3.59)	86.4 (81.8-90.1)	256	1.96 (1.79-2.16)	143	2.59 (2.31-2.91)	66.4 ^b (60.5-71.7)
L3	9	2.43 (1.88-2.98)	67.1 (28.6-91.2)	7	1.61 (1.00-2.58)	3	2.77 (1.38-5.59)	9.1 ^a (1.2-45.1)
P value		0.9727	0.9203		0.8329		0.7723	0.0417

a,b,c,d,e Means with different superscripts within column are significantly different to the P value indicated

Singleton-born lambs were heavier at birth (P<0.05) than twin-born lambs, which were heavier (P<0.05) at birth than triplets (Table 3.1.2). There was no effect of birth rank on lamb vigour scores, MBS, or lamb survival at birth (P>0.05). Male lambs were heavier at birth (P<0.05), and had greater survival (P<0.05) compared with female lambs, and there was no difference (P>0.05) between sexes for lamb vigour scores, or the percentage of lambs alive at birth. The probability for survival based on birth weight of singletons born to mature ewes or ewe lambs is presented below. Low numbers of multiples from ewe lambs meant that models for twins and triplets born to ewe lambs or mature ewes were not presented.

Probability of death of a singleton born to a mature ewe

$$= \frac{e^{(14.03475 - 5.7463xBWT + o.489xBWT^2)}}{1 + e^{(14.03475 - 5.7463xBWT + o.489xBWT^2)}}$$

Probability of death of a singleton born to a hogget

$$= \frac{e^{(9.40475 - 4.8464xBWT + o.5126xBWT^2)}}{1 + e^{(9.40475 - 4.8464xBWT + o.5126xBWT^2)}}$$

Of lambs that were alive at birth (Table 3.1.3), lambs that had a vigour score of one were 1.68 times more likely (P<0.05) to die than lambs that had a vigour score of three. Lambs that had a vigour score of two were 1.34 times more likely to die than lambs that had a vigour score of three, although there was no significant difference (P>0.05) in survival rate of lambs with a vigour score of two or three.

Table 3.1.3 Survival (% (95% CI)) until weaning, of lambs that were born alive, by lamb vigour score (Vigour; 1-3 score; 1= no struggle during catching and restraint, 3= regular struggle during catching and restraint), and maternal behaviour score (MBS; 1-5 score; 1= ewe flees and does not return during tagging, 5= ewe touches recorder during tagging). Values are back-transformed means and 95% confidence intervals.

		n	Lamb survival to weaning (%)
Vigour			
	1	388	72.5 ^a (61.6-81.2)
	2	922	77.0 ^b (67.8-84.2)
	3	1196	82.3 ^b (74.2-88.2)
	P value		0.0047
MBS			
	1	282	76.8 (65.8-85.0)
	2	900	79.0 (70.2-85.7)
	3	681	79.6 (71.1-86.1)
	4	498	75.2 (65.0-83.2)
	5	135	76.8 (63.5-86.3)
	P value		0.6017

3.1.5 Discussion

Ewe lambs had lower conception rates during the first cycle, lower pregnancy rates (number of fetuses present per 100 females joined) than mature ewes; this was consistent with previous literature (Kenyon, et al., 2004c; Kenyon, et al., 2014b). Lower conception rates during the first cycle from ewe lambs are possibly attributed to ewe lambs being shy to the rams, and not standing correctly for courtship, compared with mature ewes (Edey, et al., 1978). Birth weight was lower for lambs born to ewe lambs, than for lambs born to mature ewes (Dýrmundsson, 1981; Annett and Carson, 2006; Gootwine, et al., 2007; Young, et al., 2010), and lower for lambs born as multiples (Schreurs, et al., 2010a; Young, et al., 2010).

Lamb survival was greater at birth, and to weaning for lambs that were born to mature ewes, compared with ewe lambs (Kerslake et al., 2005; Stevens, 2010). Everett-Hincks et al. (2005) reported that lambs born to two-year-old dams had lower rates of survival than did lambs born to older dams. They also noted that female lambs had greater survival rates than did male lambs, which was also observed in the current study. Lamb survival is largely related to birth weight of lambs (Karn and Penrose, 1951; Morris et al., 2005; Schreurs et al., 2010b; Mulvaney et al., 2012). Therefore, differences in lamb birth weight due to dam age or lamb birth rank will affect survival rates of these groups. Everett-Hincks et al. (2005) reported that as litter size increased, litter survival decreased, which concur with the results of this experiment. Based on the prediction equation, to achieve a survival rate of 85% or greater, lamb birth weights needed to be in the 3.9 to 5.5 kg range for singleton lambs born to ewe lambs, and 4.3 to 7.4 kg range for singleton lambs born to mature ewes. Kerslake et al. (2005) and Young et al. (2010) reported that dystocia and starvation/exposure were the largest causes of lamb deaths in the perinatal period.

Maternal behaviour score did not differ between ewe age groups, or among litter sizes. This contradicts previous results, which suggests that higher dam age or higher litter size resulted in higher MBS, however, that research did not use ewe lambs (O'Connor et al., 1985). O'Connor et al. (1985) showed that an increase in MBS resulted in greater lamb survival, as did Everett-Hincks et al. (2005), however this was not seen in the current study, where there was no difference in lamb survival based on maternal behaviour scores. This shows that the flight or fight response to people during tagging may not indicate the ability of the ewe as a mother.

Lamb survival was affected by lamb vigour score, and lambs that had greater vigour scores had greater survival rates; Dwyer (2008) reported previously that higher lamb vigour at birth resulted in higher lamb survival rates until weaning. Smith (1977) and Owens, et al. (1985) reported that increasing ewe age resulted in fewer weak lambs at birth. However, those studies did not involve ewe lambs.

3.1.6 Conclusions

In conclusion, lambs that are born to ewe lambs are smaller at birth, have lower vigour scores and lower rates of survival at birth and until weaning, than lambs that are born to mature ewes. There was no difference in maternal behaviour score between mature ewes and ewe lambs. Poor lamb vigour may be a good indicator for farmers to use for intervention to improve survival rates.

3.2 Differences in lamb production between ewe lambs and mature ewes

3.2.1 Abstract

Currently comparisons of lamb output from either ewe lambs or mature ewes are confounded, as the age groups are bred to different sires, and lamb at different times. The aim of this experiment was to compare the reproductive performance of ewe lambs and mature ewes, bred at the same time to the same sires, and lambed in the same climatic conditions. The experiment included 1082 mature ewes and 1026 ewe lambs that gave birth to 2701 lambs. Birth weights of lambs were 3.92 ± 0.06 kg and 5.02 ± 0.06 kg, and weaning weights of lambs were 24.03 ± 0.24 kg and 26.68 ± 0.29 kg for ewe lambs and mature ewes, respectively. Lambs born to ewe lambs were less vigorous than lambs born to mature ewes, even when adjusted for their lighter birth weights. Lamb survival during the neonatal period was 92.2% and 97.3% for lambs born to ewe lambs or mature ewes, respectively. The effect of birth weight on survival within each dam age and lamb birth rank followed a quadratic form, and differed for each group. Farmers should preferentially allocate all ewe lambs and mature ewes bearing triplets to lamb in paddocks that provide better conditions for lambing.

3.2.2 Introduction

It is estimated that 30-43% of farmers in New Zealand breed their ewe lambs at eight-tonine months of age (Beef + Lamb New Zealand, 2019b). Breeding ewe lambs (also termed hoggets) can have benefits, including increased lamb output per farm per year and per ewe per lifetime, as well as increased pasture utilisation during the spring (Kenyon et al., 2004a). However, the reproductive performance from ewe lambs is poorer than the reproductive performance of mature ewes (Kenyon et al., 2004a; Morris et al., 2005; Kenyon et al., 2008b; Corner et al., 2013a; Mulvaney et al., 2013; Corner-Thomas et al., 2015a; Edwards et al., 2016; Griffiths et al., 2016; Corner-Thomas et al., 2017; Edwards and Juengel, 2017). Compared with mixed age ewes, ewe lambs produce fewer lambs, which are lighter at birth and at weaning, and have reduced survival (Kenyon et al., 2004a; Kenyon et al., 2014a; Pain et al., 2015). Ewe lambs are commonly bred a month later than mature ewes in New Zealand (Kenyon et al., 2004a). This allows more time for the ewe lamb to attain puberty and maximises the chance that they become pregnant (Corner et al., 2013a). This also confounds lambing outcomes, and a true comparison of reproductive performance between ewe lambs and mature ewes cannot be made. Additionally, mature ewes and ewe lambs require different feeding management during their pregnancy, as the ewe lambs are still growing themselves (CSIRO, 2007). Corner et al. (2013a) and Loureiro et al. (2011) bred ewe lambs and mature ewes at the same time, and reported ewe lambs had lower pregnancy rates, fewer lambs born, lower birth and weaning weights and poorer survival rates of their lambs to weaning. While significant, these studies were limited by the small number of animals used. It is important for farmers to know the differences in survival rates between lambs born to mature ewes or ewe lambs when deciding to breed their ewe lambs, so that they can prioritise better lambing paddocks for the ewe lambs.

The majority of lamb deaths between birth and weaning occur during the first three days after birth (McMillan, 1983; Everett-Hincks and Dodds, 2008). Mortality rates have been reported between 5-30% in different farming systems, including mature ewes and ewe lambs as dams (Kerslake et al., 2005; Everett-Hincks and Dodds, 2008; Stevens, 2010), with the main causes of lamb mortality being dystocia and starvation and/or exposure (Everett-Hincks and Duncan, 2008; Stevens, 2010). Lamb mortality is largely associated with lamb birth weight, with lambs at the extremes of birth weight ranges having a higher chance of mortality (McMillan, 1983; Everett-Hincks and Dodds, 2008). Mortalities of lambs with low birth weights are commonly associated with starvation and/or exposure, while mortalities of lambs with high birth weights are commonly associated with dystocia (Kerslake et al., 2005; Everett-Hincks and Duncan, 2008). Lambs born to ewe lambs as singletons have higher rates of death due to dystocia than starvation and/or exposure, and lambs born as twins and triplets have higher rates of death due to starvation and/or exposure (Stevens, 2010), however, triplets also have higher rates of death due to dystocia caused by entanglement (Brown et al., 2014).

The aim of this experiment was to compare the performance to weaning of lambs born as singletons and twins to ewe lambs and singletons, twins and triplets born to mature ewes, born during the same time, and in the same climatic conditions. Traits measured include the live weight of lambs at birth, early-life, and weaning, vigour score, and lamb survival. It was hypothesised that lambs born to ewe lambs would have poorer survival than lambs born to mature ewes, under the same climatic conditions, due to their lower birth weight and vigour score. The companion chapter, Chapter 3.1, reported that the ewe lambs were lighter and produced fewer lambs than the mature ewes. Lambs born to ewe lambs were lighter than lambs born to mature ewes at birth (Chapter 3.1). Lambs with low vigour

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score at birth were less likely to survive until weaning, but maternal behaviour score did not affect lamb survival (Chapter 3.1).

3.2.3 Materials and methods

The experiment was conducted at Riverside Farm, Massey University (latitude 40°50'S, longitude 175°37'E), 11 km north of Masterton, New Zealand, between April 2017, and January 2018. All animal procedures were carried out with the approval of the Massey University Animal Ethics Committee (MUAEC 17/16 and MUAEC 17/12).

The experiment included 1082 multiparous three- and four-year-old mature Romney ewes and 1026 nulliparous eight-month-old Romney ewe lambs. The mature ewes and ewe lambs were randomly allocated into two groups for breeding, 17 days before ram introduction (D0; April 20th 2017), each breeding group contained 541 mature ewes, and 513 ewe lambs for the breeding period. These two breeding groups were each joined with 10 vasectomised (teaser) rams, for one reproductive cycle (17 days). The ewe lambs had been previously joined with the vasectomised rams, as one cohort, for 51 days (three reproductive cycles) prior to D0.

Estimate of pre-grazing herbage mass at the start of breeding was 1980 kg DM/ha. Pasture masses were estimated using a Jenquip rising plate meter. At D17 unfasted live weights and body condition scores (BCS; 1–5 score; (Jefferies, 1961) were recorded. At D17 (May 7th, 2017) the vasectomised rams were removed, and 18 entire mature Romney rams were joined with each group, for 34 days. At D51 the mature ewes were removed from the breeding group. The ewe lambs and all 36 rams were joined as one cohort, for a further nine days. At D60 the rams were removed from the ewe lambs.

From D51 until D156 the mature ewes and ewe lambs were managed as two separate groups due to different nutritional needs, under commercial farming conditions. Ewe lambs have additional nutritional needs when pregnant, to sustain their own growth, compared with mature ewes (CSIRO, 2007). Ewe lambs had an estimated pre-grazing

herbage mass during pregnancy of 1170 kg DM/ha, and the mature ewes had an estimated pre-grazing herbage mass during pregnancy of 1000 kg DM/ha. Pregnancy detection occurred at D97 for mature ewes and D110 for ewe lambs using transabdominal ultrasound. At D104 unfasted live weights and BCS were recorded. Ewes and ewe lambs were diagnosed as carrying zero, one, two, or three fetuses, and the cycle that conception occurred was estimated. At pregnancy detection any ewes and ewe lambs carrying zero fetuses were removed from the experiment (29 and 409 for mature ewes and ewe lambs, respectively). Further detail on the management, and comparison of pregnancy results between the mature ewes and ewe lambs has been previously published (Chapter 3.1).

On D156, eight days prior to the planned start of lambing, ewes had unfasted live weights and BCS recorded, and were allocated to their lambing paddocks. Mature ewes pregnant to the first cycle of breeding (n=1019; predicted to lamb D163 to D180) were split by pregnancy rank, with ewes carrying one fetus (n=191) in three paddocks (11 ewes/ha), ewes carrying two fetuses (n=734) in 14 paddocks (8.5 ewes/ha), and ewes carrying three fetuses (n=94) in four paddocks (6.5 ewes/ha). Mature ewes pregnant to the second cycle of breeding (n=48; predicted to lamb D181 to D198) regardless of pregnancy rank were lambed together in two paddocks (7.5 ewes/ha). Ewe lambs pregnant in the first cycle of breeding (n=201; predicted to lamb D163 to D180) were split by pregnancy rank, with ewe lambs carrying one fetus (n=133) in four paddocks (9 ewes/ha), and ewe lambs carrying two fetuses (n=68) in two paddocks (8 ewes/ha). Ewe lambs pregnant in the second cycle of breeding (n=273; predicted to lamb d181 to d198) were split by pregnancy rank, with ewe lambs carrying one fetus (n=195) in two paddocks (9 ewes/ha), and ewe lambs carrying two fetuses (n=78) in two paddocks (8 ewes/ha). Ewe lambs pregnant in the third cycle of breeding (n=159; predicted to lamb D198 to D207) regardless of pregnancy rank, were lambed together in one paddock (9.5 ewes/ha). Pregrazing herbage mass estimate was 840 kg DM/ha for all groups on D156. All ewes were managed in their lambing paddocks until D208. At this time, paddocks of ewes were joined, within ewe age, pregnancy rank, and cycle pregnant, and rotationally grazed until weaning (D258). The mature ewes and ewe lambs had unfasted live weights and BCS recorded on D258.

3.2.3.1 Measurements on the lambs

Lambing occurred from D159 (26th September 2017) to D309 (15th November 2017) of the experimental period. All ewes were observed twice daily at morning and afternoon during the lambing period, and until three days after the expected end of lambing. Lambs were tagged during twice-daily lambing observations (approx. 8 a.m. and 2 p.m.), their birth rank, sex, and dam were identified, and birth weight was recorded. Lambs were only tagged once they were old enough to stand and walk, and had time to bond with their mother. Lamb vigour (adapted from Plush (2013), where 1 = no-, 2 = moderate-, and 3 = noregular struggle/movement during catching and restraint) was also recorded at this time for all live lambs. Behavioural observations were made by one of three trained operators. Unfasted live weight of the lambs was recorded in early-life, on D200 for lambs born to mature ewes, and lambs born to ewe lambs during the first cycle of lambing, and on D218 for lambs born to ewe lambs during the second and third cycles of lambing. Unfasted live weight of the lambs were recorded at D258, when they were weaned. The average age of lambs at the early-life weight was 29 days (L29), and at weaning was 82 days. Lambs that were dead at tagging were considered to be born dead for survival analysis. Lambs that were not present at L29 and at weaning were assumed dead at early-life for survival analysis. Lambs that were not recorded at L29, but were recorded at weaning (n=29) were considered alive for survival. Lambs that were not recorded at weaning were assumed to be dead for survival analysis.

3.2.3.2 Statistical analysis

Statistical analysis was carried out using SAS software (version 9.4; SAS Institute, Cary, NC, USA). Live weight of ewes at breeding, mid-pregnancy, pre-lambing, and weaning was analysed using a linear mixed model allowing for repeated measures. It included the fixed effects of mating mob, pregnancy rank, pregnancy cycle, ewe age, day of measurement, and the two-way interaction of ewe age and day of measurement, and the random effect of ewe. Body condition score of ewes at breeding, pregnancy detection, and pre-lambing was analysed using a generalised linear model allowing for repeated measures, assuming a Poisson distribution and a logit transformation. It included the fixed effects of mating mob, pregnancy rank, pregnancy cycle, ewe age, day of measurement, a two-way interaction of ewe age and day of measurement, and the random effect of ewe.

Measurements on the lambs

Live weight of lambs at tagging, at early-life, and at weaning, and average daily liveweight gains of the lambs during early, late, and the entire lactation period were analysed using a general linear model. The model included the fixed effects of age of dam, and sex of lamb, the nested effect of lamb birth rank within dam age group, and the nested effect of lambing paddock within dam age group. The model analysing live weight at birth and weaning, and average daily liveweight gain for the entire lactation included date of birth of the lambs as a covariate. Since L29 weight measurement of lambs was taken at two different time points, age of lamb at L29 weight was used as a covariate for L29 weight and the average daily liveweight gain during early and late lactation. The interaction of sex of lamb and age of dam was included in all models, but was removed as it was not significant (P>0.05). The nested effects of birth rank within sex of lamb, and birth rank within a sex of lamb and age of dam interaction were also included, but were removed as they were not significant (P>0.05). The covariate of lamb age at early-life

weight was tested, but not significant (P>0.05), and subsequently removed in the analysis of average daily gain during the late lactation period.

Lamb vigour was analysed using a generalised linear model, assuming a Poisson distribution and a logit transformation. The fixed effects of dam age group and assessor were included in the model. The covariate of date of birth of the lamb was included in the model. The nested effect of birth rank of the lamb, within dam age group was also included in the model. A secondary analysis of lamb vigour score also included the covariate of birth weight of the lamb included in the model. The fixed effects of sex of lamb, proportion of litter surviving to weaning, and lambing paddock within dam age were initially included in the model, but were not significant (P>0.05), and so were removed. The interaction of sex of lamb and age of dam was included, but was removed as it was not significant (P>0.05). The nested effects of birth rank within sex of lamb, and birth rank within a sex of lamb and age of dam interaction were also included, and removed as they were not significant (P>0.05).

Lamb survival at tagging, L29, and weaning, and lamb survival from birth to weaning considered all lambs born, and was analysed using a generalised linear model, assuming a binomial distribution and a logit transformation. The fixed effects of dam age group and paddock within dam age group were fitted. The nested effect of litter size, within dam age group was fitted in the model. The covariates of lamb birth weight and lamb birth weight squared were also fitted in the model. The models for analysing lamb survival at L29, weaning, and from birth to weaning also had the fixed effect of sex of lamb. The fixed effect of sex of lamb was initially included in lamb survival at birth, but was not significant (P>0.05), and removed. The interaction of sex of lamb and age of dam was included in all models, but was removed as it was not significant (P>0.05). The nested

effects of birth rank within sex of lamb, and birth rank within a sex of lamb and age of dam interaction were also included, and removed as they were not significant (P>0.05).

Lamb survival to weaning was also analysed using a generalised linear model, assuming a binomial distribution and a logit transformation. The fixed effects of dam age group and lamb birth rank as a contemporary group and sex of lamb were included in the model. The covariates of birth weight and birth weight squared were nested within the dam age group and lamb birth rank contemporary groups. Quadratic regressions were used to predict lamb survival at a given birth weight for each contemporary group. Confidence intervals at the 95% level were used to test for differences in lamb survival to weaning for the contemporary groups of dam age group and lamb birth rank.

3.2.4 Results

The mature ewes were heavier (P<0.001) than the ewe lambs throughout the experiment (Table 3.2.1). Mature ewes had greater BCS at breeding (P<0.001) and at mid-pregnancy (P<0.01), but lower (P<0.05) at pre-lambing than ewe lambs (Table 3.2.1). There was no difference in BCS (P>0.05) between the ewe groups at weaning of their lambs. Mature ewes gained 2.9 kg from breeding to pre-lambing, less than the expected increase in weight due to conceptus weight (Table 3.2.1), and their BCS also decreased by 0.67 of a BCS. Ewe lambs gained 10.3 kg during pregnancy and increased their BCS. During lactation the mature ewes maintained their weight, but lost BCS, while ewe lambs increased live weight, but decreased BCS. The mature ewes gave birth to 1.83 lambs and the ewe lambs 0.7 lambs per ewe presented for breeding.

Table 3.2.1: Least squares means (± S.E.M.) for live weight (kg) and least squares means (95% CI) for body condition score (BCS; 1-5 score) of mature ewes and ewe lambs from the start of breeding until the weaning of their lambs. The values presented for BCS are back-transformed LS means.

		Mature ewes	Ewe lambs	P value
Live	weight (kg)			
	Breeding	71.3 ± 0.2^{b}	48.8 ± 0.2^a	< 0.0001
	Mid-pregnancy	70.5 ± 0.2^{b}	51.5 ± 0.2^a	< 0.0001
	Pre-lambing	74.2 ± 0.2^b	59.1 ± 0.2^{a}	< 0.0001
	Weaning	74.0 ± 0.2^b	64.2 ± 0.3^{a}	< 0.0001
BCS				
	Breeding	3.30 (3.18-3.41) ^b	2.88 (2.75-3.01) ^a	< 0.0001
	Mid-pregnancy	3.05 (2.95-3.16) ^b	2.77 (2.64-2.90) ^a	0.0011
	Pre-lambing	2.88 (2.78-2.99) ^a	3.06 (2.92-3.20) ^b	0.0405
	Weaning	2.63 (2.53-2.74)	2.64 (2.50-2.79)	0.9333

^{a,b} Means with different superscripts within row are significantly different to the P value indicated

Lambs born as singletons to mature ewes were heaviest (P<0.001) compared with all other groups at birth, early-life weight (L29) and weaning (Table 3.2.2). At birth, lambs born as twins to mature ewes were heavier than lambs born as triplets to mature ewes, and lambs born to ewe lambs, regardless of birth rank. At birth, lambs born as triplets to

mature ewes, and lambs born as singletons to ewe lambs were not different to each other, and heavier than lambs born as twins to ewe lambs. At L29 and weaning, lambs born as twins to mature ewes and lambs born as singletons to ewe lambs were not different, but were heavier than lambs born as triplets to mature ewes, and lambs born as twins to ewe lambs. At L29 and weaning lambs born as triplets to mature ewes, and lambs born as twins to ewe lambs were not different.

Average daily liveweight gains during early lactation were greatest (P<0.001) for lambs born as singletons to mature ewes (Table 3.2.2). During early lactation lambs born as singletons to ewe lambs had greater average daily liveweight gains than lambs born as twins or triplets to mature ewes, and lambs born as twins to ewe lambs. Lambs born as twins to mature ewes had greater average daily liveweight gains in early lactation than lambs born as twins to ewe lambs. Lambs born as triplets to mature ewes had similar average daily liveweight gains during early lactation to lambs born as twins to both mature ewes and ewe lambs.

The average daily gains during late lactation were greatest (P<0.001) for lambs born as singletons to mature ewes (Table 3.2.2). Lambs born as twins to ewe lambs had the lowest (P<0.001) average daily gains during late lactation. Lambs born as twins or triplets to mature ewes, or as singletons to ewe lambs were intermediary, and indifferent from each other for their average daily gains during late lactation.

Lambs born as singletons to mature ewes had the greatest (P<0.001) average daily liveweight gains during the entire lactation period (Table 3.2.2). Lambs born as twins to mature ewes and lambs born as singletons to ewe lambs had greater average daily liveweight gains than twins born to ewe lambs. Lambs born as triplets to mature ewes had

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similar average daily liveweight gains during the entire lactation to lambs born as twins to both mature ewes and ewe lambs.

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Table 3.2.2: Least-squares means (± S.E.M.) for birth, early-life (L29) and weaning weight (kg), and average daily liveweight gain from birth to early-life (L29; ADG early; g/day), early-life to weaning (L29; ADG late; g/day), and from birth to weaning (ADG all; g/day) of lambs based on dam age (mature ewe vs. ewe lamb), and birth rank of lamb within dam age (mature ewe - singleton vs. mature ewe - triplet vs. ewe lamb - singleton vs. ewe lamb - twin).

	n	Birth weight (kg)	n	Early-life weight (kg)	n	ADG early (g/day)	n	Weaning Weight (kg)	n	ADG late (g/day)	n	ADG all (g/day)
Dam age												
Mature ewe	1959	5.02 ± 0.06^{b}	1653	13.28 ± 0.16^{b}	1650	287 ± 5^{b}	1618	26.68 ± 0.29^{b}	1598	255 ± 3^{b}	1615	262 ± 3^{b}
Ewe lamb	697	3.92 ± 0.06^{a}	539	11.86 ± 0.13^{a}	538	259 ± 4^a	522	24.03 ± 0.24^{a}	513	216 ± 3^a	521	239 ± 3^{a}
P value		< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001
Birth rank within	dam ag	e										
Mature ewe – singleton	214	5.65 ± 0.14^{d}	192	15.35 ± 0.42^{c}	192	$350 \pm 13^{\rm d}$	193	30.08 ± 0.75^{c}	190	284 ± 9^{c}	193	299 ± 9^{d}
Mature ewe – twin	1458	5.16 ± 0.06^{c}	1266	12.98 ± 0.15^{b}	1265	270 ± 5^{b}	1223	26.16 ± 0.28^{b}	1214	248 ± 3^b	1222	$254 \pm 3^{\rm bc}$
Mature ewe – triplet	287	4.25 ± 0.14^{b}	195	11.50 ± 0.44^{a}	193	241 ± 14^{ab}	202	23.79 ± 0.78^{a}	194	233 ± 9^{b}	200	234 ± 9^{ab}
Ewe lamb – singleton	402	4.38 ± 0.08^{b}	330	12.89 ± 0.20^{b}	330	291 ± 6^{c}	322	25.90 ± 0.37^{b}	316	239 ± 4^{b}	322	263 ± 4^{c}
Ewe lamb – twin	295	3.45 ± 0.09^{a}	209	10.83 ± 0.29^{a}	208	227 ± 9^a	200	22.16 ± 0.53^{a}	197	194 ± 6^{a}	199	214 ± 6^a
P value		< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001

a,b,c,d Means with different superscripts within column are significantly different to the P value indicated

Lambs born to ewe lambs were less vigorous than lambs born to mature ewes (P<0.001). Even with fitting birth weight of the lambs as a covariate to the model, lambs born to ewe lambs were still less vigorous (P<0.01) than lambs born to mature ewes. There was no difference (P>0.05) in the vigour score of lambs at tagging, with or without birth weight covariate adjustment for any birth ranks within dam ages (Table 3.2.3).

Table 3.2.3: Lamb vigour score (1-3 score) without (Lamb vigour 1) and with (Lamb vigour 2) lamb birth weight adjustment for lambs based on dam age group (mature ewe vs. ewe lamb), and birth rank of lamb within dam age (mature ewe - singleton vs. mature ewe - twin vs. mature ewe - triplet vs. ewe lamb - singleton vs. ewe lamb - twin). The values presented are back-transformed LS means (95% CI).

	n	Lamb vigour 1	Lamb vigour 2
Dam age			
Mature ewe	1880	2.38 (2.23-2.54) ^b	2.36 (2.21-2.51) ^b
Ewe lamb	617	1.98 (1.84-2.13) ^a	2.08 (1.92-2.24) ^a
P value		< 0.0001	0.0015
Birth rank within dam age			
Mature ewe – singleton	208	2.48 (2.25-2.74)	2.34 (2.10-2.60)
Mature ewe – twin	1415	2.39 (2.25-2.54)	2.37 (2.22-2.52)
Mature ewe – triplet	257	2.27 (2.07-2.50)	2.37 (2.15-2.62)
Ewe lamb – singleton	361	2.00 (1.84-2.18)	2.05 (1.88-2.23)
Ewe lamb – twin	256	1.97 (1.79-2.16)	2.11 (1.90-2.33)
P value		0.5130	0.9631

a,b Means with different superscripts within column are significantly different to the P value indicated

Lambs born as singletons to mature ewes had the greatest survival to tagging (P<0.001), L29 (P<0.001) and to weaning (P<0.01; Table 3.2.4). At tagging, lambs born as twins to mature ewes had greater survival than triplets born to mature ewes, singletons born to ewe lambs and twins born to ewe lambs, which were not different from each other. At L29, lambs born as twins and triplets to mature ewes, and as singletons to ewe lambs had the same rates of survival, and greater survival than lambs born as twins to ewe lambs. At weaning, lambs born as twins to mature ewes had greater survival than lambs born as triplets to mature ewes. At weaning lambs born to ewe lambs as singletons and twins had similar survival to each other, and were not different to either the twins or triplets born to mature ewes.

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Lamb survival to weaning, of lambs that were alive at tagging, was greater (P<0.05) for singletons born to mature ewes and ewe lambs than for twins and triplets born to mature ewes (Table 3.2.4). Lambs born as twins and triplets to mature ewes had the same survival from birth to weaning. Lambs born as twins to ewe lambs were not different from any of the other lamb groups.

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Table 3.2.4. Lamb survival (%) at tagging, early-life (L29), and weaning of all lambs born, and survival to weaning of all lambs born alive, based on age group (mature ewe vs. ewe lamb), and birth rank of lamb within dam age (mature ewe – singleton vs. mature ewe – twin vs. mature ewe – triplet vs. ewe lamb – singleton vs. ewe lamb – twin. The values presented are back-transformed LS means (95% CI).

	n	Survival at tagging	Survival at early- life	Survival at weaning	n	Survival from tagging to weaning
Dam age			me	weumig		tugging to wearing
Mature ewe	1959	97.3 (96.0-98.1) ^b	88.3 (85.7-90.5)	83.9 (81.1-86.3)	1860	87.0 (84.3-89.2)
Ewe lamb	697	92.2 (89.7-94.2) ^a	86.2 (83.2-88.8)	81.1 (77.6-84.1)	612	88.5 (85.6-90.9)
P value		< 0.0001	0.2526	0.1840		0.4117
Birth rank within dam age						
Mature ewe – singleton	214	99.1 (97.4-99.7) ^c	94.9 (90.7-97.2) ^c	91.0 (85.7-94.4) ^c	208	91.8 (86.2-95.3) ^b
Mature ewe – twin	1458	97.2 (96.1-98.0) ^b	86.9 (84.9-88.7) ^b	81.7 (79.5-83.8) ^b	1397	84.8 (82.7-86.7) ^a
Mature ewe – triplet	287	92.5 (88.7-95.1) ^a	78.0 (72.6-82.6) ^a	75.8 (70.2-80.6) ^a	255	82.7 (77.7-86.9) ^a
Ewe lamb – singleton	402	91.1 (87.8-93.6) ^a	86.9 (83.2-89.9) ^b	81.7 (77.5-85.3) ^{ab}	358	90.2 (86.7-92.9) ^b
Ewe lamb – twin	295	93.3 (89.7-95.7) ^a	85.4 (80.7-89.1) ^b	80.4 (75.1-84.8) ^{ab}	254	86.6 (81.9-90.3) ^{ab}
P value		< 0.0001	< 0.0001	0.0016		0.0402

a,b,c Means with different superscripts within column are significantly different to the P value indicated

Lamb survival as a function of birth weight followed a quadratic form for all dam age and birth rank of lamb contemporary groups (Figure 3.2.1). For all contemporary groups, lambs that were 2.5 kg at birth had a similar rate of survival, around 40%, except in singletons born to mature ewes, which had a minimum birth weight of 3.3 kg. Maximum birth weight for optimal survival depended on the age of the dam. Lambs that were 6.5 kg at birth had a survival range of 86-91% if they were born to a mature ewe, or a maximum of 60% if born to a ewe lamb. The maximum birth weight for twins born to ewe lambs was 5.6 kg, with a survival rate of 53%. Lambs born as twins to mature ewes, and as singletons or twins to ewe lambs had a similar quadratic shape for survival, with the extreme birth weights, having the lowest survival. Singletons born to mature ewes all appear to have a high rate of survival, with a small decrease in survival at birth weights over 7.5 kg. Triplets born to mature ewes have the continuing advantage of increasing survival with increased birth weight, but have a lower overall survival. When considering the contemporary groups, 95% of the population have good survival rates for singletons and twins born to mature ewes, 95% of the population have average survival for triplets born to mature ewes and singletons born to ewe lambs, and 95% of the population has poor survival for twins born to ewe lambs.



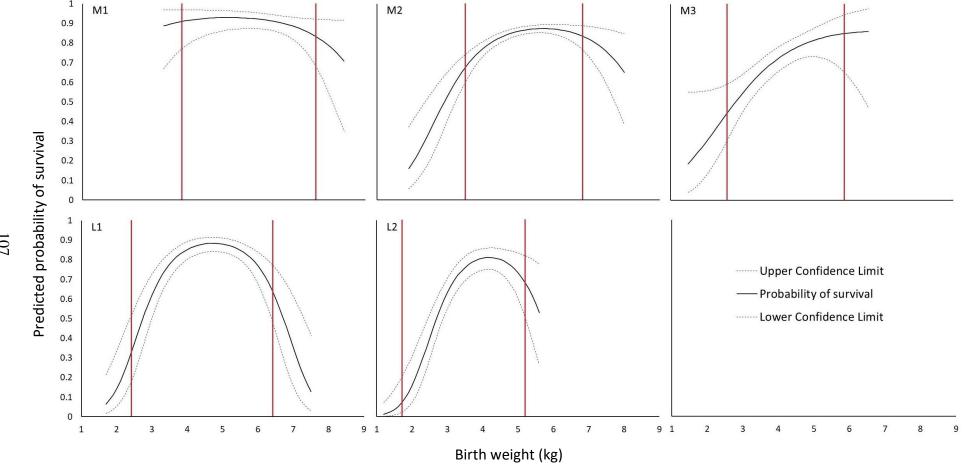


Figure 3.2.1. Predicted survival curves (solid black line) and 95% confidence intervals (dotted lines) of lambs born as singletons (M1), twins (M2), or triplets (M3) to mature ewes, or singletons (L1) or twins (L2) born to ewe lambs, based on their birth weight, and indication of where 95% (two standard deviations) of the population sit (red).

3.2.5 Discussion

It was hypothesised that lambs born to ewe lambs, especially those born as twins, would have lower rates of survival than lambs born to mature ewes, of all birth ranks, when born in the same climatic conditions, and to the same sires, due to their lower weight and vigour score at birth. Lambs born to ewe lambs were lighter than singletons and twins born to mature ewes, which is consistent with the literature. Loureiro et al. (2012), Pain et al. (2015), and Corner et al. (2013b) all reported that singletons born to ewe lambs were lighter at birth than singletons born to mature ewes. Gootwine et al. (2007) reported an intra-uterine growth restriction in litters with higher multiples of lambs, indicating why lambs born as higher multiples, within a dam age, were lighter at birth than their singleton peers. Additionally, the ewe lambs were lighter for the entirety of the experiment, by over 20 kg at the start of breeding, indicating a much smaller body size, and uterine capacity, resulting in lambs that were lighter at birth, than those born to mature ewes within the same birth rank. This means that these lambs born to ewe lambs need to have greater growth rates until weaning to be as heavy as lambs born to mature ewes at weaning.

Lambs that were born to ewe lambs were less vigorous at birth than lambs born to mature ewes. Lambs that are smaller at birth are more likely to be affected by starvation and/or exposure, and therefore likely to be less vigorous at birth. Since lambs born to ewe lambs are born smaller, it is expected that they would be less vigorous than those born to mature ewes. When adding the covariate of birth weight to the model, lambs born to ewe lambs were still less vigorous than the lambs born to mature ewes, indicating that birth weight was not the only factor affecting the vigour of lambs born to ewe lambs. Chapter 3.1 reported that lambs with lower vigour scores, regardless of contemporary group, were less likely to survive from tagging until weaning, which is in agreeance with Dwyer (2008). Interestingly, lambs born to mature ewes had greater rates of mortality after

tagging, while lambs born to ewe lambs had greater rates of mortality prior to tagging. This possibly indicates that the lower vigour lambs born to ewe lambs had already died prior to tagging, but something else contributes to lamb deaths after tagging. Therefore, farmers could identify ewes that are likely to have less vigorous lambs, and lamb them in optimal paddocks, to increase lamb survival rates of lambs, however, recording vigour at tagging may be too late to intervene with the less vigorous lambs.

Lambs born to ewe lambs had lower survival at tagging than lambs born to mature ewes, however there was no difference in survival based on dam age alone during other periods. Survival to weaning was largely related to the birth weight of the lambs, within contemporary groups, consistent with the literature (Morris et al., 2005; Mulvaney et al., 2012). Lambs born at 2.5 kg had a 35-42% survival rate, regardless of dam age group or lamb birth rank. Commonly, deaths of lambs with low birth weights are caused by starvation and/or exposure, rather than dystocia. This indicates that starvation/exposure can affect all small lambs, regardless of the age of their dam or their birth rank (Kerslake et al., 2005; Young et al., 2010). There were differing levels of survival for lambs with 6.5 kg birth weights, based on the age of the dam. This is possibly due to smaller body sizes of the ewe lambs, requiring lighter lamb birth weights to avoid dystocia, compared with mature ewes (Kerslake et al., 2005; Gootwine et al., 2007). This highlights the importance of farmers monitoring their ewe lambs during the lambing period, to intervene if there are incidences of dystocia, especially as this can result in the death of the dam as well as the lamb, if there is no intervention. It also highlights the importance of only selecting ewe lambs that are of sufficient weight at breeding, to be presented for breeding, to reduce the risk from dystocia during lambing.

Lamb weaning weight, based on birth rank and the age of dam, was consistent with the literature, where multiples were lighter than singletons across dam ages, and lambs born to ewe lambs were lighter than lambs born to mature ewes across birth ranks (Dýrmundsson, 1981; Gootwine et al., 2007; Young et al., 2010). Mature ewes that are heavier at the start of breeding are more likely to wean heavier lambs, especially twinbearing ewes (Kenyon et al., 2009a). The ewe lambs were lighter at breeding than the mature ewes, indicating that they are disadvantaged at providing for their lambs, unless preferentially fed. Since the lambs born to ewe lambs were lighter at birth, they would have to attain greater average daily gains to achieve the same weaning weights as lambs born to mature ewes. At each birth rank, lambs born to ewe lambs had lower average daily gains than lambs born to mature ewes, during early and late lactation. Milk yield in ewe lambs has not been reported, but primiparous heifers have lower milk yields than multiparous cows (Lopez et al., 2004; Wathes et al., 2007), and, therefore, it is likely that the ewe lambs will have lower milk yields than mature ewes, as they are also primiparous. Therefore, their lambs, especially those that are born as twins, will have lower milk consumption, and need to consume more pasture to obtain similar growth rates to lambs born to mature ewes. Additionally, live weight of the dam is known to affect lamb growth weights, possibly influencing their lactation potential, especially in times of nutritional hardship (Kenyon et al., 2004c). Lambs born to ewe lambs are, therefore, disadvantaged based on their dam's live weight. Lambs born to ewe lambs are also likely to have a restricted growth opportunity compared with lambs born to mature ewes, especially lambs born as twins. There were considerably fewer mature ewes lambing during the second, and none lambing in the third cycles of lambing, possibly confounding the results, however, lamb date of birth was included as a covariate in all lamb models accounting for this. Subsequently, when farmers are selecting replacements, lambs born to ewe lambs

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are not considered, based on their weights. When growing these lambs for slaughter, farmers will need to grow them for longer to achieve the same slaughter weights.

3.2.6 Conclusions

Lambs that were born to ewe lambs are lighter at birth and weaning, had lower vigour scores at birth, and lower rates of survival at birth, than lambs that were born to mature ewes within each birth rank. This highlights the importance for farmers to ensure that ewe lambs are at a sufficient live weight for breeding, to increase the chances of them weaning a lamb. Ewe lambs need to be offered better pasture during pregnancy, and have smaller, flatter paddocks, with shelter over the lambing period to increase the survival of their lambs, compared with mature ewes. Lambs with birth weights of 2.5 kg or lower have similar survival rates, regardless of their birth rank or dam age, but heavier lambs have different survival rates at the same weight, depending on their birth rank and dam age.

Chapter 4

The effect of age of dam and birth rank on the reproductive performance of ewe lambs

4.1 Abstract

Breeding ewe lambs at eight months of age can increase ewe lifetime production and rate of genetic gain, if their offspring are selected as replacements. Yet, lambs born to ewe lambs are not commonly selected as replacements because they are lighter than lambs from older dams at the time of selection, potentially reducing their reproductive performance during their first breeding as ewe lambs. The aim of this experiment was to determine the reproductive performance of ewe lamb replacements born to ewe lambs. The experiment included ewe lambs born as twins to mature ewes (M2, n=135), as singletons to ewe lambs (L1, n=135), and as twins to ewe lambs (L2, n=88). Ewe lambs that were 39 kg or heavier at approximately seven months of age were presented for breeding. All (100%) of M2, but only 70.4% (95% CI: 62.1-77.5) of L1, and 33.0% (24.0-43.4) of L2 ewe lambs reached these target minima and were presented for breeding. Of those presented for breeding, the number of ewe lambs pregnant over a 34-day breeding period did not differ for M2, L1 and L2 groups (48.9, 52.3 and 66.7% respectively). There was no difference (P>0.05) in the weight of lambs born or weaned, or lamb survival until weaning among the three groups. This indicates that replacements born to ewe lambs can be as productive as ewe lambs born to mature ewes, provided they are heavy enough to be bred in their first autumn. Farmers may need to consider preferentially feeding replacements born to ewe lambs prior to their first breeding.

4.2 Introduction

A major reason for farmers to breed ewe lambs at eight to nine months of age is to produce more lambs per ewe per lifetime, and to increase total number of lambs born on farm per year (Kenyon et al., 2004b; Kenyon et al., 2014a). There is also the potential to increase rate of genetic gain by creating a shorter generation interval using younger dams (Dýrmundsson and Lees, 1972b; Kenyon, 2008; Kenyon et al., 2014a). Increased genetic gain is only achievable if the daughters of these ewe lambs are selected as replacements. Commonly in New Zealand, ewe lamb progeny are not selected as replacements, negating this potential advantage. There is currently little information in the literature on the performance of replacements born to ewe lambs over their productive life (Pain et al., 2015; Loureiro et al., 2016).

Lambs born to ewe lambs on New Zealand farms are usually born a month later than those born to mature ewes (Kenyon et al., 2014a). Furthermore, they are lighter at birth and weaning (Annett and Carson, 2006; Loureiro et al., 2012; Corner et al., 2013a). Lambs that are born as twins, regardless of dam age, are also lighter than lambs born as singletons at both birth and weaning (Schreurs et al., 2010a; Young et al., 2010; Kenyon et al., 2014a; Chapter 3), lasting until at least eight years of age (Chapter 2). It is well documented that live weight has a positive influence on reproductive performance for both mature ewes and ewe lambs (Coop, 1962; Cockrem, 1979; Meyer and French, 1979; Kenyon et al., 2005; Corner-Thomas et al., 2015a; Griffiths et al., 2016). Therefore, it would be expected that lambs born to ewe lambs, especially those born as twins, may have greater difficulty achieving suitable live weights for breeding at seven to nine months of age and, therefore, would display poorer reproductive performance.

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The aim of this experiment was to determine whether being born as a singleton or twin to a ewe lamb compared with being born as a twin to a mature ewe caused differences in live weight, body condition score, and maternal performance (number of lambs produced and weight of lambs produced), when bred at seven months of age.

4.3 Materials and methods

This study was conducted at Massey University's Riverside farm (latitude 40° 50' S, longitude 175° 37' E) 11 km north of Masterton, New Zealand, from January 2018 to January 2019 with the approval of the Massey University Animal Ethics Committee (MUAEC 17/16).

4.3.1 Background

Three hundred and fifty eight Romney ewe lambs born during October to November 2017, to either ewe lambs, as either singletons (L1; n=135) or twins (L2; n=88), or to mature ewes, as twins (M2; n=135) were selected for this experiment (Chapter 3). This paper reports on the ewe lambs from their weaning, and follows on from Chapter 3 (D0, average age 82 days) to the weaning of their first lambs (D379). The M2 ewe lambs were selected from a larger population (n=647; Chapter 3), and included a random 135 of the heaviest 270 lambs at weaning, the L1 ewe lambs included the heaviest 135 of 184 lambs, whereas L2 ewe lambs included the entire population of female lambs present at weaning.

4.3.2 Nutritional management

The goal prior to breeding was to ensure as many ewe lambs as possible were heavy enough for breeding. The current industry recommendations include ewe lambs needing to be ideally be a minimum of 40 kg or 65% of their mature weight prior to breeding (Beef + Lamb New Zealand, 2018b). However, Chapter 2, indicates that ewes born to ewe lambs are lighter than those born to mature ewes from birth to weaning and until at least eight years of life. Therefore, for the present study a minimum live weight of 39 kg for breeding was used. This minimum was achieved by all M2 ewe lambs but not all those born to ewe lambs (i.e. 29 and 52 lambs did not achieve 39 kg for breeding for L1 and L2 ewe lambs, respectively). Therefore, the nutritional management of the treatment groups needed to differ, from their weaning (average weight of 29.6 kg, 26.0 kg, and 21.5 kg, for

M2, L1, and L2 ewe lambs selected, respectively; Chapter 3) until breeding, because lambs born to ewe lambs were much lighter at weaning (Corner et al., 2013b). Further the farm that the ewe lambs were on was exposed to drought-conditions through the autumn (February-April), and therefore the use of supplements was required to achieve target growth rates for L1 and L2 ewe lambs. This approach was taken as part of normal farm practice to ensure as many light ewe lambs as possible reached target breeding weights.

The ewe lambs were managed together from their weaning (3rd of January, 2018; D0) until d7 on ryegrass-based pasture. At D8 the M2 ewe lambs were removed from the other ewe lambs and were trained to eat a barley-grain-based supplement, with added molasses (85.8% dry matter, 12.6% crude protein, 12.9 MJ ME). Training involved the ewe lambs being confined to the sheep yards, with minimal pasture available, and ad libitum grain supplement provided, between 8 a.m. and 5 p.m. for five days, and then being returned to pasture overnight. At D13 the M2 ewe lambs were returned to the other ewe lambs, to help train the other to consume the supplement. At this time, all ewe lambs were rotationally grazed on lucerne pasture (Medicago sativa). During D13 to D34 all ewe lambs were offered the supplement at a rate of 90 g/lamb/day via troughs in their paddock, increasing to 140 g/ewe lamb/day from D35 to D46, 190 g/ewe lamb/day from D47 to D56, and to 240 g/ewe lamb/day from D57 to D75. At D76 the M2 ewe lambs were removed from the lucerne pasture and grazed on a ryegrass-based pasture (ryegrass (Lolium perenne) and white clover (Trifolium pratense)) with no supplement until D126. From D76 to D126 the L1 and L2 ewe lambs received 190 g/ewe lamb/day of grain supplement in addition to lucerne pasture. From D120 until D126 the L1 and L2 ewe lambs were grazed on ryegrass-based pasture.

At D127 (introduction of the ram, 10th May 2018) all ewe lambs that were heavier than 39 kg (n= 135, 95, and 29 for M2, L1, and L2 ewe lambs, respectively) were merged into one group and grazed on ryegrass based pasture (approximate pre-grazing pasture mass of 1200 kg DM/ha), with no grain-based supplement. Ewe lambs lighter than 39 kg (n= 0, 40, and 59 for M2, L1, and L2 ewe lambs, respectively) were grazed on a ryegrass-based pasture (approximate pre-grazing pasture mass of 1600 kg DM/ha) and offered 250 g/ewe lamb/day of grain-based supplement until D144. After D144 all ewe lambs received only ryegrass-based pasture. At D144, there were zero, 12, and seven M2, L1, and L2 ewe lambs added to the over 39 kg group.

At D161 (end of the breeding period) all ewe lambs (n=358) were re-joined as one group and grazed together on ryegrass-based pasture (approximate pre-grazing pasture mass of 800 kg DM/ha) until D265. At D265, all pregnant ewe lambs (n=66, 57, and 24 for M2, L1, and L2 ewe lambs, respectively) were paddocked for lambing, separated based on cycle pregnant (first or second 17-day period), then randomly allocated over two sets of four paddocks (average pre-grazing pasture mass of 940 \pm 30 kg DM/ha, average metabolisable energy of 12.3 MJ ME/kgDM, stocking rate of 7.6 ewe lambs/ha). At D308, until D379, the lactating ewe lambs were rotationally grazed in two groups, based on cycle pregnant (average pre-grazing pasture mass of 1270 \pm 20 kg DM/ha, average metabolisable energy of 11.6 MJ ME/kgDM). From D265 (pre-lambing) to D379 (weaning) non-pregnant ewe lambs (n=212) were managed separately, and rotationally grazed (average pre-grazing pasture mass of 1680 \pm 70 kg DM/ha, average metabolisable energy of 10.9 MJ ME/kgDM).

4.3.3 Ewe lamb live weight and body condition score measurements

The ewe lambs were weighed within two hours off pasture at 20 time points, on average 20 days apart (D0 (January 3rd, 2018, average age of 82 days), D8, D27, D41, D59, D76,

D93, D110, D120, D127 (introduction of ram), D144, D161, D177, D194, D215 (pregnancy detection), D239, D250, D265 (pre-lambing weight), D308, and D379 (weaning of first lambs). Their body condition score (BCS; Jefferies (1961); scale 1 – 5, 1=emaciated, 5=obese) was also recorded eight times during this period, average 42 days apart (D76, D127, D161, D177, D215, D265, D308, and D379).

4.3.4 Reproductive measures

At D59 (3rd of March 2018) the ewe lambs were joined with crayon harnessed vasectomised rams (ratio of approximately 1:50) for 68 days (D59-D127). At the end of each 17 day period (D76, D93, D110, and D127), crayon marks were recorded on all ewe lambs, to detect if a ewe lamb was mounted/tupped, as an indicator of oestrus and puberty attainment (Allison et al., 1975) and crayon colours were changed. Crayon marks on the ewe lamb rumps were scored using a 0-3 score, indicating the incidences of tupping (0= no marks, 1= one mark, 2= two marks, 3= three or more marks (Radford and Watson, 1960)). Ewe lambs were considered to have shown oestrus as an indicator of puberty if they had a crayon mark score on their rump of two or three at any time crayon marks were recorded (Whyman, 1980). At D76 L1 and L2 ewe lambs were separated from M2, to allow preferential feeding for the L1 and L2 ewe lambs (see earlier details), along with three vasectomised teasers (ratio of approximately 1:45), with L1 and L2 ewe lambs remaining as a second group with the remaining teaser rams (ratio of approximately 1:53). On D127 (10th of May 2018) the vasectomised rams were removed.

At D127 (May 10th 2018, average age of 209 days), all ewe lambs that were 39 kg or heavier (n=258) were joined as one group with entire, harnessed Romney rams for 34 days (two 17-day reproductive periods), at a ratio of approximately 1:39 (n=135, 95, and 29 M2, L1, and L2 ewe lambs, respectively). At the end of each reproductive cycle (17 days; D144 and D161) crayon marks were recorded on ewe lamb's rumps. Crayon colours

were changed on D144. At D144 any ewe lambs that were then subsequently found to be 39 kg or above, and not already in the breeding group (n= 0, 12, and 7 for M2, L1, and L2 ewe lambs, respectively) joined with the breeding group. One additional ram was also added, creating a ratio of approximately 1:38 of rams to ewe lambs. At D161 crayon marks on the rump were recorded, and the rams were removed from the ewe lambs. Only 81 ewe lambs (n=0, 29 and 52 for the M2, L1, and L2 ewe lambs respectively) of the total 358 were not presented for breeding, due to being too light.

Pregnancy detection occurred at D211 (August 2nd, 2018), via transabdominal ultrasound, to detect the number of fetuses, for all ewe lambs that were presented for breeding. The cycle of pregnancy was determined using crayon marks, for all ewe lambs diagnosed as pregnant. Ewe lambs were identified as having conceived during the first 17-day period of breeding if they displayed only the first crayon colour on their rumps. Those displaying only the second crayon colour on their rumps were identified to have conceived in the second 17-day period of breeding. Any ewe lambs that were had both or none of the crayon colour marks on their rumps were considered to have conceived during the second 17-day cycle, for lambing management purposes.

4.3.5 Fleece weight

At D48 the ewe lambs were shorn, and fleece weight was not recorded. At D250 (September 11th, 2018) the ewe lambs were shorn, and the individual greasy fleece weights, including bellies and pieces were collected, as described by Blair et al. (1984).

4.3.6 Lambing period

During lambing (D265-D308) ewe lambs were checked twice daily at approximately 9 a.m. and 3 p.m., by one of two trained operators. The first lamb was born on D268, and the last lamb on D305. Lambs that were old and strong enough to stand were tagged and

identified to their dam, and if any lambs were not yet standing, the entire litter was left until the next check. The sex of the lamb(s), its birth rank, date and paddock of birth, and birth weight were recorded. Maternal behaviour score (1-5 score; O'Connor et al. (1985)) was recorded for all dams that had a live lamb at tagging. Any dead lambs were weighed and recorded. Lambs that were dead at the time of tagging were considered born dead, and lambs that were collected after tagging, until 3 days after the end of the lambing period (D308), were considered to have died between birth and the end of the lambing period. At D308 (average of day 24 of lactation; L24) all lambs were weighed and the tail removed using a hot iron (docked), and all male lambs were castrated using a rubber ring. At D379 (average of day 95 of lactation) lambs were weaned, and weighed.

4.3.7 Data handling

The trait of percentage of ewe lambs showing oestrus (and therefore assumed to have achieved puberty) prior to the introduction of the ram (Oestrous %) was defined based on the presence or absence of crayon marks from the vasectomised rams. Ewe lambs with a 2-3 crayon score while joined with the vasectomised rams were considered to have shown oestrous, as an indicator of puberty attainment. The number of ewe lambs presented for breeding in both reproductive cycles of breeding, or just the second reproductive cycle of breeding, or not presented for breeding were recorded. Based on these results, those that were presented for both reproductive cycles, and only for the second reproductive cycle were considered presented for breeding. The entire population included all ewe lambs that either were or were not presented for breeding for each treatment group. The number of ewe lambs that were pregnant, was considered firstly as a percentage of all ewe lambs presented for breeding, and secondly for the entire population, within each treatment group. The percentage of ewes that were multiple bearing at the time of pregnancy detection was based on only those that were diagnosed as pregnant at pregnancy detection

for each treatment group. The percentage of ewe lambs pregnant during the first cycle of breeding was determined retrospectively, using the date of lambing, and considered only ewe lambs that were presented for breeding during both reproductive cycles of breeding. The number of lambs present at birth (NLB) and weaning (NLW) was determined as a percentage, for the ewe lambs that were presented for breeding, and the total population for each treatment group.

Lamb survival to tagging was determined based on whether a lamb was alive or dead at the time of tagging. Lamb survival to weaning was determined on the weaning weight measurements, with lambs not present at weaning considered to have died between tagging and weaning.

4.3.8 Statistical analysis

Statistical analysis was carried out using SAS version 9.4 software (SAS Institute, Cary, NC, USA). Live weight of ewe lambs was analysed with a linear mixed model, with the fixed effects of treatment group, paddock at lambing, day of measurement, pregnancy rank (zero, one, or two fetuses), and the interaction of treatment group and day of measurement. This selection among only the heaviest (42%) of lambs caused skewness and kurtosis in live weight of the M2 ewe lambs. However, the skewness and kurtosis, was considered insufficient to adversely affect ANOVA tests of significance because the ratio of population sizes was equal to 150% and, therefore, ANOVA without transformation of the data was conducted. A univariate analysis was carried out for live weight on each day of measurement among the three groups, as a test for normality using the Kolmogorov-Smirnov method. A general linear model was used with a Levene's test for homogeneity of variance for live weight within each day of measurement among the three groups. The random effect of animal was included to account for repeated measures.

Ewe lamb BCS was analysed with a generalised linear model, assuming a Poisson distribution, with fixed effects of treatment group, day of measurement, and the interaction of treatment group and day of measurement. Paddock at lambing, and pregnancy rank (zero, one, or two fetuses), were initially considered, but not significant (P>0.05), and so were removed from the model. The random effect of animal was included to account for repeated measures.

Using the data of ewe lambs that were heavy enough to be bred, for either reproductive cycle, the probability of pregnancy occurring, based on pregnancy scanning results using live weight at the introduction of the ram as the independent variable, was analysed using logistic regression. A generalised linear model was used to analyse reproductive traits, based on a binomial distribution, and using the fixed effect of treatment group.

The number of lambs present at birth and weaning per ewe bred and per ewe of the entire population were analysed using a generalised linear model, assuming a Poisson distribution, with the fixed effect of treatment group.

Fleece weight was analysed using a general linear model, with the fixed effect of treatment group, and the covariate of live weight at the time of measurement. The analysis of fleece weight also had the fixed effect of pregnancy rank (zero, one, or two fetuses).

Lamb birth weight, L24 weight, and weaning weight (L95) were analysed using a mixed linear model, with the fixed effects of treatment group and birth rank of the lamb. Date of birth was added as a covariate, and the random effect of ewe lamb was included to account for repeated measures of twin lambs. The interaction of treatment group and birth rank of the lamb was initially tested, but was not significant (P>0.05) and so was removed. Lamb birth weight had the additional fixed effect of sex of lamb in the model, which were both tested, and not significant (P>0.05) for lamb L24 and weaning weight, and so were

removed from these models. Lambing paddock was considered for all models, but was not significant (P>0.05), and was removed. Two lambs born prematurely (identified via post-mortem examination) were removed from birth weight analysis.

Lamb survival to tagging (used as an indicator of survival at birth) and to weaning were analysed using a generalised linear model, assuming a binomial distribution, and included the fixed effects of treatment group and lamb birth rank. Confidence intervals at the 95% level were used to test for differences in lamb survival to weaning for the treatment groups of dam age and lamb birth rank. The interaction of treatment group and birth rank of the lamb, and the fixed effect of lambing paddock were initially tested, but were not significant (P>0.05) and so were removed from the model. Maternal behaviour score was analysed using a generalised linear model, assuming a Poisson distribution, and had the fixed effect of treatment group. The fixed effects of birth rank, operator, and lambing paddock were also tested, but were not significant (P>0.05) and so were removed from the model.

4.4 Results

4.4.1 Ewe lamb live weights

The average live weights at weaning (and live weight range) were 29.6 (23.4-42.8), 26.0 (16.0-35.2), and 21.5 (12.0-28.0) kg for the M2, L1, and L2 ewe lambs, respectively. The M2 ewe lambs were consistently heavier (P<0.0001) than the L1 ewe lambs by 1.3 to 4.3 kg from their weaning (D0) until the weaning of their first lambs (D379; Figure 4.1, Table 4.1). The L1 lambs were heavier (P<0.0001) than L2 lambs by 2.1 to 4.6 kg from their weaning (D0) until the weaning of their first lambs (D379). Of the ewe lambs that were presented for breeding, the M2 ewe lambs were consistently heavier (P<0.0001) than the L1 and L2 ewe lambs, across all time points. The L1 ewe lambs were heavier than the L2 ewe lambs at their own weaning and pre-breeding. There was no difference in live weight (P>0.05) between the L1 and L2 ewe lambs at pregnancy detection, pre-lambing, and the weaning of their first lambs, in those that were presented for breeding (Table 4.1).

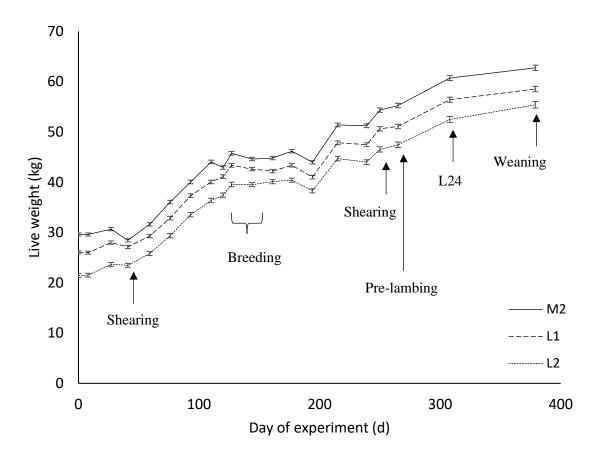


Figure 4.1: Least-squares means (error bars of \pm S.E.M.) of live weight (kg) of the entire population for ewe lambs born to mature ewes as twins (M2; —), or born to ewe lambs as singletons (L1; —) or as twins (L2; —) from their weaning (D0) to the weaning of their first lambs (D379).

Table 4.1: The live weight $(kg \pm S.E.M.)$ of ewe lambs at their own weaning, prebreeding, pregnancy detection, pre-lambing, and the weaning of their first lambs for the ewe lambs that were presented for breeding only, and for the entire population, for ewe lambs born to mature ewes as twins (M2), or born to ewe lambs as singletons (L1) or as twins (L2).

	Own	Pre-	Pregnancy	Pre-	Weaning
	weaning	breeding	detection	lambing	first lambs
Presented f	or breeding ¹				
M2	29.6 ± 0.3^{c}	45.7 ± 0.4^{c}	51.4 ± 0.4^{b}	55.2 ± 0.4^{b}	62.7 ± 0.5^{b}
L1	26.1 ± 0.3^{b}	44.2 ± 0.4^{b}	48.5 ± 0.4^{a}	52.3 ± 0.5^{a}	59.1 ± 0.6^{a}
L2	23.5 ± 0.6^{a}	42.7 ± 0.6^{a}	47.3 ± 0.6^{a}	51.5 ± 0.8^{a}	57.5 ± 1.0^{a}
P value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Entire popu	ılation ²				
M2	29.6 ± 0.3^{c}	45.7 ± 0.4^{c}	51.4 ± 0.4^{c}	55.2 ± 0.4^{c}	62.7 ± 0.5^{c}
L1	26.0 ± 0.3^{b}	43.4 ± 0.4^{b}	47.8 ± 0.4^{b}	51.1 ± 0.4^{b}	58.5 ± 0.5^{b}
L2	21.5 ± 0.4^a	39.5 ± 0.4^{a}	44.7 ± 0.5^a	47.4 ± 0.5^{a}	55.4 ± 0.7^{a}
P value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

a.b.c Means with different superscripts within column are significantly different at the p value indicated ¹ Ewes that were heavy enough (above 39 kg) at either the start of breeding, or the start of the second 17-day period (reproductive cycle) of breeding, over a 34-day (two reproductive cycles) breeding period. ²All ewes in the population, including those that were heavy enough to be bred (greater than 39 kg, as stated in 1), and those that were not heavy enough to be bred (n=0, 29 and 52 for the M2, L1, and L2 ewe lambs respectively).

4.4.2 Ewe lamb body condition score

The entire population of ewe lambs had similar (P>0.05) BCS throughout the experimental period, except at the start of breeding (D127) when the M2 ewe lambs had a lower (P<0.0001) BCS than the other two treatment groups (Figure 4.2, Table 4.2). At breeding (D127), when considering only those ewe lambs that were presented for breeding, the M2 ewe lambs had a lower (P<0.0001) BCS than L1 and L2 ewe lambs (Table 4.2). At all other time points there were no differences (P>0.05) in BCS among the ewe lamb groups.

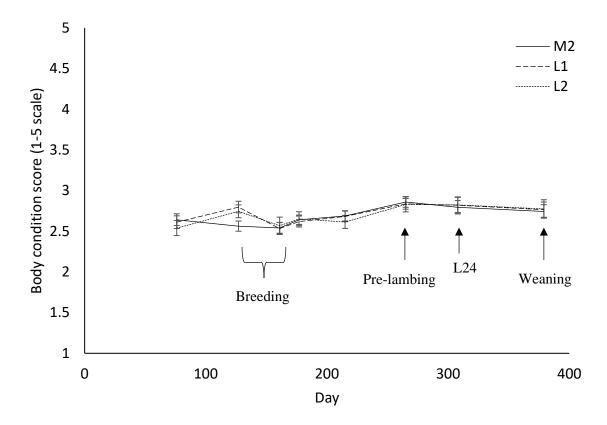


Figure 4.2: Body condition score (BCS; 1-5 score) of the entire population for ewe lambs born to mature ewes as twins (M2; —), or born to ewe lambs as singletons (L1; --) or as twins (L2; ---), from D76 after their weaning (D0) to the weaning of their first lambs (D379). Values are back-transformed LS means and error bars indicate 95% confidence intervals.

Table 4.2: The body condition score (BCS; 1-5 score) of ewe lambs at pre-breeding, pregnancy detection, pre-lambing, and the weaning of their first lambs for the ewe lambs that were presented for breeding only, and for the entire population, for ewe lambs born to mature ewes as twins (M2), or born to ewe lambs as singletons (L1) or as twins (L2). Values are back-transformed LS means and 95% confidence intervals.

	Pre-breeding	Pregnancy	Pre-lambing	Weaning first		
		detection		lambs		
Presented f	or breeding ¹					
M2	2.56 (2.50-2.71) ^a	2.69 (2.63-2.75)	2.86 (2.79-2.93)	2.74 (2.66-2.83)		
L1	$2.87 (2.80-2.95)^{b}$	2.70 (2.63-2.78)	2.83 (2.76-2.91)	2.74 (2.63-2.86)		
L2	2.97 (2.87-3.08) ^b	2.72 (2.61-2.83)	2.90 (2.76-3.05)	2.75 (2.55-2.97)		
P value	< 0.0001	0.8069	0.5967	0.9962		
Entire popu	Entire population ²					
M2	2.56 (2.50-2.71) ^a	2.69 (2.63-2.75)	2.86 (2.79-2.93)	2.74 (2.66-2.83)		
L1	2.79 (2.73-2.87) ^b	2.68 (2.62-2.75)	2.84 (2.77-2.90)	2.76 (2.67-2.86)		
L2	$2.74(2.67-2.82)^{b}$	2.61 (2.54-2.69)	2.83 (2.74-2.92)	2.77 (2.67-2.89)		
P value	0.0003	0.8724	0.8978	0.8876		

^{a,b} Means with different superscripts within column are significantly different at the p value indicated ¹ Ewes that were heavy enough (above 39 kg) at either the start of breeding, or the start of the second 17-day period (reproductive cycle) of breeding, over a 34-day (two reproductive cycles) breeding period. ²All ewes in the population, including those that were heavy enough to be bred (greater than 39 kg, as stated in 1), and those that were not heavy enough to be bred (n=0, 29 and 52 for the M2, L1, and L2 ewe lambs respectively).

4.4.3 Ewe lamb reproductive performance

Fewer (P<0.01) L2 ewe lambs reached puberty prior to the introduction of the ram compared with M2 ewe lambs, while L1 ewe lambs did not differ from either the M2 or L2 groups (Table 4.3). In addition, fewer (P<0.05) L2 ewe lambs were presented for breeding in the first and second 17-day periods of breeding than L1 ewe lambs. All M2 ewe lambs were presented for breeding in the first cycle.

Table 4.3: Percentage of ewe lambs showing oestrous (as an indicator of puberty) prior to the introduction of the ram (Puberty; %), presented for breeding for both of the reproductive cycles (Presented both cycles; %), presented for breeding total (Presented total; %) during both, or the second reproductive cycle of breeding, for ewe lambs born to mature ewes as twins (M2), or born to ewe lambs as singletons (L1) or as twins (L2) during their first breeding. Values are back-transformed LS means and 95% confidence intervals.

	M2	L1	L2	P value
n	135	135	88	
Puberty (%) ¹	21.5 (15.4-29.2) ^b	15.6 (10.4-22.7) ^{ab}	6.8 (3.1-14.4) ^a	0.0085
Presented both cycles (%) ²	100*	70.4 (62.1-77.5) ^b	33.0 (24.0-43.4) ^a	<0.0001
Presented total (%) ³	100*	79.3 (71.6-85.3) ^b	40.9 (31.2-51.4) ^a	<0.0001

^{*} M2 ewe lambs were all presented for breeding at the start of the breeding period, therefore were not included in the analysis.

At the time of introduction of entire rams (D127) and at a given live weight, there was no difference (P>0.05) among treatment groups in the percentage of ewe lambs likely to become pregnant (Figure 4.3). As live weight at the introduction of the ram increased so did the likelihood of the ewe lamb conceiving during the breeding period, irrespective of treatment group.

¹ The percentage of ewe lambs with recorded crayon marks from vasectomised rams prior to the introduction of the ram, as an indicator of puberty attainment.

² The percentage of ewe lambs presented for both reproductive cycles of breeding.

³ The percentage of ewe lambs presented for breeding (either for both or just the second reproductive cycles).

a,b Means with different superscripts within row are significantly different at the p value indicated

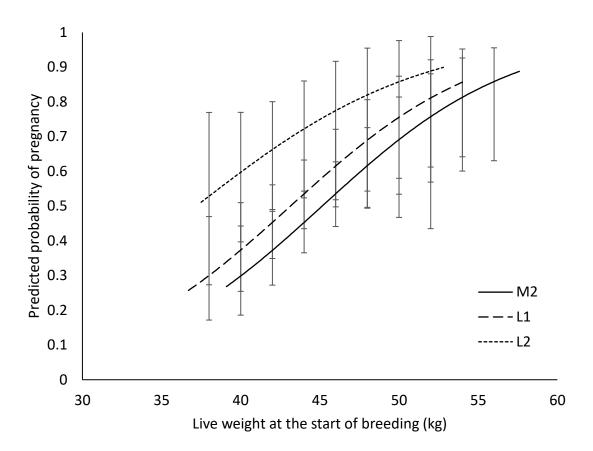


Figure 4.3: The effect of live weight (kg) at the start of breeding on the probability of pregnancy occurring over the breeding period, for the ewe lambs born to mature ewes as twins (M2; —), or born to ewe lambs as singletons (L1;—) or as twins (L2; ---) during their first breeding. Values are back-transformed LS means and error bars are 95% confidence intervals.

There was no difference (P>0.05) in the proportion of ewe lambs pregnant from each treatment group, when analysed based only on ewe lambs that were presented for breeding (either both cycles, or just the second cycle; Table 4.4). However, when analysed based on the entire population, there were fewer (P<0.01) L2 ewe lambs pregnant than both L1 and M2 ewe lambs. There was no difference (P>0.05) in the proportion of pregnant ewe lambs bearing multiples, or those pregnant in the first cycle of breeding of those that were presented for the entire breeding period among the treatment groups.

Of the ewe lambs presented for breeding (either both cycles, or just the second cycle), there was no difference (P>0.05) in the number of lambs weaned per treatment group (Table 4.4). Of the entire population, M2 and L1 ewe lambs weaned more (P<0.02) lambs than L2 ewe lambs.

Table 4.4: Percentage of ewe lambs diagnosed as pregnant, and number of lambs born (NLB) and weaned (NLW) of those that were presented for breeding and of the entire population, percentage of ewe lambs diagnosed as multiple bearing of those that were diagnosed pregnant, and percentage of ewe lambs conceiving during the first reproductive cycle of breeding (first 17 days) of those that were presented for breeding during both reproductive cycles, for ewe lambs born to mature ewes as twins (M2), or born to ewe lambs as singletons (L1) or as twins (L2) during their first breeding. Values are back-transformed LS means and 95% confidence intervals.

	M2	L1	L2	P value		
n	135	135	88			
Ewe lambs presented for breeding ¹						
Pregnant	48.9 (40.6-57.3)	52.3 (42.9-61.6)	66.7 (50.0-80.0)	0.1594		
(%)						
NLB (%)	54.1 (43.0-68.0)	59.8 (46.8-76.4)	75.0 (51.4-109.4)	0.3641		
NLW (%)	45.2 (35.2-58.1)	47.7 (36.2-62.7)	52.8 (33.7-82.7)	0.8391		
Entire populatio	on of ewe lambs ²					
Pregnant	48.9 (40.6-57.3) ^b	41.5 (33.5-50.0) ^b	27.3 (19.0-37.5) ^a	0.0049		
(%)						
NLB (%)	54.1 (43.0-68.0) ^b	47.4 (37.1-60.6) ^{ab}	30.7 (21.0-44.7) ^a	0.0309		
NLW (%)	45.2 (35.2-58.1) ^b	37.8 (28.7-49.7) ^b	21.6 (13.8-33.9) ^a	0.0115		
Ewe lambs diag	nosed pregnant					
Multiple	15.2 (8.4-25.9)	19.6 (11.2-32.1)	12.5 (4.1-32.4)	0.6801		
bearing (%)						
Ewe lambs prese	ented for breeding in	both cycles only2				
Pregnant 1st	41.5 (33.5-50.0)	43.2 (33.6-53.3)	51.7 (34.1-68.9)	0.6953		
cycle (%)						

a,b Means with different superscripts within row are significantly different at the p value indicated ¹ Ewes that were heavy enough (above 39 kg) at either the start of breeding, or the start of the second 17-day period (reproductive cycle) of breeding, over a 34-day (two reproductive cycles) breeding period.

²All ewes in the population, including those that were heavy enough to be bred (greater than 39 kg, as stated in 1), and those that were not heavy enough to be bred (n=0, 29 and 52 for the M2, L1, and L2 ewe lambs respectively).

4.4.4 Ewe lamb fleece weights

The M2 ewe lambs had greater (P<0.0001) fleece weights at D250 than the L1 and L2 ewe lambs (2.88 ± 0.03 kg, 2.74 ± 0.03 kg, and 2.65 ± 0.06 kg, respectively). When the covariate of live weight was added, there was no difference among treatment groups for their fleece weight (P>0.05).

4.4.5 Lamb production

There was no interaction (P>0.05) between treatment group (M2, L1, or L2) and progeny birth rank (singleton or twin) on the weight of progeny at birth, L24, or weaning. There was no difference (P>0.05) in the birth weight, weight at 24 days of lactation, or weaning weight of progeny born to M2, L1 and L2 ewe lambs (Table 4.5). At all ages, progeny born as singletons were heavier (P <0.0001) than progeny born as twins (Table 4.5).

Table 4.5: Least squares means (± S.E.M.) of progeny weights at birth (BWT), day 24 of lactation (L24), and weaning (WWT) for ewe lambs born to mature ewes as twins (M2), or born to ewe lambs as singletons (L1) or as twins (L2), and by birth rank of the progeny (singleton or twin), during their first lambing.

	n	BWT (kg)	n	L24 (kg)	n	WWT (kg)
Treatment grou	p					_
M2	73	4.56 ± 0.10	61	11.55 ± 0.30	60	25.71 ± 0.53
L1	63	4.58 ± 0.10	51	11.08 ± 0.34	50	24.73 ± 0.55
L2	26	4.41 ± 0.17	20	11.22 ± 0.47	19	24.57 ± 0.82
P value		0.7678		0.4597		0.2991
Progeny birth ra	ınk					
Singleton	119	4.97 ± 0.08^{b}	101	12.74 ± 0.23^{b}	100	27.26 ± 0.41^{b}
Twin	43	4.07 ± 0.12^{a}	31	9.83 ± 0.41^a	29	22.75 ± 0.67^{a}
P value		< 0.0001		< 0.0001		< 0.0001

a,b Means with different superscripts within column are significantly different at the p value indicated

There was no interaction (P>0.05) between treatment group (M2, L1, or L2) and progeny birth rank (singleton or twin) on the survival of progeny at tagging, or to weaning (Table 4.6). There was no difference (P>0.05) in the survival of progeny at tagging, or to weaning

of progeny born to M2, L1 and L2 ewe lambs, or between progeny birth ranks (singleton vs. twin; Table 4.6).

Table 4.6: Progeny survival at tagging and at weaning (%) for ewe lambs born to mature ewes as twins (M2), or born to ewe lambs as singletons (L1) or as twins (L2), and by birth rank of the progeny (singleton or twin), during their first lambing. Values except are back-transformed LS means and 95% confidence intervals.

	n	Survival at	Survival to
		tagging (%)	weaning (%)
Treatment group			
M2	73	91.6 (82.0-96.3)	79.3 (67.4-87.7)
L1	63	88.7 (77.8-94.7)	77.1 (64.3-86.3)
L2	26	80.4 (59.8-91.9)	68.5 (47.0-84.2)
P value		0.3429	0.5929
Progeny birth rank			
Singleton	119	88.1 (80.4-93.0)	83.0 (74.7-89.0) ^b
Twin	43	87.2 (72.4-94.6)	65.4 (49.3-78.6) ^a
P value		0.8842	0.0239

a,b Means with different superscripts within column are significantly different at the p value indicated

There was no interaction among treatment groups (M2, L1, and L2) and progeny birth rank (singleton or twin; P>0.05) for maternal behaviour score (data not shown), and no difference (P>0.05) among treatment group (MBS 2.7 (95% CI: 2.2-3.2), 2.6 (2.1-3.2), and 2.4 (1.8-3.3) for M2, L1, and L2 ewe lambs, respectively) or progeny birth rank for maternal behaviour score.

4.5 Discussion

The aim of this experiment was to determine whether being born as a singleton or twin to a ewe lamb or as a twin to a mature ewe caused differences in live weight, body condition score, and reproductive performance, when bred first at seven-months-old. One limitation of this experiment was being able to select the M2 group of ewe lambs based on their weaning weight, while having to include all female progeny available from the L1 and L2 groups to have enough numbers. This situation is likely to reflect that seen commercially, however, where the population of lambs born to ewe lambs is fewer in number and lighter in weight at weaning. Therefore, some of the L1 and L2 ewe lambs were not heavy enough to be presented for breeding. At all measurements, M2 ewe lambs were heavier than L1 ewes, which were heavier than L2 ewes. This is in agreement with Loureiro et al. (2016), who reported that ewes born to ewe lambs were lighter than ewes born to mature ewes, until at least 2.5 years of age. Interestingly, there were few differences in body condition score among treatment groups, throughout the experimental period. This indicates, that at any given live weight, the L2 ewe lambs were possibly at a greater BCS than the L1 ewe lambs, which were possibly greater BCS than the M2 ewe lambs. The differences in live weight, but not body condition score, may be explained by differences in the frame size of the ewe lambs, but this was not measured. Previous studies by Atta and El Khidir (2004) and Cam et al. (2010) demonstrated high correlations between ewe live weight and wither height in Nilotic and Karayaka sheep, respectively. While the fleece was heavier for M2 ewes, the 0.2 kg advantage was insufficient to account for the differences in live weight.

The lambing percentage (number of lambs weaned per ewe presented for breeding) ranged between 45.2-52.8% among the three groups, which is lower than the national average of 65.4% for ewe lambs in 2018 (Beef + Lamb New Zealand, 2018a), but within

the range of 36.0-69.0% reported by Kenyon et al. (2014a). The ewe lambs in the present study were born in October, making them 7-months old at breeding. This is a month younger than replacements in the industry, which are generally born to mature ewes, in September. This likely explains why they are less likely to have attained puberty prior to breeding, resulting in a reduced reproductive performance (Dýrmundsson, 1981). The ewe lambs in this study were also bred at a minimum of 39 kg, while Beef and Lamb New Zealand recommend a minimum of 40 kg (Beef + Lamb New Zealand, 2018a). Removing the ewe lambs who were less than 40kg at the start of the breeding period only increased lambing percentage by 2 percentage points, which does not explain the difference between the current results, and the industry average. The percentage of the each group showing oestrous activity prior to breeding was significantly lower than that previously reported (van der Linden et al., 2007). The ewe lambs were on average 207 days old at the start of breeding, while van der Linden et al. (2007) reported that ewe lambs first achieved oestrous at an average of 260-264 days old. The impaired performance of these ewes is, therefore, possibly due to them being younger than traditional replacements at breeding, and more likely to be attaining puberty during, rather than before, the breeding period. This could possibly be avoided by selecting ewe lambs that are born earlier in the lambing period, rather than those that are born later in the lambing period. The largest impact farmers could make to ensure that lambs born to ewe lambs will be suitable for breeding as ewe lambs themselves is to ensure that they are heavy enough to be bred.

Due to only a proportion of the L1 and L2 populations being heavy enough to be bred, the reproductive analysis was carried in two ways: performance per ewe presented for breeding, and performance per ewe of the population for each treatment group. When considering the entire population, there were fewer lambs produced by the two groups born to ewe lambs, especially those born as twins. This is due to the proportions of each

group that were not presented for breeding, and, therefore, not given the opportunity to produce a lamb. When considering just the populations that were presented for breeding only, there were no differences in the number, or weight of lambs weaned among the three groups, or rates of lamb survival, suggesting there is no consequence of breeding ewe lambs that were born to ewe lambs if they are heavy enough to be bred. Loureiro et al. (2016) reported that there was no difference in the number of lambs born or weaned between ewes born as singletons or twins, to mature ewes or ewe lambs, during their first lambing, at two years of age.

In an average flock of 3000 breeding ewes, where ewe lambs are bred, with a 30% replacement rate (Griffiths et al., 2017), there would be 900 ewe lambs presented for breeding. Assuming they have a 65% weaning rate from the ewe lambs presented for breeding (Beef + Lamb New Zealand, 2018a), and half of the offspring were female, this leaves 293 ewe lambs born to ewe lambs to select from. If farmers were to select the top 55% of these ewe lambs based on weaning weight, that would mean 161 replacements would be born to ewe lambs, while the other 739 of the 900 replacements would be born to mature ewes. This experiment used additional feed during the weaning-to-breeding period to increase growth rates of the replacements born to ewe lambs. Depending on the individual farm, and the proportion of replacements born to ewe lambs, and the resulting average weaning weights, farmers would need to consider prioritising feeding for the replacements born to ewe lambs, however, farmers may also choose to try and increase growth rates pre-weaning with additional supplements. This needs a systems analysis to determine whether potential increases in genetic gain and efficiency are worth the additional feed costs, and to determine the most feasible proportion of replacements born to ewe lambs to keep and utilise.

Differing proportions of the treatment groups were found to be heavy enough to be bred as ewe lambs, driven by the limitation of having to select all lambs born to ewe lambs. In the current experiment, there were 127 days between weaning and the start of ewe lamb breeding, with an average daily liveweight gain of 134 g/d during that period. The minimum recommended breeding weight for ewe lambs is 40 kg (Beef + Lamb New Zealand, 2018b). Based on these requirements ewe lambs would need to have been a minimum of 23 kg at weaning to ensure they were able to be bred at seven months of age. Based on this minimum weaning weight, 100% of the selected M2 ewe lambs, 61% of the L1 ewe lambs, and 22% of the L2 ewe lambs would have been heavy enough for selection at weaning. Beef + Lamb New Zealand (2014) recommend weaning lambs from their dams at an average of 24 kg. With replacement rates being around 30% of the ewe flock, farmers can select ewe lambs are 23 kg or heavier at weaning, to achieve breeding weight targets.

4.6 Conclusions

Replacements born to ewe lambs have the same lamb production (number and weight of lambs weaned) as replacements born to mature ewes during their first breeding as ewe lambs, provided they are heavy enough at the start of breeding. The average weaning weight of lambs born to ewe lambs is lower than lambs born to mature ewes, making them less likely to achieve the weight targets that allow them to be bred as ewe lambs. Therefore, farmers can choose to select replacements out of the lamb crop from their ewe lambs, if they are heavy enough to reach breeding weight on time. Ewe lambs born as singletons or twins to ewe lambs were lighter than the twins born to mature ewes, but there was no difference in body condition score. Despite the differences in ewe lamb live weight, there were no differences in the number and weight of lambs produced at weaning per ewe lamb bred, during their first lambing. If the replacements born to ewe lambs are lighter in live weight for their lifetimes, while still producing the same number and weight of lambs, it is possible that they may be more efficient than replacements born to mature ewes, but further investigation, including a lifetime performance analysis, and an economic analysis would need to be carried out.

Chapter 5

Reproductive performance of ewes born to ewe lambs as singletons or twins, or to mature ewes as twins, as two-year-olds

5.1 Abstract

Currently, 30-43% of New Zealand sheep farmers breed their ewe lambs, but few retain the offspring as replacements for their flock. No difference in lamb production as a yearling among singletons and twins born to ewe lambs and twins born to mature ewes has been reported, provided the ewe lambs had reached the 60-65% of their likely mature weight prior to breeding at seven to eight months of age. The aim of this experiment was to determine the lamb production from singletons and twins born to ewe lambs and twins born to mature ewes during their second year of lambing. The experiment included 18month-old ewes born as twins to mature ewes (M2, n=133), singletons born to ewe lambs (L1, n=133), and twins born to ewe lambs (L2, n=87), bred during the same period to the same rams. The M2 ewes were consistently heavier (P<0.05) than the L1 ewes, which were heavier (P<0.05) than the L2 ewes, but there were no differences in body condition score among the ewe groups. There was no difference (P>0.05) in weaning weight of the lambs (25.09 \pm 0.36, 24.29 \pm 0.36, and 24.45 \pm 0.44 kg, for M2, L1, and L2, respectively) or number of lambs weaned per ewe bred (1.22 (95% CI: 1.05-1.42), 1.15 (0.98-1.35), and 1.05 (0.85-1.29), for M2, L1, and L2, respectively) among the ewe groups during their second breeding. Efficiency of lamb production (total litter weight at weaning divided by the pre-breeding weight of the ewe, for all ewes presented for breeding) after two years of production, was not significantly different (P>0.05) among the groups (0.40 \pm 0.02, 0.39 \pm 0.02, and 0.39 \pm 0.03, for M2, L1, and L2, respectively.

5.2 Introduction

Currently 30-43% of farmers breed their ewe lambs at eight months of age in New Zealand, increasing the lifetime production efficiency of the flock, and on-farm profitability (Kenyon et al., 2014a). Selecting lambs born to ewe lambs can increase the rate of genetic gain, by decreasing the generation interval of the flock, however, lambs born to ewe lambs are not commonly retained as replacements in the ewe flock in New Zealand (Dýrmundsson and Lees, 1972b; Kenyon, 2008; Loureiro et al., 2012; Kenyon et al., 2014a). Therefore, there is little knowledge of the reproductive performance of ewes that are born to ewe lambs compared with lambs born to mature ewes (Pain et al., 2015; Loureiro et al., 2016). It is well documented that lambs born to ewe lambs are lighter than lambs born to mature ewes at birth and to weaning (Annett and Carson, 2006; Loureiro et al., 2012; Corner et al., 2013a). Typically, lambs born to ewe lambs are slaughtered for meat production, with measurements of maternal performance not being well documented.

Loureiro et al. (2011) reported that lambs born as singletons or twins to ewe lambs were lighter at birth, and to 12 months of age, than lambs born as singletons or twins to mature ewes, and Loureiro et al. (2016) reported this difference continued until the weaning of their first lambs, when first bred at 18 months of age. The same authors also reported that singletons born to ewe lambs were lighter than singletons born to mature ewes for the first 12 months of their life, but then had similar live weight until three years of age (Loureiro et al., 2012) and until four years of age (Pain et al., 2015). All of these studies reported there were no differences in the number or weight of lambs produced at birth (Pain et al., 2015) and weaning (Pain et al., 2015; Loureiro et al., 2016) among the respective comparisons. Furthermore, ewes born to ewe lambs produced greater weight of lambs at birth (Loureiro et al., 2012; Loureiro et al., 2016) and weaning (Loureiro et al., 2016) and weaning (Lo

al., 2012). There were also no differences in the body condition score of the ewes among the respective groups (Loureiro et al., 2011; Loureiro et al., 2012; Pain et al., 2015; Loureiro et al., 2016). These studies had limited numbers of ewes in each group, ranging from 17 to 41, and did not breed their ewes as ewe lambs, so further experiments with larger population sizes are warranted.

This chapter continues from Chapter 4 of this thesis, which aimed to determine the ability for lambs born to ewe lambs to successfully be bred at seven to eight months of age. The aim of this experiment was to determine whether being born as a singleton or twin to a ewe lamb or a twin to a mature ewe caused differences in live weight, body condition score, and reproductive performance during their second breeding, and to calculate the cumulative lamb production to weaning at 28 months of age. It was hypothesised that there would be no difference in lamb production among the ewe groups during their second year of breeding, while their live weights would remain significantly different.

5.3 Materials and methods

The study was conducted at Massey University's Riverside farm (latitude 40° 50' S, longitude 175° 37' E) 11km north of Masterton, and Keeble farm (latitude 41° 10' S, longitude 175° 36' E) 5 km south of Palmerston North, New Zealand. The experiment ran from January 2019 to December 2019 with the approval of the Massey University Animal Ethics Committee (MUAEC 17/16).

5.3.1 Background

The animals in this experiment are described in Chapter 4. Briefly, 353 Romney ewes, born during the October to November 2017 period (Chapter 3), to yearling dams, as either singletons (L1; n=133) or twins (L2; n=87), or born as twins to mature ewe dams (M2; n=133) were utilised in this chapter. This chapter reports on these ewes from 16 months of age (D379, 17th January 2019, Chapter 4) until 28 months of age (D714, 18th December 2019). The ewes were managed at Riverside farm from their birth (September-November 2017, Chapter 3), and were relocated to Keeble farm in January 2019 (D392), where they remained for the duration of the experiment.

5.3.2 Ewe live weight and body condition score measurements

The ewes were weighed within two hours off pasture at 15 time points (D379 (January 17th 2019, average age of 461 days, weaning of first lambs, Chapter 4), D418, D449, D463, D469, D481 (pre-breeding), D498, D518, D532, D574, D597, D615 (pre-lambing), D660 (average day 24 of lactation; L24), and D714 (weaning of their second lambs)). Their body condition score (BCS; Jefferies (1961); scale 1 – 5, 1=emaciated, 5=obese) was also recorded nine times during this time period (D379, D449, D469, D481, D518, D574, D615, D660 and D714).

5.3.3 Reproductive measures

At D481 (April 29th, 2019), ewes were joined with entire, crayon-harnessed Romney rams at a ratio of approximately 1:59 for 34 days (two 17-day reproductive cycles; rams removed D515). The crayon harness colours were changed on d498 to detect if a ewe was mounted/tupped during either 17-day cycle. On D498 and D518 crayon marks on the ewe's rump were scored using a 0 to 3 score, indicating the incidences of tupping (0= no marks, 1= one mark, 2= two marks, 3= three or more marks (Radford and Watson, 1960)).

Pregnancy detection occurred at D568 (July 25th, 2019), via transabdominal ultrasound, to detect the number of fetuses. The breeding cycle that conception occurred was estimated based on crayon marks, for all ewes diagnosed pregnant, to determine paddocks for lambing. Pregnant ewes were identified as becoming pregnant during the first 17-day period of breeding if they had only the first crayon colour on their rumps (n=254). Those pregnant and showing both or only the second crayon colour on their rumps, were identified as becoming pregnant in the second 17-day period of breeding (n=25). Pregnant ewes that had no crayon marks at the end of the breeding period (n=28) were also assumed to be pregnant during the second 17-day cycle, for lambing management purposes.

5.3.4 Fleece weight and height

At D552 (July 9th, 2019) the ewes were shorn, and the individual greasy fleece weights, including bellies and pieces were collected, as described by Blair et al. (1984). Height at the withers was recorded on the ewes at D449, D574, D615, and D714, as described by (Cockrem and Rae, 1959). Height at the hip was also recorded at D449.

5.3.5 Lambing period

During the lambing period (D621-D663) the ewes were monitored twice daily at approximately 8:30 a.m. and 3 p.m., by one of two trained operators. During the twice-

daily lambing checks, litters that were strong enough to stand were tagged and identified to their dam. Lambs that were not yet standing were left until the next check. The sex of the lamb(s), birth rank, date of birth, paddock, and birth weight were recorded, irrespective of whether they were dead or alive. Maternal behaviour score (1-5 score; O'Connor et al. (1985)) was recorded for all ewes that had at least one lamb that was alive at tagging. Dead lambs were weighed and recorded. Lambs that were dead at the time of tagging were considered born dead, and lambs that were recorded after tagging, until 3 days after the end of the lambing period (D663), were considered to have died between birth and the end of the lambing period. At D660 (lambs were an average of 24 days old; L24) all lambs that were born were weighed and the tail removed via hot iron (docked), and all male lambs were castrated using a rubber ring. There were five lambs born on or after the docking date, that had all birth measurements taken, and were additionally tail docked and castrated (if male) using a rubber ring when tagged. At D714 (average of day 78 of lactation) lambs were weaned and weighed. Lambs that were not present at weaning were considered to have died between tagging and weaning.

5.3.6 Ewe health

At D398 and D442 ewes were dosed with zinc capsules (Time Capsule® Adult Sheep, AgriTrade) to provide protection against facial eczema. At D450, D498, and D567 faecal samples were taken to determine faecal egg counts for drench management. Ewes were drenched with Genesis Ultra Hi Min (Boehringer-Ingelheim) sheep drench at D450, D503, and D597. Ewes were crutched (removal of the wool from the breech and belly area of the fleece) at D484. During the duration of the experiment there were 16 (M2 n=3, L1 n=8, and L2 n=5) ewe deaths that occurred prior to the lambing period, and nine (M2 n=5, L1 n=2, and L2 n=2) that occurred during the lambing period. These death rates

(M2: 6%, L1: 8%, L2: 8%) were within the normal ranges (2.8-20% per annum) for New Zealand ewes, as reported by Griffiths et al. (2017).

5.3.7 Ewe and grazing management

The 16-month-old ewes had their first lambs weaned on D379 (Chapter 4). From D379, all ewes were managed as one group (previously managed with non-pregnant ewes separate to pregnant ewes, and pregnant ewes managed in two mobs), and at D392 (30th January 2019), they were moved from Riverside farm to Keeble farm. At Keeble farm the ewes were managed as one group grazing a predominant ryegrass/white clover-based pasture from D392 to D615. Due to drought conditions, grass baleage was provided to ewes from D421 (28th February 2019), at a rate of one bale per day (estimated 0.4 kgDM/ewe/day). At D449, it was identified that the ewes had lost live weight (average 3.8 kg loss) and/or body condition (average 0.3 score loss) since d379. Therefore, at D451 ewes were also provided with 200g/ewe/day of a wheat-, barley- and maize-based feed (Sharpes Stock Feeds, Multifeed Nuts). Ewes were rotationally grazed, being shifted every two to three days, depending on paddock size. At D486 the grass baleage was reduced to half a bale per day (estimated 0.2 kgDM/ewe/day). At D506 baleage supplementation was ceased. At D525 the wheat-, barley- and maize-based supplementation was ceased.

Pre- and post-grazing pasture masses were estimated during the experimental period, and are presented in Appendix 9.3 Table 9.3.1 (non-lambing period) and Table 9.3.2 (lambing period only). Samples of the pasture, baleage, and supplemented feed also were collected for nutritive analysis. Pasture was analysed using near infrared reflectance (NIR; Smith and Flinn, 1991), and supplemented feed and baleage were analysed using wet chemistry (Corson et al., 1999). Pre- and post-grazing pasture masses, and corresponding nutritive values are presented in Appendix 9.3 Table 9.3.1.

At D615, 13 days before the planned start of lambing, the ewes were allocated to their paddocks for the lambing period. Ewes identified as not pregnant at pregnancy detection (n=17) were removed, and rotationally grazed separately to pregnant ewes. Pregnant ewes were separated based on the breeding cycle that conception occurred (determined by crayon marks), with the ewes with no recorded tupp mark (n=25) added into the second cycle group. Ewes were split into the lambing paddocks based on their pregnancy rank and cycle pregnant. There were eight paddocks for the first cycle ewes and three paddocks for the second cycle ewes. Pre-grazing pasture masses ranged from 1190-2730 kgDM/ha, so stocking rates were calculated accordingly, and ranged from 11-15 ewes per hectare. Ewes bearing either singletons or twins from each group, within each cycle, were placed into each paddock, with a minimum of two from each sub-class per paddock. There was one exception, with only five L2 ewes bearing singletons and in the second cycle, and three paddocks, they were placed in two of the paddocks, ensuring a minimum of two ewes per sub-class per paddock. All triplet bearing ewes from the three groups (n=9) were in the first cycle, and so were placed in one paddock together. At D660, ewes in neighbouring paddocks were merged to create two cohorts, and rotationally grazed in these two groups until D714. Ewes that were identified as not pregnant at pregnancy detection were joined with one of the mobs at D660.

5.3.8 Statistical Analysis

Statistical analysis was carried out using SAS version 9.4 software (SAS Institute, Cary, NC, USA). Live weight of the ewes was analysed with a linear mixed model, with the fixed effects of treatment group, day of measurement, and pregnancy rank (zero, one, two, or three fetuses). The interaction of treatment group and day of measurement was also included in the model. The random effect of animal was included to account for repeated measures. Lambing performance of the previous year (not pregnant, pregnant

but did not wean a lamb, and pregnant and did wean a lamb) was initially considered, but it was not significant (P>0.05), and so was removed from the model. Ewe lamb BCS was analysed with a generalised linear model, assuming a Poisson distribution, with fixed effects of treatment group, day of measurement, and pregnancy rank (zero, one, two, or three fetuses), and the interaction of treatment group and day of measurement. The random effect of animal was included to account for repeated measures. Lambing performance of the previous year (not pregnant, pregnant but did not wean a lamb, and pregnant and did wean a lamb) was initially considered, but it was not significant (P>0.05), and so was removed from the model.

Ewe height at the wither was analysed with a linear mixed model, with the fixed effects of treatment group, and day of measurement, and the interaction of treatment group and day of measurement. The random effect of animal was included to account for repeated measures. Height at the hip was measured once, and was analysed with a linear mixed model with the fixed effect of treatment group. Lambing performance of the previous year (not pregnant, pregnant but did not wean a lamb, and pregnant and did wean a lamb) was initially considered, but it was not significant (P>0.05), and so was removed from the model for height at the wither. Ewe fleece weight was analysed with a mixed linear model, with the fixed effect of treatment group and lambing performance of the previous year (not pregnant, pregnant but did not wean a lamb, and pregnant and did wean a lamb). An additional analysis was carried out with the added covariate of live weight prior to shearing (D532).

For the second lambing only, the number of ewes diagnosed as pregnant per ewe bred was analysed using a generalised linear model, assuming a binomial distribution, with the fixed effect of treatment group. The number of lambs present at pregnancy detection per

ewe bred, and the number of lambs present at weaning per ewe bred were analysed using a generalised linear model, assuming a Poisson distribution, with the fixed effect of treatment group.

Lamb birth weight, L24 weight, and weaning weight (L78) were analysed using a mixed linear model, with the fixed effects of sex of lamb, lamb birth rank, and treatment group. Lamb date of birth was also added to the model as a covariate. The interaction of treatment group and lamb birth rank was initially considered, but it was not significant (P>0.05) and was removed from the model.

Lamb survival at the time of tagging and to weaning were analysed using a generalised linear model, assuming a binomial distribution, and included the fixed effects of treatment group, lamb birth rank, and sex of lamb. Lamb survival from those alive at tagging to weaning was analysed using a generalised linear model, assuming a binomial distribution, with the fixed effect of maternal behaviour score at tagging. Ewe maternal behaviour score at tagging was analysed for all litters with at least one lamb alive at tagging, using a generalised linear model, assuming a Poisson distribution. The fixed effects of treatment group and litter size (including dead lambs) were included in the model.

For both lambing periods, the average number of lambs weaned per ewe bred was analysed using a generalised linear model, assuming a Poisson distribution, with the fixed effects of treatment group and year. The random effect of animal was included to account for repeated measures. The average ewe efficiency was calculated as the total litter weaning weight of lambs divided by the breeding weight of the ewe, within each year of production. Ewes that were not presented for breeding as ewe lambs did not have a value calculated for their first year but did have an efficiency calculation for their second year. The average litter weight at weaning per ewe bred and the average ewe efficiency, were

analysed using a mixed linear model with the fixed effects of treatment group and year.

The random effect of animal was included to account for repeated measures for ewes that were presented for breeding in both years.

Ewe survival analysis was carried out using exit data of all ewes that died or were removed prior to the end of the experiment (D714). All ewes alive at the weaning of their 2nd lamb (D714) were censored at that date for the survival analysis. In addition, hypothetical culling was imposed, retrospectively, if a particular ewe was barren at pregnancy detection or weaning during the second breeding, as per commercial farming conditions. No culling for non-production was imposed during the first year, breeding as ewe lambs. All ewes that were alive, and not culled at the end of the experiment were censored on D714 for the survival analysis.

5.4 Results

5.4.1 Ewe live weight

The M2 ewes were heavier (P<0.0001) at all time points than the L1 ewes, which were heavier than the L2 ewes, from 16 months of age (D379) until 28 months of age (D714, Figure 5.1). All ewes were heaviest at D615, prior to lambing, when they were carrying conceptus weight.

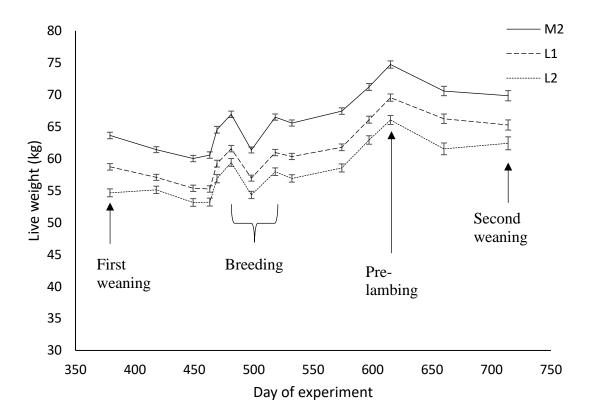


Figure 5.1: Least-squares means (error bars of \pm S.E.M.) of live weights for ewes born to mature ewes as twins (M2; —), or born to ewe lambs as singletons (L1, – –) or as twins (L2; - - -) from 16 months of age (d379) until 28 months of age (d714).

5.4.2 Ewe body condition score

There was no significant difference (P>0.05) in the BCS of ewes from 16 months of age (D379) until 28 months of age (D714, Figure 5.2).

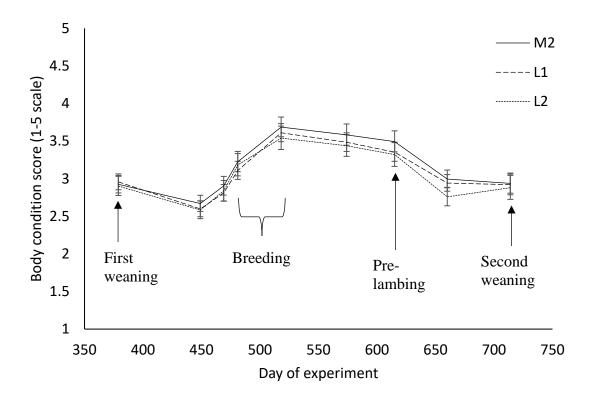


Figure 5.2: Body condition score (BCS; 1-5 scale) of live weights for ewes born to mature ewes as twins (M2; —), or born to ewe lambs as singletons (L1, —) or as twins (L2; ---) from 16 months of age (D379) until 28 months of age (D714). Values are backtransformed LS means and 95% confidence intervals.

5.4.3 Ewe height

The M2 ewes were taller (P<0.01) at the wither at all time measurements than both L1 and L2 ewes (Figure 5.3). At D449 the L1 and L2 ewes did not differ (P>0.05) for height at the wither. At all other time points L1 ewes were taller (P<0.01) than the L2 ewes. Hip height of the ewes at D449 was significantly different (P<0.0001), with the M2 ewes tallest (68.0 \pm 0.3 cm), and the L1 ewes (66.2 \pm 0.3 cm) taller than the L2 ewes (64.9 \pm 0.3 cm).

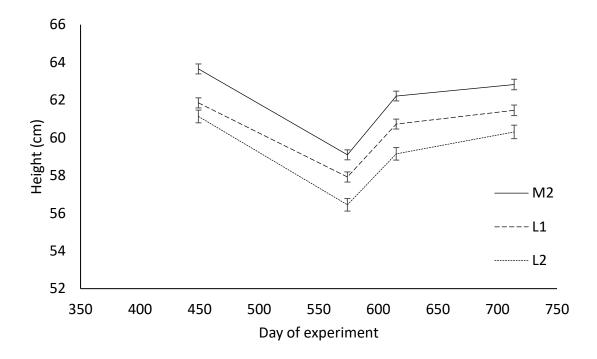


Figure 5.3: Least-squares means (error bars of \pm S.E.M.) of height (cm) at the wither for ewes born to mature ewes as twins (M2; —), or born to ewe lambs as singletons (L1, — —) or as twins (L2; - - -) from 16 months of age (D379) until 28 months of age (D714).

5.4.4 Ewe fleece weight

The M2 ewes had heavier (P<0.0001) fleeces than the L1 ewes which had heavier (P<0.05) fleeces than L2 ewes (4.39 ± 0.05 , 4.14 ± 0.05 , and 4.00 ± 0.06 kg, for M2, L1, and L2, respectively). With the addition of live weight at D532 (nearest timepoint to fleece measurements) as a covariate, there was no difference (P>0.05) in fleece weight among the treatment groups (4.21 ± 0.05 , 4.11 ± 0.04 , and 4.08 ± 0.05 kg, for M2, L1, and L2, respectively).

5.4.5 Ewe reproductive measures

There was no difference (P>0.05) in the pregnancy rate (number of ewes identified as pregnant per ewe presented for breeding) among the three groups (0.96 (95% CI: 0.92-0.99), 0.94 (0.88-0.97), and 0.94 (0.86-0.97) for M2, L1, and L2 ewes, respectively).

There was no difference (P>0.05) in the pregnancy rank (number of lambs identified at pregnancy detection per ewe presented for breeding) among the three groups (1.51 (95% CI: 1.31-1.74), 1.58 (1.37-1.81), and 1.51 (1.26-1.80) for M2, L1, and L2 ewes, respectively). There was no difference (P>0.05) in the number of lambs weaned per ewe presented for breeding based on the ewe treatment group (1.22 (95% CI: 1.05-1.42), 1.15 (0.98-1.35), and 1.05 (0.85-1.29) for M2, L1, and L2, respectively).

5.4.6 Lamb live weights

There was no interaction (P>0.05) between ewe treatment group and lamb birth rank on the weight of the lambs at birth, L24, and at weaning. At birth, lambs born to M2 ewes were 0.3 kg heavier (P<0.05) than lambs born to L1 and L2 ewes, which were not different (P>0.05; Table 5.1). There was no difference (P>0.05) in the weight of lambs at L24, and at weaning (L78) among the three treatment groups (Table 5.1). Lambs that were born as singletons were heavier (P<0.0001) than lambs born as twins or triplets at birth, L24, and weaning. Lambs born as twins did not differ in weight (P>0.05) at birth to lambs born as triplets, but twins were heavier (P<0.0001) than triplets at L24 and weaning.

Table 5.1: Least squares means (± S.E.M.) of lamb weights at birth (BWT), day 24 of lactation (L24), and weaning (WWT) for ewes born to mature ewes as twins (M2), or born to ewe lambs as singletons (L1) or as twins (L2) and by birth rank of the lambs (singleton, twin or triplet) during their second breeding.

	n	BWT (kg)	n	L24 (kg)	n	WWT (kg)
Ewe group						
M2	188	6.79 ± 0.10^{b}	159	12.14 ± 0.22	160	25.09 ± 0.36
L1	187	6.49 ± 0.10^{a}	155	11.97 ± 0.22	153	24.29 ± 0.36
L2	114	6.49 ± 0.12^{a}	92	11.69 ± 0.27	90	24.45 ± 0.44
P value		0.0136		0.2760		0.1094
Birth rank						
Singleton	136	7.92 ± 0.09^{b}	117	14.63 ± 0.20^{c}	118	29.11 ± 0.33^{c}
Twin	326	6.42 ± 0.06^{a}	268	11.54 ± 0.12^{b}	264	24.11 ± 0.22^{b}
Triplet	27	5.43 ± 0.22^{a}	21	9.76 ± 0.57^{a}	21	20.61 ± 0.78^{a}
P value		< 0.0001		< 0.0001		< 0.0001

a,b,c Means with different superscripts within column are significantly different to the P value indicated

5.4.7 Lamb survival

There was no interaction (P>0.05) between ewe treatment group and lamb birth rank for lamb survival at tagging (as an indicator of survival at birth) or at weaning. There was no difference (P>0.05) in the survival of lambs at tagging or at weaning among the treatment groups, or among the lamb birth ranks (Table 5.2).

Table 5.2: Lamb survival (%) at tagging and weaning for ewes born to mature ewes as twins (M2) or born to ewe lambs as singletons (L1) or as twins (L2) and by birth rank of the lambs (singleton, twin or triplet) during their second breeding. Values are backtransformed LS means and 95% confidence intervals.

	n	Survival at tagging	Survival to weaning
		(%)	(%)
Ewe group			
M2	188	93.7 (87.7-96.9)	86.6 (79.2-91.6)
L1	187	92.5 (86.2-96.0)	83.3 (75.7-88.9)
L2	114	90.6 (81.7-95.4)	80.5 (70.3-87.9)
P value		0.5687	0.3577
Birth rank			
Singleton	136	91.2 (85.0-95.0)	86.9 (80.0-91.7)
Twin	326	92.5 (88.9-95.1)	82.0 (77.1-85.9)
Triplet	27	93.2 (75.7-98.4)	81.5 (61.8-92.3)
P value		0.8609	0.4064

5.4.8 Ewe maternal behaviour score at tagging

There was no difference (P>0.05) in maternal behaviour score among the groups, with maternal behaviour score of 2.89 (95% CI: 2.45-3.41), 2.78 (2.33-3.27), and 2.53 (2.07-3.09) for the M2, L1, and L2 groups, respectively. There was also no difference (P>0.05) in maternal behaviour score based on the size of the litter, with maternal behaviour score of 2.84 (95% CI: 2.54-3.16), 2.70 (2.44-2.99), and 2.64 (1.77-3.94) for singletons, twins, and triplets, respectively. There was also no difference (P>0.05) in lamb survival to weaning, of all lambs born alive, based on the maternal behaviour score of the dam during tagging.

5.4.9 Ewe average production and efficiency at two years of age

In their first year of lambing the ewes were lighter than their second year of lambing (Figure 5.4), and produced lighter litters at weaning, for all ewe groups. In the second year of lambing there were noticeably more twin-ranked litters weaned than the first year, as indicated by the higher cluster of points in Figure 5.4. Actual ewe survival was similar (P>0.05) among the three ewe groups, with 85-91% of ewes surviving until the weaning of their second lambs (Figure 5.5a). When culling was imposed for non-production during the second breeding, as per commercial conditions, there was still no difference (P>0.05) among the three groups, but survival was decreased to 70-82% (Figure 5.5b). Ewes that did not successfully wean a lamb, but were presented for breeding, were given a value of zero for litter weaning weight. The values for total litter weaning weight and ewe breeding weight were used to calculate total ewe efficiency (Table 5.3).

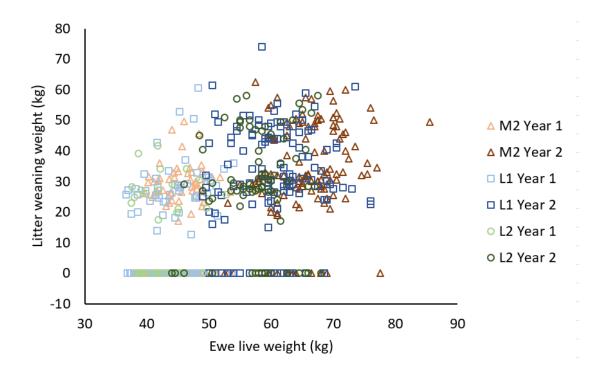


Figure 5.4: Scatter plot of total litter weight (kg) at weaning by ewe live weight (kg) at breeding when lambing as a one-year-old (Year 1; light) and as a two-year-old (Year 2; dark) for ewes born to mature ewes as twins (M2; red triangles), or born to ewe lambs as singletons (L1; blue squares) or as twins (L2; green circles). Data presented are raw values.

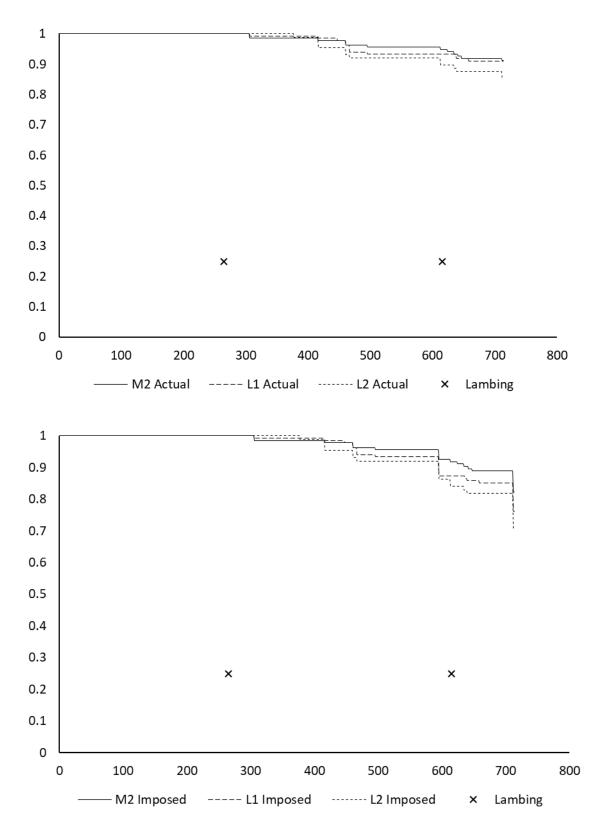


Figure 5.5: The actual (Figure 5.5a) and imposed culling for non-production (Figure 5.5b) survival curves of ewes born as twins to mature ewes (M2), born as singletons to ewe lambs (L1) and born as twins to ewe lambs (L2). Times marked with an x indicate the start of the lambing period each year (D268 and D624).

Average lamb production for the first two years of production was measured per ewe bred within each year and is presented in Table 5.3. The average number of lambs weaned per ewe bred, average litter weight at weaning per ewe bred, and average efficiency (ratio of total progeny litter weight to ewe breeding weight per year, for all ewes presented for breeding) were not different (P>0.05) among the treatment groups.

Table 5.3: The average number of lambs weaned (NLW), litter weight and efficiency (ratio of total progeny litter weight to ewe breeding weight) per year for the first two years of breeding for ewes born to mature ewes as twins (M2), or born to ewe lambs as singletons (L1) or as twins (L2). Values for average number of lambs weaned are back-transformed LS means and 95% confidence intervals, and values for litter weight and efficiency are LS means ± S.E.M.

Ewe group	Average NLW ¹	Average litter weight $(kg)^2$	Average efficiency ³
M2	0.75 (0.68-0.82)	21.4 ± 1.0	0.40 ± 0.02
L1	0.74 (0.65-0.83)	20.1 ± 1.1	0.39 ± 0.02
L2	0.67 (0.58-0.78)	19.0 ± 1.6	0.39 ± 0.03
P Value	0.4110	0.3973	0.9686

¹ Average number of lambs weaned each year per ewe presented for breeding

² Average litter weight at weaning each year per ewe presented for breeding

³ Average efficiency of ewes as a ratio of total progeny litter weight to ewe breeding weight per year for each ewe presented for breeding.

5.5 Discussion

The aim of this chapter was to add performance as a two-year-old ewe to the one-year-old performance from Chapter 4 thereby providing a combined lifetime reproductive performance of singletons and twins born to ewe lambs and twins born to mature ewes (acting as a control). This chapter reports on the reproductive performance of their second lambing, and the average cumulative production on lambs until the weaning of their second lambs. It was hypothesised that there would be no differences in lamb production among the ewe groups, while their live weights would remain significantly different.

Chapter 4 reported that the M2 ewes were heavier than L1 ewes, which in turn were heavier than L2 ewes, but there were no differences in body condition score, or lamb production during their first lambing, provided that the ewe lambs were heavy enough to be bred. From 16 months of age until 28 months of age, live weights continued to differ as they did during their first lambing, with M2 ewes being heavier than L1 ewes which were heavier than L2 ewes. Similar differences were seen in Chapter 2, where twins born to mature ewes and singletons born to ewe lambs were similar in live weight, and both were heavier than twins born to ewe lambs. Body condition score in this earlier experiment was also not different among the groups. Height at the wither and the hip showed the same pattern as the live weight of the ewe groups. Given there were no differences in body condition score, this suggests that the differences in live weight are likely due to differences in frame size. Fleece weight was heavier for M2 ewes than L1 ewes, which had heavier fleeces than L2 ewes. But, the differences in fleece weights (maximum difference of 0.39 kg) were not sufficient to explain the differences live weight among the ewe groups, again suggesting the live weight differences are caused by differences in frame size.

The ewe groups all grew from 16 months to 28 months of age, with increases of 6.3 – 7.7 kg. At the weaning of the second crop of lambs, ewe live weights ranged from 62.4 kg to 69.9 kg, indicating that they are not likely to be at mature weight. Mature weight is achieved at about 3.5 years of age (Chapter 2). Since the ewes are not yet at their mature weight, their production is expected to be less than the national average for number of lambs weaned per ewe bred. The national average lambing percentage in 2019 was 127.1% (Beef + Lamb New Zealand, 2019b), while the ewe groups in this experiment weaned at rates between 105% and 122%. The decrease in live weight prior to the breeding period due to drought conditions will have also impacted reproductive rates, as it is well recognised that a decrease in live weight prior to breeding will decrease ovulation rate (Ducker and Boyd, 1977; Morley et al., 1978; Rattray et al., 1981; Montgomery et al., 1988; Smith, 1988; Lassoued et al., 2004; Scaramuzzi et al., 2006).

In the current experiment, there was no difference among the ewe groups for the average lamb weight at weaning, which is consistent with results in Chapters 2 and 4, and with the literature (Loureiro et al., 2012; Pain et al., 2015; Loureiro et al., 2016). The M2 ewes produced heavier lambs at birth than the L1 and L2 ewes. This is possibly a maternal constraint on the fetus (Gluckman and Hanson, 2004; Jenkinson et al., 2007), with the M2 ewes being heavier and larger than the other two groups. The difference in lamb birth weight was only 0.3 kg, and did not affect either the survival rate, or future live weight measurements of the lambs. Therefore, the age of dam and birth rank of the ewe had no effect on the total lamb production during their second lambing.

Lifetime efficiency was measured as the average number, and weight of lambs weaned per ewe presented for breeding, and the efficiency, as a ratio of litter weight at weaning to ewe breeding weight, for the two lambing opportunities had by the ewes. There was unavoidable bias in this analysis, whereby each ewe group had a different proportion of the population presented for breeding during their first year, based on achieving a suitable breeding weight. All M2 ewes, 79.3% of L1 ewes, and 40.9% of L2 ewes were presented for breeding as ewe lambs (Chapter 4). Consequently, a higher percentage of the breeding records for efficiency were from the second year of breeding for L1 and especially L2 ewes, compared with M2 ewes. With higher rates of production expected from two-year old ewes than ewe lambs (Kenyon et al., 2008d; Corner et al., 2013a; Kenyon et al., 2014a), this presents a bias for the analysis. The fixed effect of year was used in the analysis to account for the differences in production between the ewes as one-year-olds versus two-year-olds. Alternatively, a "zero" production value could have been imposed for the first year of breeding for ewe lambs that were not presented for breeding, but this imposes an even larger bias, as those ewe lambs may have been able to produce but were not given the opportunity. Given the different proportions of each group presented and not presented for breeding, this would impose a large negative bias against the L2 ewes.

While not statistically significant, the L2 ewes produced 2.4 kg less in total litter weaning weight than the M2 ewes, per ewe bred, however, the lighter live weight of L2 ewes at breeding, and throughout the experimental period, counter this, resulting in very similar efficiency for the two ewe groups. This was also seen in Chapter 2, where the L2 ewes had a lower total litter weaning weight than the other groups and were also lighter at breeding than the other groups, the combined effect showing no difference in efficiency among the groups. The lifetime efficiency values (0.68-0.75; Chapter 2) are higher than the efficiency values for the two combined lambings (0.39-0.40; current chapter), likely due to the differences in the ewe ages during the analysis, and the corresponding reproductive rates. The current chapter was the only one to analyse the efficiency including the less-productive year as a one-year-old, and Chapter 2 analysed the ewes

during their older years, when they have reached their peak reproductive performance. Pain et al. (2015) reported that there was no difference in the litter weight of lambs weaned from singletons either born to ewe lambs or mature ewes, but that singletons born to ewe lambs tended to produce heavier litters than singletons born to mature ewes. They also reported that there was generally no difference in ewe live weight after one year of age for singletons born to ewe lambs or mature ewes, and the efficiency of progeny production was also not significantly different among groups. Based on these combined results, if farmers are selecting ewe replacements at weaning, the live weight of the ewe lamb is a much more important criteria to select on, than the age of the dam or the birth rank of the lamb.

5.6 Conclusions

From 16-to-28 months of age, ewes born to ewe lambs as singletons and twins had lower live weight than ewes born as twins to mature ewes, but they have no difference in body condition score. Differences in live weight among the groups were attributed to differences in frame size, determined by differences in height among the groups. There were no differences in lamb production during the second year of lambing, or the average lamb production over two years of breeding for those ewes presented for breeding. This suggests that if farmers select ewe lamb replacements from the lamb crop born to ewe lambs based on live weight, they will not sacrifice ewe productivity. Ewes born to ewe lambs have the same lamb production, but lighter live weight, possibly making them more efficient, although that was not seen in this experiment. The results reported in this chapter suggest that continued investigation of production of these ewes for their lifetime productivity, and longevity is warranted to make more robust recommendations to farmers regarding the selection of lambs born to ewe lambs as flock replacements.

Chapter 6

Single nucleotide polymorphisms (SNPs) associated with live weight at first breeding and pregnancy status of ewe lambs bred at eight-months of age

6.1 Abstract

By understanding more of the genetic controls of reproduction, especially as a ewe lamb, farmers and scientists can use this information to increase the accuracy of selection and increase production. There were 1513 ewe lambs, from eight different contemporary groups, over two years used in the experiment. Traits considered were live weight at the start of breeding at eight months of age, and the occurrence of pregnancy when bred for two reproductive cycles (34 days) for the first time at eight months of age. Thirteen singular SNPs were found to be significantly associated with live weight, and one singular SNP and four nearly significant SNP regions were associated with pregnancy occurrence. There were five SNPs associated with live weight that had corresponding gene functions, including meat area in *Musculus longissimus dorsi*, ubiquitination, regulation of collagen mRNA, protein translocation in the Golgi apparatus, and positive regulation of GTPase activity. There were two SNPs associated with the occurrence of pregnancy that had corresponding gene functions, including influencing litter size in first-kidding goats, and gamete formation in males and decreased granulosa cells in human females with polycystic ovarian syndrome. These gene functions can be related to live weight at eight months of age, or the occurrence of pregnancy when bred for the first time at eight months of age, however, further investigation is required.

6.2 Introduction

Farmers can increase farm profitability by breeding their ewe lambs at eight months of age (Kenyon et al., 2004a; Kenyon et al., 2014a). The likelihood of pregnancy occurring at this age is influenced by the live weight of the ewe lamb (Kenyon, 2008; Kenyon et al., 2014a), which is affected by genetic and environmental effects. The heritability of live weight at five-to-eight months of age ranges from 0.27-0.41 (Waldron et al., 1992; Fossceco and Notter, 1995; Safari and Fogarty, 2003; Safari et al., 2005), and the heritability of fertility as a ewe lamb (defined as the number of ewes lambing per ewe presented for breeding) is 0.08-0.10 (Fogarty et al., 1994; Safari and Fogarty, 2003; Safari et al., 2005). There are negative genetic correlations (-0.25) between live weight of the ewe lamb and fertility (defined as pregnant or not; Fossceco and Notter, 1995). In firstlactating dairy cattle there are negative genetic correlations (-0.45) between live weight during lactation and first luteal activity (Veerkamp et al., 2000). The negative genetic correlation between these traits indicate that ewe lambs that have a genetically heavier mature weight, will need to be a heavier at the start of breeding in order to attain 60-65% of their mature weight, associated with puberty attainment (Fossceco and Notter, 1995). Therefore, genetically heavier ewe lambs will have a lower fertility, at a given weight, than genetically lighter ewe lambs, based on the percentage of their mature weight that they have achieved. Given the heritability of fertility is low, and the genetic correlation between live weight and fertility is low to moderate, one option to increase genetic gain is to select for candidate genes involved in the expression of the trait (McEwan, 2009). With genomic technologies becoming cost effective, selection of replacements via genomic information is an increasingly realistic tool for farmers to use, and could be used to select replacement animals at an earlier age (Auvray et al., 2014; Brito et al., 2017; Dominik et al., 2019). The use of genomic breeding values in replacement selection has

been projected to increase the rate of genetic gain in the dairy industry by 50-70% (McEwan, 2009). In order for genomic selection to be successful, a knowledge of genetic markers associated with particular traits is needed (Auvray et al., 2014; Fortes et al., 2016; Brito et al., 2017).

Single nucleotide polymorphisms (SNPs) are chromosomal locations where there are substitution mutations associated with the expression of the gene (McEwan, 2009). Some SNPs have significant associations with phenotypic traits, indicating that the gene region they are part of, or are near to, has an impact on the expression of the trait (McEwan, 2009). Both pregnancy occurrence and live weight at the start of breeding are complex traits, with many genes and environmental factors directly and indirectly influencing their phenotypic expression (Fortes et al., 2016). Commonly associated with muscle growth and meat production, the myostatin gene has been identified as one of the most important regulators of growth and development (Han et al., 2010; Trukhachev et al., 2015). Additionally, SNPs associated with growth hormone genes have a significant effect on the phenotypes of live weight at 120 days of age, and average daily liveweight gain until 120 days of age in Harri sheep (Abdelmoneim et al., 2017). A ewe lamb needs to attain puberty prior to the breeding period. The attainment of puberty, and the regulation of the oestrous cycle have similar genetic and hormonal control (Kinder et al., 1987), and, therefore, genes associated with the attainment of puberty can potentially be used as a substitute for pregnancy occurrence. The insulin-like growth factor 1 (IGF1) pathway is associated with the attainment of puberty in heifers (Fortes et al., 2016), and there are associations with mutations in the leptin receptor gene, and a delayed onset of puberty (Haldar et al., 2014; Juengel et al., 2016) and decreased ovulation rates in prolific Davisdale sheep (Juengel et al., 2016). Therefore, combined this suggests that there are many genetic factors influencing live weight and fertility in ewe lambs.

Chapter 6

The aim of this study was to perform a genome-wide association analysis using 15,000 SNP markers to identify candidate genes associated with live weight at eight months of age, and the occurrence of pregnancy in Romney ewe lambs, when bred for the first time, at eight months of age.

6.3 Materials and Methods

The experiment was conducted at Massey University's Riverside farm (latitude 40° 50' S, longitude 175° 37' E) 11 km north of Masterton, New Zealand, from January 2017 until July 2018, with the approval of the Massey University Animal Ethics Committee (MUAEC 17/16 and MUAEC 17/12).

6.3.1 Animal measurements

The ewe lambs described in Chapter 3 (n=1026, born in 2016) and Chapter 4 (n=358, born in 2017), and 135 additional ewe lambs (born in 2017), were bred for the first time at eight months of age, in 2017 and 2018, respectively. Data editing was performed to enable consistent analysis of the same trait between the two different year cohorts. The first trait considered was achievement of pregnancy during the two cycles (34 days) of breeding. In 2017, ewe lambs were presented for breeding for 44 days, so for the purpose of this analysis, any that conceived after day 34 were considered non-pregnant. Date of conception was determined retrospectively based on the date of lambing, and assuming a gestation length of 147 days (Holst et al., 1986). In the 2017 experiment, a minimum live weight of 39 kg at the start of breeding was set for ewe lambs to be given the opportunity to conceive. In 2017 (Chapter 3), the minimum weight for being presented for breeding was 38 kg, so all ewe lambs that were lighter than 39 kg at the start of breeding, were considered not heavy enough for breeding, regardless of true pregnancy outcome. In 2018, there were ewe lambs that were not heavy enough at the start of the first cycle of breeding, that were joined later in the breeding season. These ewe lambs were also considered as not heavy enough for breeding, whether they ultimately became pregnant or not. The second trait considered was the live weight of the ewe lambs at the start of the breeding period. There were no data handling or censoring adjustments made to the live weight data, and all experimental animals with a live weight record were included,

however, there was selection imposed on the animals from their original populations, and the animals in the population were censored.

Genetic connectedness among the cohorts is indicated in Figure 6.1. In 2016, the two mature ewe groups were bred with different rams. In 2017, there were two ewe lamb groups (Mob A and Mob B), presented to different rams, with mature ewes present in each mob. The contemporary groups within these cohorts for all animals with a viable SNP profile are shown in Table 6.1. A summary of the live weight ranges per group, and the number of ewe lambs either pregnant or not pregnant are presented in Table 6.2.

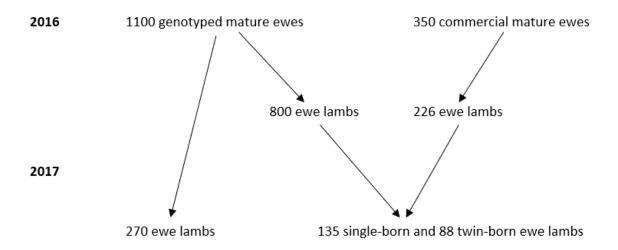


Figure 6.1: The genetic connectedness of ewe lambs born in 2016 and 2017 and presented for breeding for the first time at eight months off age in 2017 or 2018. The n values presented are the total for each group, including those without phenotype and/or genotype records.

Table 6.1: Summary of the contemporary group effects used in the analysis of SNPs based on the year of birth, dam age group, birth rank, feed treatment, and cohort during breeding. The n values presented are total numbers used in the analysis, with both a genotype and phenotype record present.

Contemporary group	n	Year Born	Dam age/type	Birth Rank	Feed treatment	Cohort during breeding
16GenA	375	2016	Genotyped mature ewes	Singletons and twins	Normal	Mob A
16GenB	360	2016	Genotyped mature ewes	Singletons and twins	Normal	Mob B
16ComA	56	2016	Commercial mature ewes	Singletons and twins	Normal	Mob A
16ComB	61	2016	Commercial mature ewes	Singletons and twins	Normal	Mob B
M2	134	2017	Genotyped mature ewes	Twins	Normal	Mob C
M2 Preferential	135	2017	Genotyped mature ewes	Twins	Preferential from weaning to breeding	Mob C
L1	133	2017	Genotyped ewe lambs	Singletons	Preferential from weaning to breeding	Mob C
L2	88	2017	Genotyped ewe lambs	Twins	Preferential from weaning to breeding	Mob C

Table 6.2: The live weight range and number of ewe lambs either pregnant or not pregnant, based on contemporary group for animals analysed for SNPs relating to live weight at breeding and pregnancy occurrence.

Contemporary group	Live weight minimum	Live weight maximum	N pregnant	N not pregnant	N not presented
	(kg)	(kg)			for
					breeding
16GenA	36	58	180	187	8
16GenB	34	58.5	166	193	1
16ComA	40.5	51	34	22	0
16ComB	43	60.5	45	16	0
M2	39.1	57.6	63	71	0
M2	41	60.2	99	36	0
Preferential					
L1	29.8	54	48	46	39
L2	26.8	52.8	20	9	59

6.3.2 Single nucleotide polymorphism analysis

Ear tissue samples were collected from each individual animal for DNA isolation. Of the 1,519 ewe lambs with phenotype records collected, 1,342 were successfully genotyped for 15,000 SNPs, using a custom Infinium Array (Illumina, San Diego, CA, USA) designed by EPAGSC (Dodds, 2007). Individuals were removed for call rates lower than 90%, or for not having both phenotypic and genotypic records (Table 6.1). The assumed map positions of the SNPs were based on the ovine genome assembly (Oar v3.1) produced by the International Sheep Genome Consortium (ISGC). The average distance between SNPs was 304,834 bp. There were 268 SNPs located on the X chromosome, and 27 SNPs that could not be mapped to the *ovis aries* (Oar v3.1) chromosomes, and were assigned to Oar Z. The SNPs on Oar Z and the X chromosome were included in the study.

6.3.3 Statistical analysis

A single SNP genome-wide association study (GWAS) was performed using an univariate animal in ASReml that had the model:

$$Y_{ijk} = \mu + contemporary group_i + SNP_j + animal_k + e_{ijk}$$

Where y was the phenotype; μ was the overall mean; contemporary group was the fixed effect of contemporary group, as described in Table 6.1; SNP was the fixed effect of SNP genotype; animal was the random additive genetic effect, distributed as N (0, $\mathbf{A}\sigma_a^2$), where A is the additive genetic relationship matrix among the animals and σ_a^2 the additive genetic variance; and e is the random residual distributed as N (0, $\mathbf{I}\sigma_e^2$), where I is an identity matrix of size of number of animals with records and σ_e^2 is residual variance. A genome-wide false discovery rate (FDR) was calculated for each trait individually. Associations with a genome-wide FDR <0.05 were considered significant. A 'region' was determined by SNPs that were significant for one trait and located near each other. A region was determined by the first significant SNP and continued as long as there were further significant SNPs within 10 MBP (1,000,000 base pairs) of each other.

6.4 Results

Figure 6.2 shows the genome-wide plot of $-\log_{10}(P\text{-values})$ of the GWAS for ewe lamb live weight at eight months of age. There were no significant (FDR > 0.05) regions associated with the trait, but there were 13 singular SNPs that were considered significant (FDR < 0.05). Figure 6.3 shows the genome-wide plot of $-\log_{10}(P\text{-values})$ of the GWAS for the occurrence of pregnancy when bred for the first time at eight months of age. There were no significant (FDR > 0.05) regions associated with the trait, but there was one singular SNP that was considered significant (FDR < 0.05), and four peaks indicating regions that were almost significant (FDR < 0.1).

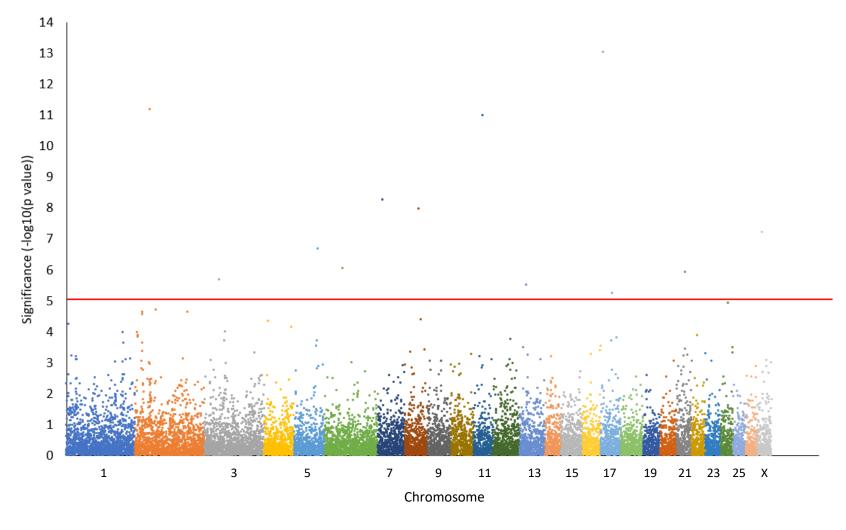


Figure 6.2: Genome-wide association plot for live weight at eight months of age in ewe lambs. The red line indicates significance (-log(10(p value)).

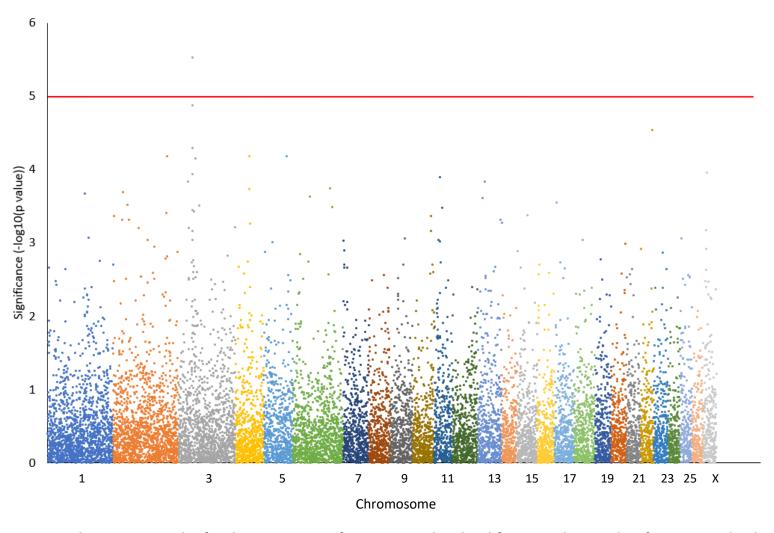


Figure 6.3: Genome-wide association plot for the occurrence of pregnancy when bred first at eight months of age in ewe lambs. The red line indicates significance (-log(10(p value)).

Chapter 6

Table 6.3 summarises the significant SNPs associated with either live weight at eight months of age, or the occurrence of pregnancy when bred at eight months of age, and the candidate gene that they are located on or are near to. There were 12 SNPs that did not have a known gene associated with them. Table 6.4 summarises the gene ontology (GO) analysis, with the gene name, function, and any literature associated with the genes associated with either trait. Five genes were identified to be associated with live weight at eight months of age, and two genes were identified to be associated with the occurrence of pregnancy at eight months of age.

Table 6.3: Significant SNPs or nearly significant SNP regions (with the most significant SNP reported) associated with ewe lamb live weight (LWT) or the occurrence of pregnancy (Preg) when bred for the first time, at eight months of age, chromosome (Chr) and position, effect, standard error of the effect (Effect SE), -10log(Pvalue), variant ID, and gene (if found).

Trait	Locus	Chr	Position	Effect	Effect SE	-10logPvalue	Variant ID	Gene
LWT	oar2_29709813.1	2	29709813	0.748	0.176	4.638656	rs401050506	ASPN
LWT	oar2_59801118	2	59801118	4.085	0.5895	11.17889	rs404800765	-
LWT	oar3_55514616.1	3	55514616	1.965	0.4121	5.684518	rs427593827	-
LWT	oar5_93455457_dup	5	93455457	3.241	0.6211	6.677514	-	-
LWT	oar6_36050035	6	36050035	2.939	0.5959	6.036725	rs416970076	HERC3
LWT	oar7_17500515	7	17500515	3.162	0.5382	8.270783	rs430071075	LARP6
LWT	oar8_59893627	8	59893627	3.531	0.6132	7.975107	rs410236644	-
LWT	oar11_s73325.1	11	29548082	4.800	0.6994	10.98264	-	-
LWT	oar13_24549545	13	24549545	2.139	0.4569	5.502348	rs403443685	ARHGAP21
LWT	oar17_4857385_a	17	4857385	5.672	0.7533	13.02302	-	-
LWT	oar17_42785548.1	17	42785548	1.360	0.2983	5.250315	rs401077696	RAPGEF2
LWT	oar21_39656527	21	39656527	2.455	0.5034	5.916832	-	-
LWT	oarX_50971111	X	50971111	2.705	0.4962	7.223827	-	-
Preg	oar2_218241732.1	2	218241732	-0.08	0.0207	4.180644	Rs409223720	PARD3B
Preg	oar3_55503740.1	3	55503740	-0.10	0.0205	5.524553	Rs416449662	-
Preg	oar4_58541568.1	4	58541568	0.094	0.0234	4.176824	Rs406324215	-
Preg	oar11_22759389	11	22759389	0.099	0.0258	3.892272	Rs410553473	SMG6
Preg	oarX_49002889.1	X	49002889	0.133	0.0342	3.960041	-	-

Table 6.4: Trait, gene, gene ontology reference (GO reference), biological function, and reference from the literature regarding each gene associated with ewe lamb live weight (LWT) or the occurrence of pregnancy (Preg) when bred for the first time, at eight months of age

Trait	Gene	Name	GO reference	Biological function	Reference
LWT	ASPN	Asporin	GO:0030512	Negative regulation of transforming growth factor beta receptor signalling pathway	(Stratil et al., 2006)
LWT	HERC3	HECT and RLD domain containing E3 ubiquitin protein ligase 3	GO:0016567	Protein ubiquitination	(Cruz et al., 2001)
LWT	LARP6	La ribonucleoprotein 6, translational regulator	GO:0006396	RNA processing	(Martino et al., 2015)
LWT	LARP6	La ribonucleoprotein 6, translational regulator	GO:0006417	Regulation of translation	(Martino et al., 2015)
LWT	LARP6	La ribonucleoprotein 6, translational regulator	GO:0032967	Positive regulation of collagen biosynthetic process	(Zhang and Stefanovic, 2016; Guo et al., 2017)
LWT	ARHGAP21	Rho GTPase activating protein 21	GO:0005096	GTPase activator activity	(Menetrey et al., 2007)
LWT	ARHGAP21	Rho GTPase activating protein 21	GO:0007030	Golgi organization	(Menetrey et al., 2007)
LWT	RAPGEF2	Rap guanine nucleotide exchange factor 2	GO:0043547	Positive regulation of GTPase activity	-
Preg	PARD3B	Par-3 family cell polarity regulator beta	GO:0005515	Protein binding	(Guan et al., 2016)
Preg	SMG6	SMG6 nonsense mediated mRNA decay factor	GO:0032204	Regulation of telomere maintenance	(Redon et al., 2007)

6.4 Discussion

Knowledge of specific gene regions can be used to improve genomic approaches for selective breeding, and can be investigated further to determine the practical implications linked to the gene regions (Fortes et al., 2016). This can be through marker-assisted selection to create genomically enhanced estimated breeding values (gEBVs) or causal mutation selection, knowing the function of a candidate gene and mutations associated (Dodds, 2007; Swan et al., 2014). Farmers are able to use genetic technologies for parentage determination, and can use gEBVs to predict the genetic merit of an animal (Dodds, 2007). Genomic predictors of merit are especially beneficial in increasing the accuracy of prediction of those traits that are hard to measure at the time of replacement selection, such as meat quality traits and future reproductive traits (Swan et al., 2014). Many production traits are affected by multiple genes, with small additive effects, making genetic selection for these traits harder to achieve (Spelman et al., 2013). By investigating genetic markers and regions associated with production traits, more information is available that can be added to existing genomic predictors of production.

There were five gene regions (ASPN, HERC3, LARP6, ARHGAP21, and RAPGEF2) associated with live weight at eight months of age, and two gene regions (PARD3B and SMG6) almost significantly associated with the occurrence of pregnancy when bred for the first time at eight months of age. No literature could be found on the RAPGEF2 gene that was related to the functions stated by the GO analysis or related to live weight traits.

The ASPN gene region belongs to the small secreted leucine-rich proteoglycans (SLRP) family, and is an important regulator of cellular growth and collagen fibrillogenesis (Stratil et al., 2006). The ASPN gene is associated with meat area on *Musculus longissimus dorsi* at the 13th and 14th rib and loin and neck meat weight in pigs (Stratil et

al., 2006), indicating that this could be related to growth until breeding in ewe lambs, and live weight at eight-months-of-age.

Ubiquitination is the addition of lysine residues to target proteins to facilitate the process of protein degradation (Xu and Jaffrey, 2011). During periods of body growth, there is a high rate of protein turnover, requiring the synthesis and degradation of several proteins (Welcker and Clurman, 2008). The HERC3 gene region is involved in regulating the process of ubiquitination (Cruz et al., 2001). Al-Mamun et al. (2015) reported that HERC5 and HERC6 gene regions (regulating the process of ubiquitination) were also associated with live weight in Merino sheep, The HERC3, HERC5, and HERC6 genes are from the HERC family of ubiquitin ligases, located near each other on the ovine chromosome 6, with similar function (Kalaldeh et al., 2019) indicating that the HERC3 gene could also be associated with live weight in sheep.

The LAPR6 gene region is involved in post-transcriptional regulation of collagen mRNA, and recruits other proteins, including non-muscle myosin, to contribute to this process (Zhang and Stefanovic, 2016). Type I collagen is the most abundant protein in vertebrates, found in bone, tendons, skin, ligaments, the cornea, arterial blood vessel walls, and many connective tissues (Cai et al., 2010; Zhang and Stefanovic, 2016). The replacement rate of type I collagen is low, except during wound healing and during adolescence, when the animal is growing rapidly (Zhang and Stefanovic, 2016; Guo et al., 2017). Therefore, animals undergoing rapid growth are likely to have a high replacement rate of type I collagen, indicating LARP3 could be involved.

The Golgi apparatus is functions to package proteins and other molecules for use within the cell or extracellular space (Benli et al., 1996). GTPases are also required for translocation of proteins through membranes, and the regulation of cell proliferation and division (Benli et al., 1996). The ARHGAP21 gene region codes for the Rho GTPase activity protein 21, responsible for inducing GTP hydrolysis to promote dynamics of the actin filament on the Golgi membranes (Menetrey et al., 2007). Therefore, the ARHGAP21 gene region could be associated with greater live weight at breeding, with faster growing animals requiring protein translocation for protein synthesis.

The PARD3B gene region has been reported to have a low association with litter size at first breeding in Jining Gray goats (Wang et al., 2020) and with gamete generation, spermatid development, spermatid differentiation, and male gamete generation in goats (Guan et al., 2016). Similarly, in the present study reported that there was a small association with fertility, but this only involved female animals. This may suggest that there are further reproductive implications in females, similar to those reported in males, that have not yet been identified. Interestingly, Lu et al. (2020) found that there was an association between PARD3B and adult weight in Chinese fine-wool sheep, which was not found in this study. Understanding more about the relationship between live weight and the occurrence of pregnancy in ewe lambs may help to explain this further.

The SMG6 gene region is associated with decreased granulosa cells in humans with polycystic ovarian syndrome (PCOS), causing a decrease in ovulation rate (Vazquez-Martinez et al., 2019). In humans, the SMG6 polypeptide is also associated with telomerase activity, with overexpression of the gene resulting in chromosome bridges during anaphase of mitosis and meiosis, and subsequent rapid apoptotic response (Redon et al., 2007). The SMG6 gene region is also involved in non-sense-mediated mRNA decay, a process that degrades mRNA that contains premature termination codons (Redon et al., 2007; Schmidt et al., 2014). Considering these actions of the SMG6 region, sheep with mutations in this gene may be less likely to become pregnant as a ewe lamb.

There was a possibility of cryptic relatedness causing false positive associations, due to relatedness in the population that is not accounted for in the analysis (Sul et al., 2018). In the 2017 population, there were 40 possible sires for the ewe lambs, but the actual sire for each individual was unknown. Additionally, the ewe lambs born to commercial ewes in 2016 had no parentage records, but it likely included relatives of each other. This could explain the significant SNPs and nearly significant SNP regions that did not appear to have a known function. Another limitation of this research was the relatively small population size, and the censoring of the animals through replacement selection, based on live weight at breeding. Larger populations with all lambs born to that population being analysed are required, especially when investigating binomial traits, to ensure there is sufficient power for the analysis and to increase the reliability of the results (Liu et al., 2011). The inclusion of males (with a strict definition of fertility at eight months of age) in the analysis would also help to identify further gene regions, or further validate the current results.

6.5 Conclusions

There were five genes associated with live weight at eight months of age, influencing the development of bone, protein degradation and turnover, transportation of proteins within cells, and cellular growth. All of these functions are required for growth, indicating that these genes could be associated with the live weight of an animal as an adolescent. There were two genes associated with the occurrence of pregnancy at eight months of age, influencing litter size, gamete generation, and the number of granulosa cells present. These functions will affect the likelihood of a ewe lamb conceiving during her first breeding, at eight months of age. Further analysis of these genes, and SNPs that were deemed significant, but did not have an identified gene, should be conducted to identify further regulators of live weight and occurrence of pregnancy in ewe lambs. Further research, with more conclusive results, could aid scientists in determining the genetic contributors that underly puberty attainment and therefore the occurrence of pregnancy when bred as a ewe lamb. This could then be applied by farmers when selecting their replacement ewe lambs, using genomically enhanced EBVs, to successfully breed at eight months of age.

Chapter 7

General discussion and conclusions

7.1 General Introduction

Currently, 30-43% of farmers breed their ewe lambs at eight months of age (Ferguson et al., 2014; Morris and Hickson, 2016; Beef + Lamb New Zealand, 2019b). Lambs born to ewe lambs are generally born a month later than lambs born to mature ewes, are sired by different rams (Edwards and Juengel, 2017) and are smaller than lambs of the same birth rank born to mature ewes (Quirke and Hanrahan, 1983; Annett and Carson, 2006; Kenyon, 2008; Kenyon and Blair, 2014; Kenyon et al., 2014a). The differences in lambing time, and the use of different sires, mean there are few valid comparison trials reported in the literature (Kenyon and Blair, 2014). Being smaller at a given age, and younger at the time of selection, lambs born to ewe lambs are not commonly considered for selection as replacement ewe lambs (Corner-Thomas et al., 2015c; McHugh et al., 2020). While it is well documented that lambs born to ewe lambs are smaller from birth to weaning, literature also indicates that they are lighter to up to four years of age (Loureiro et al., 2012; Pain et al., 2015; Loureiro et al., 2016). There is little information on how these differences in weight affect reproduction and longevity of replacements born to ewe lambs. It is well-established that live weight of the ewe influences her reproductive rate (Corner et al., 2006a; Kenyon et al., 2010; Corner-Thomas et al., 2014; Corner-Thomas et al., 2015a; Corner-Thomas et al., 2015b; Piaggio et al., 2015; Edwards and Juengel, 2017), but currently unknown if differences in live weight based on dam age affect reproductive performance. By selecting replacements that are born to ewe lambs, it is possible to better utilise the pool of replacement ewes and to increase rates of genetic gain. It is important to establish the effects of being born to a ewe lamb on lifetime reproductive performance of ewes to determine if keeping replacements born to ewe lambs is a viable option.

7.2 Overview of thesis

The overall objective of this thesis was to determine the effects on reproductive performance of ewes born to ewe lambs. More specific objectives, and their outcomes are listed below:

- 1. To investigate the maternal performance of ewes born as either singletons or twins, to either mature ewes or ewe lambs, until eight years of age (Chapter 2).
 - Ewes born as singletons to mature ewe were heaviest from birth until eight years of age, while twins born to mature ewes and singletons born to ewe lambs were similar and intermediate, and twins born to ewe lambs were lightest until eight years of age.
 - There was no difference in the number of lambs born or weaned per ewe bred, and no difference in lamb survival among the ewe groups. Twins born to mature ewes produced heavier litters at weaning than twins born to ewe lambs.
 Ewes born as singletons to either dam age were not different to each other or the other groups.
 - The lifetime efficiency of production (total lamb weaning weight divided by estimated pasture intake of the ewe) was not different among the four ewe groups.
- 2. To compare the lambing performance to weaning of mature ewes and ewe lambs when bred to the same rams at the same time (Chapter 3).
 - Ewe lambs produced 0.70 lambs and mature ewes produced 1.83 lambs per ewe presented for breeding.
 - At birth, lambs born as twins to ewe lambs were lightest, and lambs born as singletons to mature ewes were heaviest. At birth, lambs born as twins to

- mature ewes were intermediary, but heavier than triplets born to mature ewes and singletons born to ewe lambs, which were not different from each other.
- At weaning, lambs born as twins to ewe lambs and as triplets to mature ewes were of similar live weight, and were lighter than all other groups. Lambs born as twins to mature ewes and as singletons to ewe lambs were not different to each other, and were intermediate, while lambs born as singletons to mature ewes were heaviest at weaning.
- At tagging and from tagging to weaning, singletons born to mature ewes had the greatest survival, twins born to mature ewes had intermediate survival, and triplets born to mature ewes had the poorest survival. At tagging, singleton and twin lambs born to ewe lambs had similar survival rates as triplets born to mature ewes. To weaning, both singleton and twin lambs born to ewe lambs had similar survival to both twins and triplets born to mature ewes.
- 3. To investigate the live weight effects and reproductive performance of singletons and twins born to ewe lambs during their first breeding (Chapter 4), as ewe lambs, and second breeding (Chapter 5), compared with twins born to mature ewes.
 - Ewes born as twins to mature ewes were heaviest, and ewes born as singletons to ewe lambs were heavier than twins born to ewe lambs from their own weaning until the weaning of their second lambs. There was only one time point (prior to first breeding) when twins born to mature ewes had poorer body condition score than the other groups. At all other time points there was no difference in body condition score among the groups.
 - All twins born to mature ewes were presented for their first breeding at eight months of age, while 79.3% of singletons born to ewe lambs, and 40.9% of twins born to ewe lambs were presented for breeding based on a minimum

live weight threshold of 39 kg. All ewes were presented for breeding at 20 months of age. Of ewes presented for breeding, there was no difference in the number of ewes diagnosed as pregnant or number of lambs born or weaned among the groups for either year.

- Within each year, there was no difference in the average weaning weight of lambs among the ewe groups. There was also no difference in lamb survival at tagging and from tagging to weaning among the ewe groups.
- There was no difference in the efficiency of ewe groups for either lambing period, when calculated as the ratio of total progeny litter weight to ewe breeding weight for each year, for all ewes presented for breeding.
- 4. To identify SNPs that are associated with the live weight of ewe lambs at eight months of age and associated with the occurrence of pregnancy for ewe lambs first bred at eight months of age (Chapter 6).
 - Of the 13 SNPs identified to be related to live weight at eight months of age, five were associated with genes (LARP6, HERC3, ARHGAP21, RAPGEF2, and ASPN), with functions influencing bone development, protein degradation and turnover, transportation of proteins within cells, and cellular growth.
 - Of the five SNPs identified to be related to the occurrence of pregnancy, two
 were associated with genes (PARD3B and SMG6), with functions affecting
 litter size, gamete formation, and the number of granulosa cells present.

7.3 Practical implications of the study

The results of this study indicate that farmers can select singleton or twin lambs born to ewe lambs, as replacement ewes, if they reach a suitable weight for breeding; ~40 kg for a Romney type (Kenyon et al., 2012). Farmers should consider preferentially feeding their ewe lamb replacements from weaning until their first breeding to have a successful reproductive performance during their first year. This could allow farmers to decrease the weaning weight threshold that they base selection of these ewe lambs on. For example, assuming 120 days between weaning and the start of breeding, and a minimum breeding threshold of 40 kg, lambs growing 50 g/d would grow 6 kg, requiring a minimum weaning weight threshold of 34 kg. Meanwhile, lambs growing 100 g/d or 200 g/d would gain 12 or 24 kg, respectively, and require a minimum weaning weight threshold of 28 kg or 16 kg, respectively. The minimum threshold for breeding, and, therefore, weaning, would need to be determined based pasture allowance and quality. Farmers would also need to focus on increasing conception rates from their ewe lambs, using vasectomised rams, and selecting for ewe lamb conception, to increase the number of lambs produced, and available to be selected as replacements.

Ewes born to ewe lambs were lighter than their peers born to mature ewes, but produce similar weights and numbers of lambs at weaning, indicating they could be more efficient, but further lifetime studies are needed to determine the stayability and lifetime production of the ewes. Initially (Chapter 2) there was a lower rate of survival from the L2 ewes, compared with the other ewe groups, which would require an increased replacement rate, and therefore decrease the lifetime efficiency of the group. The new dataset possibly suggests a similar trend for L2 ewes, however, was this not significant until two years of age. In the initial study, each animal made up a large percentage, so the death or culling of one animal drastically influenced the survival curves. By following the lifetime of the

ewes from Chapters 4-5, a clearer representation of the longevity of the ewe groups can be established, before recommendations can be made to farmers about selecting these animals as potential replacements. Additionally, once lifetime data is collected, the causes of mortality and culling could be compared among groups to determine whether changes in management practices could be used to enhance survival of the ewes born to ewe lambs.

If the ewes prove to be more efficient, farmers would be able to stock greater numbers of ewes, contributing the same maintenance cost, and produce greater amounts of lamb. Additionally, ewes that are smaller, while still producing the same volume of lamb, are likely to contribute to a lower greenhouse gas footprint (Hegarty et al., 2010). Lighter mature weights may also indicate potential lighter minimum breeding weights. The current standard of 40 kg minimum for breeding is based on the idea that a ewe lamb achieves puberty at about 60% of mature weight (Kenyon et al., 2014a), and that mature weight is around 66 kg. If ewes born to ewe lambs have a lighter mature weight, by up to 5 kg, than ewes born to mature ewes, it would suggest that farmers may be able to breed lambs born to ewe lambs at up to 2 kg lighter than lambs born to mature ewes, as long as their body condition is not compromised (Cave et al., 2012; Corner-Thomas et al., 2015a).

If farmers were interested in selecting replacements born to ewe lambs, it would be probable that they were wanting to breed those replacements as ewe lambs themselves. Additionally, if they did not breed the lambs born to ewe lambs at eight months of age, they would lose out on the potential increased rate of genetic gain, by delaying the generation interval by an extra year. In this study a very high proportion of the available lambs born to ewe lambs as singletons and twins were selected, whereas farmers are likely to only select lambs that are heavy enough at weaning, decreasing the chances of the

replacements not being heavy enough to be bred at their first breeding. In this study, only 79.3% of L1 and 40.9% of L2 ewes lambs heavy enough to be bred, whereas this could indicate the proportion of each group farmers would select. The stricter the selection criterion for live weight imposed at weaning, the fewer twin-born lambs born to ewe lambs that would be selected.

By deciding to select replacements from those born to ewe lambs, farmers would need to consider their crossbreeding policy. If they commonly breed their ewe lambs to a low birth weight terminal sires, for easy lambing and increased growth, they would not be able to select the lambs as replacements. Selecting replacements that are born from ewe lambs can open the opportunity for farmers to breed some of their older ewes to a terminal sire, without compromising the number of lambs available to select replacements from.

By selecting lambs born to ewe lambs as replacements, there is the potential to increase the rate of genetic gain in the flock. This is achieved by decreasing the generation interval through having a younger ewe flock and increasing the selection intensity, while still selecting the same number of animals (Rendell and Robertson, 1950). There is a possibility for a slight offset to these advantages, by selecting from younger parents, they have fewer records of their own performance, decreasing the accuracy of selection (Rendell and Robertson, 1950). For nucleus ram breeders, the reduction in accuracy of selection may affect genetic gain, but for commercial farmers that are selecting based on the live weight of the individual at weaning, and rather than parental records, there will be no impact on accuracy of selection. With greater progress in genomic selection technologies, it could be possible for farmers to select animals more accurately, even with fewer records, increasing the rate of genetic gain.

7.4 Limitations of the study

The initial lifetime study (Chapter 2) utilised 115 ewes, across four groups, with group sizes ranging from 17 to 41. As this was a pilot study, contemporary group numbers of this size are adequate to determine likely trends, but for binomial traits it did not have had the statistical power to generate conclusive results. Therefore, the second study (Chapters 4-5), using group sizes of 88-135 animals was generated. This study has given more conclusive results and showed further differences in live weight between the twins born to mature ewes and singletons born to ewe lambs that were not apparent in Chapter 2. When investigating binomial traits, there is still a need for greater numbers to achieve conclusive results. The current results for number of lambs weaned per ewe bred (1.22) for M2 and 1.05 for L2 ewes), with a statistical significance of P<0.05 would require contemporary groups of >6,000 animals to detect significance at a power of 0.8. In addition, there was a considerable portion of the singletons and twins born to ewe lambs not heavy enough to be presented for breeding during their first year, reducing the power of analyses for lamb production. However, the overarching aim of the experiment was to compare the efficiency of the ewe groups, with the weight of lamb weaned per ewe, not the number of lambs weaned, and the current experiment has sufficient power to test this hypothesis. To improve this study further, greater numbers of ewe lambs should be used, consisting of ewe lambs heavy enough to be bred, and produce more conclusive results. Additionally, this experiment used two populations only, and would benefit from a larger variation of genotypes being used.

In order to make a direct comparison (Chapter 3), and to breed replacements that have the same genetic backgrounds, the same sires were used to breed with mature ewes and ewe lambs at the same time. The majority of the ewe lambs used to generate the experimental ewe lambs were daughters of the mature ewes used to generate the experimental ewe

lambs. This decreased the chance of differences in production of the experimental ewe lambs (Chapters 4-5) being genetically driven, but did mean that the experimental ewe lambs produced were younger than traditional replacements, being born one month later. Breeding in mixed-aged mobs potentially created a bias in conception rates during the first cycle of breeding, due to mature ewes possibly monopolising the attention of the ram. Ewe lambs are shy to rams, and tend not to stand correctly for courtship, compared with mature ewes, thus when bred together, rams will take preference to mature ewes, and some ewe lambs that are behaving favourably (Edey et al., 1978). With high conception rates during the first reproductive cycle of breeding for the mature ewes, there were fewer than 60 mature ewes seeking the attention of the ram during the second reproductive cycle of breeding, and the mature ewes were removed for the final 10 days of breeding. This breeding pattern influenced the performance of the resulting lambs until weaning (Chapter 3), but likely also affected the replacement ewe lambs selected that were born to ewe lambs, being born on average 10.5 days later than those born to mature ewes. This later birth date, given their average growth rate of 140 g/d, likely resulted in 1.47 kg of difference at the start of breeding, with lower birth weights also impacting later weights and growth rates. By adjusting for date of birth in the weaning weight analysis in Chapter 3, the model approximated a similar distribution of lamb birth dates between the ewe age group, possibly inflating the performance of lambs born to ewe lambs. The purpose of this experiment was to compare the two groups lambing at the same time, however, this was not entirely achieved due to the differences in conception rate early in the mating period for ewe lambs and mature ewes.

There were enough twins born to mature ewes to select based on live weight at weaning for the ewe lambs selected, which is what a farmer would do. There was a small selection (heaviest 73% selected) placed on the singletons born to ewe lambs, whereas all twins

born to ewe lambs, that were alive and healthy at weaning, were selected. The difference in age at weaning between the lambs born to mature ewes or born to ewe lambs could have been avoided by using different sires, and mating separately, however, this allows for potential genetic bias between the groups. Instead, a lower ratio was used (1 ram to 50 females) to combat this, rather than the usual 1 ram to 100 females (Kenyon et al., 2010), although this was still not enough to maintain conception rates of ewe lambs during the first reproductive cycle of breeding, compared with the national average breeding performance of ewe lambs.

Traditionally, commercial farmers select their replacement ewe lambs at weaning based on their current live weight, sometimes separated for birth rank to prioritise selecting twins. This gives a similar type of selection as was used in this experiment, however, for lambs born to ewe lambs, especially those born as twins, there was no selection imposed. In a realistic farming situation, there would be selection imposed on all of the groups, and fewer lambs born to ewe lambs would be selected as ewe lamb replacements. Based on those ewe lambs that were heavy enough at the start of breeding, there would have been 135 twins born to mature ewes, 95 singletons born to ewe lambs, and only 29 twins born to ewe lambs, creating a large population size discrepancy, and a reduction in statistical power. Subsequently, there was no criteria for breeding in the second year, and all ewes were presented for breeding, as all ewes would have reached maturity/puberty by 20 months of age, regardless of live weight.

By selecting almost all female offspring weaned from ewe lambs in this experiment, there was a need to preferentially feed these lambs from their weaning to first breeding, in order to increase the number of ewe lambs heavy enough to be bred, increasing feed demand and introducing potential costs. This was not needed for lambs born to mature ewes, with

all achieving the breeding weight target without supplementary feeding. This is an additional consideration for farmers, when deciding whether to select lambs born to ewe lambs as their replacement ewes. This may be of more importance in areas exposed to dry summer/autumn weather when pasture availability may restrict lamb growth. Therefore, the decision to select replacements born to ewe lambs, and to then breed ewe lambs, needs to be made each year, based on the current farm conditions, and the cost of additional feed required. If ewe lambs are not bred, and therefore no replacements can be selected from those born to ewe lambs, generation interval will increase.

During the second year (Chapter 5) there was a drought and spore counts were high, indicating facial eczema was present. Ewes were treated with zinc capsules, as per the manufacturer's recommendations, to prevent facial eczema. Unfortunately, a high proportion of ewes were losing condition during this time and 16 ewes either died or had to be euthanised, with some submitted for post-mortem examination to determine the cause of the liveweight loss. Zinc toxicity was detected, and likely caused underlying issues that resulted in weight loss, particularly in ewes that were already lighter/of lower body condition. Due to this occurring prior to breeding, breeding was delayed by one month to try and preferentially feed all ewes to increase live weight for breeding. Ewes that survived, but lost a considerable amount of live weight/body condition, were disadvantaged during the subsequent breeding, but were split evenly among all three ewe groups. Therefore, results among the groups were not biased, but were impacted on when comparing to the national average lamb production.

When analysing SNPs with phenotypic traits to identify candidate genes for a trait, large numbers of animals are required to conclusively find associations. This study utilised two populations with one quantitative trait (live weight at eight months of age) and one

binomial trait (the occurrence of pregnancy when bred for the first time at eight months of age), however, there were eight contemporary groups within the two populations, giving an additional complication to the model. Because sires were unknown for the second population, with 40 possible sires, the animal model caused cryptic relatedness (Sul et al., 2018). This issue can reduce the power of the analysis, causing false positive associations between the genetic markers and the traits compared with them. It is possible that some of the weak positive associations could be due to cryptic relatedness, and, therefore, further research is required to confirm the relevance of the SNPs identified. Additionally, censoring the data, by selecting lambs based on their live weight to enter the cohort, and not allowing the opportunity of breeding for ewe lambs that were not heavy enough, may have impacted some of the associations with both traits.

7.5 Future research

Continuing the current experiment of Chapters 4-5 to get lifetime information on replacement ewes born to ewe lambs, that were bred as ewe lambs themselves, will be of great interest to the sheep industry in New Zealand. This would add to the information already available in Chapter 2, giving two populations of data, and, thus, more certainty of the results. Using the lifetime data continued from Chapters 4-5 will also give greater information on the efficiency of ewes born to ewe lambs, as they appear to be lighter for their lifetimes, based on results from Chapter 2, while producing the same weight of lamb at weaning, compared with ewes born to mature ewes.

Selecting a second generation of lambs born to ewe lambs would be of interest (i.e. selecting lambs born in Chapter 4), to determine if selecting these lambs, generation after generation, affects the productivity of the ewes. In order to do this, it would be beneficial to use a larger industry farm, with 3000 dams (1000 mature ewes and 2000 ewe lambs) at the start of the experiment, to generate equal populations of 135 replacements selected for each ewe group, and continue over multiple generations. This would give indication if future generations of lambs born to ewe lambs are able to be selected as replacements, and if there are further live weight differences among the groups.

An economic analysis using feed intake, growth and reproductive data to calculate the benefits of selecting replacements from ewe lambs is required to evaluate the profitability of retaining replacements from ewe lambs. Analysis of the assumption that lambs born to mature ewes do not require additional feed from weaning to breeding, but that some lambs born to ewe lambs may need additional feed, depending on the proportion of them selected, needs to be addressed. An economic model, showing multiple scenarios will benefit farmers in making the decision of whether or not to select lambs born to ewe

lambs alongside those born to mature ewes. Additionally, an analysis determining the optimum proportion of lambs born to ewe lambs selected compared with lambs born to mature ewes is required. An economic analysis was beyond the scope of this thesis, however, with the data now available this could be achieved.

A more comprehensive investigation into SNPs associated with the attainment of puberty in ewe lambs would be of benefit to the industry. Additional phenotypes, such as the use of ultrasound detection of puberty, to more accurately determine the onset of puberty, and more animals involved is needed. Ideally, this would have fewer contemporary groups, and more knowledge of the genetic relatedness of the animals, giving more accurate results. Identifying SNPs that are associated with earlier or later attainment of puberty could be used by farmers to improve the reproductive performance of ewe lambs, by increasing the number of ewe lambs attaining puberty prior to breeding, and not selecting those that are likely to take longer to attain puberty.

7.6 Conclusions

The results presented in this thesis provide evidence that farmers are able to select lambs born as singletons or twins to ewe lambs as replacements, and breed them successfully at eight months of age if suitable live weights are achieved. It appears that replacements born to ewe lambs, especially those born as twins, are lighter than replacements born to mature ewes for their entire lives. The differences in live weight do not appear to impact lambing performance, providing body condition score is not affected. This indicates that these ewes have a smaller frame size, which does not affect their lifetime lamb production, compared with ewes born to mature ewes. Therefore, ewes born to ewe lambs appear to be more efficient than ewes born to mature ewes, and by selecting them, could increase in the rate of genetic gain. Collectively, these results indicate farm efficiency could be increased by selecting ewe replacements from ewe lambs.

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Appendices

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9.1 Appendix 1

Does being born a singleton or twin, or to a yearling or mature dam affect efficiency of ewes?

9.1.1 Summary

By breeding ewes at eight months of age as ewe lambs, ram breeders are able to reduce the female generation interval and thereby increase the annual rate of genetic gain. Farmers need to know which replacements to select. This experiment investigated the effect of having a ewe lamb (12 months old at lambing) or mature ewe dam, as well as birth rank on the lifetime performance of ewe progeny. The study used 17 singleton-born and 41 twin-born lambs born to mature ewes (M1 and M2, respectively), and 28 singleton-born and 29 twin-born lambs born to ewe lambs (L1 and L2, respectively), and recorded their lifetime production as breeding ewes. Throughout their lifetime M1 ewes were the heaviest, L2 ewes were lightest (P<0.05), while M2 and L1 ewes were intermediate and similar to each other. The L2 ewes produced the heaviest lambs at birth (P<0.05; 4.86 kg), but the lightest at weaning (P<0.05; 29.9 kg). M1 ewes had the lowest efficiency per year (0.70 kg of lamb weaned per 1 kg of ewe bred), L2 had the highest (P<0.05; 0.81 kg/kg), while M2 and L1 were indifferent from each other (P<0.05), and intermediate to the other groups (0.75-0.76 kg/kg). It is recommended that farmers consider lambs that are born as singletons to ewe lambs as potential replacements.

9.1.2 Introduction

Only 30-43% of ewe lambs are bred when they are eight-to-nine months of age in New Zealand (Beef + Lamb New Zealand, 2019a). Lambs that are born to ewe lambs are generally smaller than lambs born to mature ewes at birth (Everett-Hincks and Dodds, 2008; Young et al., 2010; Pain et al., 2015), weaning (Young et al., 2010; Loureiro et al.,

2011; Pain et al., 2015), and until 12 months of age (Loureiro et al., 2011; Pain et al., 2015). A similar effect is observed for birth rank; with lambs born as twins are smaller than singletons from birth to at least weaning (Schreurs et al., 2010a; Young et al., 2010; Corner et al., 2013a; Kenyon et al., 2014a).

Farmers do not commonly select lambs born to ewe lambs as replacements (Kenyon et al., 2004b), and the reproductive performance of ewes that were born to ewe lambs is not well documented. Ram breeders can reduce the generation interval by mating ewes to first lamb as one-year-olds, this will minimise the generation interval (Blair and Garrick, 2007). In addition to improving the rate of genetic gain, mating ewe lambs at 8 months of age will increase flock meat-production efficiency (Kenyon et al., 2014a). Pain et al. (2015) reported that singleton lambs born to ewe lambs are smaller than singleton lambs born to mature dams, from birth to weaning, and occasionally until four years of age, but had no differences in lamb output (number or live weight) during their first two lambing opportunities. Loureiro et al. (2011) and Loureiro et al. (2016), using the same dataset, reported that there was an effect of birth rank and age of dam on the live weight of female progeny until the weaning of their first lamb, with no difference in lamb output. The purpose of this paper was to continue with the data that Loureiro et al. (2011) and Loureiro et al. (2016) used, to determine whether the live weight effects of age of dam and birth rank last for the lifetime (to eight years) of female progeny, and whether there is a difference in lifetime production.

9.1.3 Materials and Methods

This experiment was undertaken at Massey University's Keeble Farm (latitude 41°10′S, longitude 175°36′E) 5 km south of Palmerston North, New Zealand. The experiment ran from March 2011 until January 2017. The experiment was conducted with the approval of the Massey University Animal Ethics Committee (MUAEC12/21).

9.1.3.1 Experimental design

Four ewe groups, representing a two (singleton or twin birth rank) by two (born to a ewe lamb or mature ewe) factorial were founded. These included singleton progeny born to multiparous mature ewes (M1, n=17), twin progeny born to multiparous mature ewes (M2, n=41), singleton progeny born to ewe lambs (L1, n=28), and twin progeny born to ewe lambs (L2, n=29), which were selected from a larger sub-set at weaning, and maintained as one mob (n=115) for their lifetime (Loureiro et al., 2011; Loureiro et al., 2016). These ewes were followed for six years (2011-2017) which encompassed six lambing opportunities.

Ewe live weights were recorded yearly at pre-breeding, pregnancy detection in midpregnancy, pre-lambing (one week prior to lambing), and at weaning. Ewes were first bred in 2011, at 18 months of age (Loureiro et al., 2016). Rebreeding subsequently occurred annually from 2011 to 2016, starting between the 24th of March and 24th of April of the respective years. Pregnancy detection occurred each year between 72 and 86 days after ram introduction. Pre-lambing live weights were recorded seven days before the planned start of lambing each year. Lambs were weighed, and identified to their dam within 18 hours of birth. These lambs had additional live weights measured at weaning (average age of 99 days).

9.1.3.2 Statistical analysis

Statistical analysis was carried out using SAS software (version 9.4; SAS Institute, Cary, NC, USA).

A linear mixed model, allowing for repeated measures to account for ewes being sampled repeatedly, was used to analyse ewe live weights. Birth rank, dam age, and day of measurement were included as fixed effects. A two-way interaction of dam age (age of

the ewe's dam) and birth rank, and a three-way interaction of dam age, birth rank and day were included in the model.

A general linear model was used to analyse the birth and weaning weight of progeny born to ewes in the experiment. Fixed effects of age of grand-dam, dam birth rank, lamb birth rank, lamb rearing rank, year, sex of lamb, and lamb date of birth (at weaning only), as well as the random effect of dam were included in the model. Two-way interactions of dam age and dam birth rank, dam age and lamb date of birth, and dam birth rank and lamb date of birth, and a three-way interaction of dam age, birth rank and year were included in the model. The random effect of dam was nested within the treatments of dam age and birth rank.

Individual ewe efficiencies were calculated for each year using total litter weights, divided by ewe live weights at breeding. Fixed effects of dam age, birth rank, lamb rear rank, year, and lamb date of birth were included in the model. A two-way interaction of dam age and birth rank and a three-way interaction of dam age, birth rank and year were included in the model. Repeated measures of ewe were included in the model.

9.1.4 Results and discussion

Ewes that were born as twins to ewe lambs (L2) remained lightest throughout their lifetimes (P<0.05), compared with ewes that were born as singletons to ewe lambs (L1) and born as twins to mature ewes (M2). These were in turn lighter than ewes that were born as singletons to mature ewes (M1), as seen in Figure 9.1.1. This is in agreement with other studies that showed lambs born to ewe lambs were smaller than lambs born to mature ewes from birth until weaning (Young et al., 2010) and up to one year of age (Pain et al., 2015) and that lambs born as twins were smaller than those born as singletons from birth until weaning (Schreurs et al., 2010a; Young et al., 2010). Therefore, age of dam,

and birth rank have effects on their lambs' live weights for their first six lambings. At yearling breeding, M1 ewes were the heaviest (P<0.05), with M2 heavier than L1, and L1 heavier than L2, which were the lightest, as seen in Table 9.1.1.

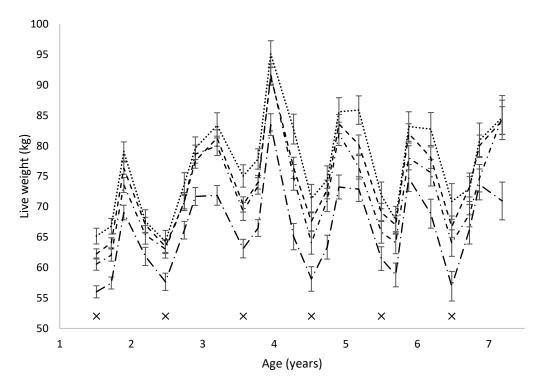


Figure 9.1.1: Means (\pm SE) depicting the live weight of ewes at mating, mid-pregnancy, pre-lambing, and weaning from their first mating at 18 months of age (March 2011) to the end of the experimental period (sixth weaning – December 2016) for ewe categories of M1 (ewes born to mature dams as singletons;), M2 (ewes born to mature dams as twins; ----), L1 (ewes born to yearling dams as singletons;). Dates marked with an x indicate pre-breeding for each year of their reproductive life.

L2 ewes produced the heaviest lambs at birth (P<0.002), as seen in Table 9.1.1. At weaning, lambs of M2 ewes were heavier than lambs of L1 and L2 ewes (P<0.05). Loureiro et al. (2012) showed that there were no differences between singleton-born ewes born to mature dams or to yearling dams in their lamb production to three years of age. Therefore, it is possible that milk production is not the only factor affecting the growth of lambs and that there must be other factors driving this.

Table 9.1.1: Average live weight of ewes at breeding (over 6 years), and their progeny at birth and weaning, as well as ewe efficiency (kilograms of lamb weaned per kilogram of ewe bred each year) based on age of dam or granddam (mature or yearling ewe; E or H, respectively), birth rank (singleton or twin; 1 or 2, respectively), and the interaction of dam age and birth rank (M1, M2, L1 and L2) for the 6 years of lambing. Values are LS means (± standard error).

	n	Ewe breeding weight (kg)	Lamb birth weight (kg)	Lamb wean weight (kg)	Ewe efficiency
Е	474	68.2 ± 0.52^{b}	4.51 ± 0.12^{a}	30.6 ± 1.14^{b}	0.725 ± 0.040^{a}
Н	427	61.7 ± 0.50^{a}	4.73 ± 0.12^{b}	29.9 ± 1.15^{a}	0.783 ± 0.040^{b}
P value		0.0001	0.0001	0.0357	0.0001
1	359	67.1 ± 0.56^{a}	4.52 ± 0.13^{a}	30.0 ± 1.15	0.730 ± 0.039^{a}
2	542	62.7 ± 0.46^{b}	4.71 ± 0.12^{b}	30.4 ± 1.14	0.778 ± 0.040^{b}
P value		0.0001	0.0008	NS	0.0001
M1	139	69.8 ± 0.87^{d}	4.45 ± 0.13^{a}	30.2 ± 1.2^{ab}	0.700 ± 0.041^{a}
M2	335	66.6 ± 0.56^{c}	4.57 ± 0.12^{a}	30.9 ± 1.4^{b}	0.751 ± 0.040^{b}
L1	220	64.5 ± 0.69^{b}	4.60 ± 0.13^{a}	29.8 ± 1.2^{a}	0.760 ± 0.040^{b}
L2	207	58.9 ± 0.73^{a}	4.86 ± 0.13^{b}	29.9 ± 1.2^{a}	0.806 ± 0.041^{c}
P value		0.0192	0.0012	0.0205	0.0043

Differences among the efficiencies (kilograms of lamb weaned per kilogram of ewe bred each year) of ewes shows that, while L2 ewes were lighter, and produced lighter lambs at weaning than M2 ewes, they had a greater efficiency than M2 and L1 ewes (Table 9.1.1), which had a greater efficiency than M1 ewes. This suggests that while these L2 ewes' live weights were negatively impacted by their birth rank and age of dam, it did not result in a proportional decrease in lamb output. Being able to produce a similar weight of lamb at weaning, while being lighter themselves increases efficiency and reduces maintenance costs per ewe (Sise et al., 2009). Therefore, there is potential to increase flock productivity by selecting L2 progeny as replacements.

9.1.5 Conclusions

Selection of twin-born lambs born to ewe lambs for replacements may offer a means of increasing efficiency. These ewes produce statistically lighter weights of lambs at weaning time compared with twin-born lambs born to mature ewes. However, because of their lower live weights, these are more efficient than ewes that are born to mature ewes,

regardless of birth rank, or ewes that were born as singletons to yearling dams. Further research is needed to confirm the effects of being born to a ewe lamb or as a twin on live weight, production, and efficiency.

9.1.6 Acknowledgements

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9.2 Appendix 2

Calculations for maintenance, growth, gestation and lactation requirements for ewes in Chapter 2.

9.2.1 Maintenance

Maintenance = $0.52 \times Predicted$ live weight $^{\circ}0.75$

9.2.2 Liveweight gain or loss

Liveweight gain = 55 x change in live weight

Liveweight loss = $30 \times change in live weight$

9.2.3 Gestation requirement

$$y = \frac{\text{Total birth weight}}{4} \times \text{Exp}(7.64 -$$

 $11.46 \times (Exp(-0.00643 \times Day \text{ of gestation})))$

$$\frac{dt}{dy}$$
 = 11.46 x 0.00643 x Exp(-0.00643 x Day of gestation) x y

Conversion of energy to gestational growth = 0.133

Daily gestational requirement =
$$\frac{\frac{dy}{dt}}{0.133}$$

9.2.4 Lactation requirement

Daily milk yield was predicted from (Peart et al., 1975) for days in milk, and number of lambs reared.

Lamb growth was assumed linear from birth to weaning.

$$Lamb \ average \ daily \ gain \ (ADG) = \frac{(Weaning \ weight-birth \ weight)}{Age \ at \ weaning}$$

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Energy in milk = $(0.0328 \times 0.08 + 0.0025 \times \text{day of lactation} +$

2.203) x Milk yield

Conversion of energy to milk production = 0.6

Conversion of energy in milk to lamb growth = 0.38

Energy consumed by the ewe to make milk = $\frac{\text{Energy in milk}}{0.6}$

Energy consumed by the lamb from milk = Energy in milk \times 0.38

Additional lamb requirement from grass

= (Lamb maintenance + Lamb growth) - Energy from milk

9.2.5 Total daily requirement

Total energy = Ewe mainenance + Ewe liveweight change + Energy to make milk + additional lamb requirements

9.2.6 Other assumptions

- Lambs that did not have a birth weight (n=2), and/or date of birth (n=1), were given a birth weight average and/or date of birth average, respectively, for the ewe group for the year they were born.
- Lambs that did not have a weaning weight were assumed to have died. Any lambs that died were assumed to have died at birth, and had no energy requirements from birth to weaning.
- Ewes that died prior to pregnancy detection were assumed to be non-pregnant.
- Ewes that died between pregnancy detection and lambing, and were carrying one or more lambs, were given an average lamb birth weight and date of birth for their ewe group of the year they died to calculate gestational energy requirements prior to death.

9.3 Appendix 3

Pasture measurements for ewes in Chapter 5

Table 9.3.1: The pre- and post-grazing pasture masses, dry matter of and metabolisable units offered to the ewes during the experimental period, excluding paddocks for lambing in 2019.

Day	Treatment (if any) ¹	Feed type	Pregrazing mass (kgDM/ha)	Post- grazing mass (kgDM/ha)	Dry matter (%)	Metabolisable energy (MJME/kgDM)
450	-	Pasture	2410	1720	-	-
457	-	Pasture	-	-	95.5	9.4
461	-	Pasture	1640	1380	-	-
461	-	Bailage			91.7	-
468	-	Grain	-	-	86.2	
485		Pasture			97.1	10.1
498	-	Pasture	3440	-	96.4	11.6
532	-	Pasture	2620	-	94.9	>12.5
567	-	Pasture	1680	1150	96.6	11.8
601	-	Pasture	1430	970	97.6	9.9
614	-	Pasture	-	1260		
666	Mob A	Pasture	1310	-	96.7	12.3
666	Mob B	Pasture	1690	-	95.9	10.5
684	Mob A	Pasture	2410	1490	95.9	10.8
684	Mob B	Pasture	2160	1280	95.2	10.4
700	Mob A	Pasture	2060	1680	97.5	9.7
700	Mob B	Pasture	2360	2380	95.3	10.6

¹ Treatment: Ewes were merged from their lambing paddocks into two mobs after L24 weight

Table 9.3.2: The pre- and post-grazing pasture masses, dry matter of and metabolisable units offered to the ewes during the lambing period, based on individual lambing paddock in 2019.

Lambing paddock	Day	Current grazing mass (kgDM/ha)	Dry matter (%)	Metabolisable energy (MJME/kgDM)
A	601	2000	95.6	>12.5
	614	2230	96.5	11.8
	632	2040	95.9	10.9
	642	1910	96.6	10.6
	656	2160	97.1	11.2
В	601	2170	97.2	12.5
	614	2330	96.2	11.8
	632	1940	97.0	11.2
	642	1730	96.4	10.6
	656	1680	96.4	10.7
С	601	2330	96.4	12.3
=	614	2470	96.7	11.9
	632	1890	95.4	10.6
	642	1440	96.2	10.3
	656	1350	96.3	11.5
D	601	2730	96.5	>12.5
_	614	3340	95.5	12.1
	632	2150	96.2	11.2
	642	2210	94.8	10.7
	656	1900	94.9	11.6
Е	601	2330	96.9	12.1
	614	2770	97.2	12.0
	632	2050	95.4	11.5
	642	2050	95.5	11.0
	656	1650	95.4	11.5
F	601	2160	96.1	>12.5
	614	2040	95.1	12.0
	632	1660	96.3	10.6
	642	1700	97.7	10.4
	656	1400	97.0	11.1
G	601	1640	95.5	>12.5
	614	2000	96.4	>12.5
	632	1550	94.8	11.6
	642	1240	96.1	10.9
	656	1110	94.8	11.2
Н	601	1900	97.8	>12.5
	614	2290	96.7	12.2
	632	1810	95.6	11.3
	642	1640	96.7	10.6

Table 9.3.2 continued:

Lambing paddock	Day	Current grazing mass (kgDM/ha)	Dry matter (%)	Metabolisable energy (MJME/kgDM)
I	601	1420	97.2	>12.5
	614	1660	96.7	>12.5
	632	1200	96.3	11.7
	642	1100	94.9	10.8
	656	1050	96.2	11.9
J	601	1190	95.5	11.4
	614	1300	97.0	>12.5
	632	1070	96.0	11.7
	642	990	95.6	11.5
	656	1150	95.0	12.1
K	601	1330	97.6	12.1
	614	1550	96.5	>12.5
	632	1230	96.7	12.1
	642	920	96.1	11.0
	656	1160	95.1	11.8



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