

Chapter 1. Introduction

Ultimately, farming enterprises need to be profitable to survive. Regardless of enterprise type, flock reproductive efficiency is one of the key drivers of farm profitability (Sidwell and Miller 1971; Martin *et al.* 2004). For sheep producers, flock reproductive efficiency can best be thought of as the ratio of lambs born in a breeding season to the number of females on the property during joining. Historically, Australian sheep production systems were dominated by Merino sheep, where most emphasis in the breeding program is placed on wool (Rowe 2010). The last 20 years has seen big changes in Australia's sheep population with the industry moving from a wool-focussed industry to a dual-purpose industry. Over this period, the value of lamb production relative to wool has increased significantly and has now overtaken wool (Rowe 2010; Curtis 2014). This is also reflected through changes in the ewe base population, where, although Merino ewes make up approximately three quarters of the ewe flock, just under 50% of these ewes are mated to Merino rams (Curtis 2014). The shift to a dual-purpose industry and an increased value of meat relative to wool is resulting in greater emphasis being placed on flock reproductive rate in most sheep enterprises (Barnett 2007).

Up until 2007, Australia's national marking rate had been relatively stagnant at 77% (Barnett 2007). Whilst there are indications it has improved by approximately 8% between 2005 and 2012 (Curtis 2014), it still lags considerably behind New Zealand's average marking percentage of 118% (Beef + Lamb NZ 2015). Improving average net reproduction rate is an obvious way to improve reproductive efficiency; another method is to lower the age at first mating and join ewes prior to 1 year of age. Bio-economic modelling was used by Young *et al.* (2014) to identify critical control points for improving the reproductive performance of sheep in Australia. Improving reproduction from ewe lambs was identified as the second most important research area after twin lamb survival.

Ewes first mated prior to 1 year of age typically have lower lambing percentages than mature ewes (Dýrmundsson 1973, 1981; Corner *et al.* 2013). In addition to this, reproductive performance of young ewes is highly variable from year to year and season to season (Dýrmundsson 1973; Fogarty *et al.* 2007).

A survey of New Zealand farmers by Kenyon *et al.* (2004c) found that there are a number of negative perceptions surrounding the mating of ewes prior to 1 year of age including detrimental effects on second mating, poor weaning weights of ewe lamb progeny, negative effects on wool production, and poor reproductive performance. Whilst it is not clear whether Australian farmers have the same perceptions as those in New Zealand, in both countries the percentage of ewes mated early is low; less than 20% (Curtis and Croker 2005) and 40% (Kenyon *et al.* 2014) for Australia and New Zealand, respectively.

Yearling reproduction traits¹ were recently identified as genetically different traits to reproduction traits measured at 2 years of age (Bunter and Brown 2013). This suggests that the genes controlling yearling reproductive performance are not identical to those controlling later reproductive performance. Given that a ewe is at a different physiological development stage at 7 months compared to at 18 months of age, it is also possible that different factors contribute to reproductive success and failure. For instance, when ewes are mated at 18 months of age it can be assumed that they are sexually mature and have commenced oestrus cycles. While many ewes reach puberty prior to 1 year of age, it is not safe to assume all ewes will be sexually mature at this age. A need exists to better quantify the factors that influence successful joining of ewes prior to 1 year of age as well as to understand the relationships that exist between early and later reproductive performance.

In breeding programs there is an incentive to mate animals at a younger age so that the generation interval can remain low. With genomic selection now possible (Swan *et al.* 2014), it has become more optimal to mate more breeding animals earlier, e.g. within their first year. Whilst the effect of the use of young rams on flock genetic gain is well understood, the implications of using ewes at younger ages on flock genetic progress has not been considered to the same extent. In particular, the lower and more variable fertility rate seen in young ewes is usually not considered in existing literature on modelling sheep breeding programs. In order to encourage breeders to consider adopting the practice of mating of ewes prior to 1 year of age it will be necessary to demonstrate the impact of young ewe fertility rate, including any possible adverse effects, on flock genetic progress.

¹ The outcomes from breeding ewes prior to 1 year of age are termed yearling reproduction traits in this thesis

With a focus on yearling reproductive performance the aims of this thesis were fourfold:

1. To assess the impact of early mating and selection of ewes on flock genetic progress relative to other breeding program changes.
2. To better understand the role of pubertal traits and their relationship with yearling reproductive performance.
3. To gain a better understanding of and quantify the factors which influence yearling reproductive performance.
4. To quantify the relationship between reproductive performance at different parities.

Broadly speaking, these aims were achieved through two methods: using stochastic simulation to model breeding programs, and through the analysis of historical data from the Sheep CRC Information Nucleus Flock and industry data collected from the middle of 2012 to the beginning of 2015.

Chapter 2, the review of the literature, first considers the importance of ewe reproduction on breeding programs in terms of both age at first mating and reproductive rate. The second section of Chapter 2 reviews neuroendocrine control of puberty and the oestrus cycle in sheep and how puberty can be defined and measured. The factors influencing the onset of puberty and reproductive performance are considered before existing knowledge on the genetic components of reproduction are summarised. Finally, the impact of mating prior to 12 months of age on lifetime performance is reviewed.

The first study in this thesis, Chapter 3, used stochastic simulation to compare and contrast different sheep breeding programs. The aim of this study was to assess the impact that age at selection and different ewe fertility levels at 1 year of age have on expected genetic gain and breeding program risk relative to other parameter changes, such as the early mating of rams and the availability of genomic information.

Probability distribution functions were used to create an assessment of breeding program risk that accounted for both mean and variation in response after 10 years of selection.

In the second study, Chapter 4, historical data collected from the Sheep CRC Information Nucleus Flock was used to quantify the relationship between age at first oestrus, as detected by teaser wethers, and

yearling reproductive performance in maternal-cross ewes. In addition, the relationship between reproductive performance across parities was estimated.

The final two studies were based on industry data collected as part of this PhD project. Data on the novel trait, progesterone concentration at joining, reproductive outcomes, additional liveweight and condition score measurements, and management information were collected from 12 industry ram-breeding flocks. The overall aim was to determine whether the trait progesterone concentration at joining was a useful indicator of sexual maturity and subsequent reproductive success as well as gain a better understanding of the relationships existing between yearling reproductive performance, later reproductive performance, and key production traits. The third experimental chapter focused on gaining an understanding of the trait, progesterone concentration at joining. Influential fixed effects and covariates were identified and several trait definitions were trialled in estimating heritability.

The final study, Chapter 6, aimed to quantify the relationship between yearling reproduction traits, progesterone concentration, and other key production traits including liveweight and condition score at joining. The genetic and phenotypic relationship between reproductive performance at 1 and 2 years of age were quantified and the impact that lambing at 1 year of age had on subsequent 2-year-old performance was also assessed.

Chapter 7, the general discussion, brings together the key outcomes of each of the experimental chapters. These are: 1) The impact of young ewe fertility rate on rate of genetic progress and breeding program risk, 2) measuring the attainment of sexual maturity in ewes and its' relationship with yearling reproductive performance, 3) other factors influencing yearling reproductive performance and 4) the relationship between yearling reproductive performance and reproductive performance at later parities. The general discussion concludes with a number of recommendations for industry.

Chapter 2. Literature Review

2.1 Introduction

Reproduction efficiency is one of the key drivers of profit on farm regardless of enterprise type (Sidwell and Miller 1971; Martin *et al.* 2004). Flock reproductive efficiency encompasses many aspects of reproduction (Sidwell and Miller 1971; Martin *et al.* 2004) but can essentially be summarised as the ratio of the number of lambs weaned to the number of flock ewes. As on-farm costs continue to rise (ABARES 2014) and farm profit margins tighten, improving flock reproductive efficiency is gaining greater importance. Over the last 20 years the value of meat relative to wool has increased considerably and the two sectors now have a similar economic value (Rowe 2010), so it can be argued that improving reproductive efficiency is also of increased importance to wool enterprises (Barnett 2007). The early mating of ewes may offer the opportunity to improve reproductive efficiency by cutting one year from the production cycle, hence reducing the number of ewes in the flock not mated.

For both stud and commercial operations there are a number of potential benefits to adopting early mating of ewes including increased profitability (Young *et al.* 2010), the opportunity to better utilise pasture, as well as greater income from sale lambs due to higher lamb numbers (Kenyon *et al.* 2014). There may also be additional benefits for flock genetic progress. The selection of replacement ewes at younger ages reduces the generation interval and the rate of genetic progress can be increased (Falconer 1989), which is of particular relevance to the stud sector.

Under Australia's extensive sheep management systems ewes have historically been first mated at 1.5 to 2.5 years of age, though there is potential to mate ewes prior to this. The most recent national survey of Australian sheep producers found that only 18% of non-Merino producers and 3% of Merino producers attempted to join ewes to lamb at 12 months of age (Curtis and Croker 2005). As the survey targeted producers with a flock size greater than 500 sheep, this mainly applies to commercial enterprises. In New Zealand more ewes are joined prior to 12 months of age, and it is estimated that 40% of ewes are mated to lamb at 12 months of age (Kenyon *et al.* 2014). Based on feedback from stud breeders and the volume of

data submitted into the Australian genetic evaluation system for sheep, it is likely that more than 20% of Australian stud breeders mate ewes prior to 12 months of age and the number of stud producers who have adopted or are considering adopting early mating programs has increased in the last decade.

To date barriers to adoption of early mating in industry have been lower and more variable reproductive performance in young ewes (Dýrmundsson 1973); potential negative effects on future production (Kenyon *et al.* 2014) or progeny performance (Corner *et al.* 2013); additional feed requirements to prepare ewes for early mating (Whale 2013); and the potential for additional time, labour and costs associated with ewe management. Although these are important considerations in the mating of ewes prior to 1 year of age, it is crucial that improvements in ewe reproductive performance and flock efficiency are made. As improving reproduction from ewe lambs was recently identified as the second most important area for future national research in reproduction behind twin lamb survival (Young *et al.* 2014), it is clear that scope exists for further work in this area. Improving reproductive efficiency will be important in helping to ensure future global lamb demands can be met (Palmer 2010) and to secure future farm profitability (Young *et al.* 2010).

Reproduction traits are complex quantitative traits influenced by multifaceted neuroendocrine pathways (Goodman and Inskeep 2006), environmental cues (Dýrmundsson 1981), farm management decisions (Trompf *et al.* 2011) and have an underlying genetic component (Safari and Fogarty 2003). All these factors and their interactions must be considered together in seeking to improve individual ewe or flock reproductive performance. The improvement of reproductive performance in ewes mated prior to 1 year of age has the additional challenge of considering the impact of pubertal development and animal growth. As ewes are at a different stage of maturity at 7 months relative to 18 months, it is highly probable that different and even more complex factors influence reproductive outcomes at 1 year of age.

Placing emphasis on yearling reproductive performance, this review considers the current reproductive performance of ewes, the importance of ewe reproduction rate and age at first mating on the breeding program, and how the relative risks and opportunities of breeding program changes can be assessed.

Neuroendocrine control of the oestrus cycle and the onset of puberty are then summarised, followed by a

discussion of effects that influence puberty and reproduction in ewes before a review of the literature covering the genetic components of reproduction rate in sheep. The review concludes with an examination of the impact of yearling reproduction on later performance.

2.2 Current ewe reproduction rate

Historically there has been little improvement in Australia's sheep reproduction rate with the national marking percentage remaining at approximately 80% until 2007 (Barnett 2007). More recently, improvements have been made with the national flock marking percentage still estimated at 80% for Merinos but at 88% for Merino-cross lambs and 98% for other breeds (Curtis 2014). Since early settlement in Australia wool has been a significant export industry (Bardsley 1994). Wool used to be the main source of income in sheep enterprises (Rowe 2010), and wool prices were stabilised by the Wool Reserve Price Scheme (Bardsley 1994), so there was little incentive to improve reproduction rate on farm. This is reflected in historical Merino breeding objectives where reproduction rate is given little emphasis and greater value placed on wool traits. The collapse of the Wool Reserve Price Scheme and the emergence of the lamb industry has seen a shift in the structure of the sheep industry. A higher proportion of Merino ewes are mated to non-Merino breeds and there are a growing number of non-Merino ewes in the national flock shifting the national focus more towards meat production and thus a higher reproduction rate.

Australia's national reproduction rate is lower than that of other major sheep producing countries. In New Zealand the lambing percentage for the last financial year was 118% (Beef + Lamb NZ 2015). Whilst the level of cross-breeding and composite ewe types is much higher in New Zealand, considerable improvements in New Zealand's lambing percentage have also been seen over the last 20 years (Corner-Thomas *et al.* 2013). Higher weaning percentages are also seen in the United Kingdom, with the English national average ranging from 132 to 142% across production systems (EBLEX 2014). Whilst the average weaning percentage in Scotland in marginal environments is 88%, in more productive systems it is as high as 161% (Quality Meat Scotland 2014). Australia's overall reproductive performance is lagging behind other major sheep-producing countries.

Reproductive performance of ewes at first mating is lower than at later parities whether the ewes are joined to lamb at 24 months of age (Turner and Dolling 1965) or 12 months (Dýrmundsson 1981). A ewe typically reaches her reproductive potential at her fourth parity (Hafez 1952). A large-scale study of maternal breeds found the average weaning percentage from yearling lambing to be only 54% (Bunter and Brown 2013). After receiving two mating opportunities prior to 1 year of age, Rosales Nieto *et al.* (2013) reported a conception rate of 36% in Merino ewes. Both these estimates are considerably lower than what is expected in mature ewes of that breed (Curtis 2014). In New Zealand, pregnancy rates from yearling lambing, termed hogget mating, also tend to be lower than their national average pregnancy rate across ages. Pregnancy rate in Romney ewes joined at 8 to 9 months of age ranged from 41% to 48% in the study of Kenyon *et al.* (2008a) whilst Corner *et al.* (2013) reported pregnancy rates of 40% and 97% across two studies of Romney ewes mated at 8 months of age. Reproduction outcomes from yearling ewes also tend to be more variable. Fogarty *et al.* (2007) reported differences in weaning percentage from cross-bred ewes mated at 7 months. Weaning percentage from ewes at Hamilton, Victoria varied from 30% to 41% over 2 years and at Cowra, NSW, weaning percentages varied from 54% to 64% over 3 years. A larger difference was observed by Robertson (2011); over a three-year period pregnancy scanning results in ewes mated prior to 1 year of age ranged from 8% to 58%. Based on the range of yearling reproductive outcomes previously achieved, it is clear there is potential to lift the reproduction rate of ewes at yearling age.

2.3 The importance of ewe reproduction in production systems

The main economic driver of breeding programs is the rate of genetic gain over time (Dekkers 2012). Genetic gain for an individual trait can be predicted using the breeder's equation (Falconer 1989):

$$R = i h^2 \sigma_p$$

Where:

R = response to selection per generation

i = selection intensity

h^2 = heritability

σ_p = phenotypic standard deviation.

Replacing i with the equation below, which partitions out selection intensity for males (i_m) and females (i_f) and accounts for male (L_m) and female (L_f) generation interval, permits response per year to be calculated.

$$i_y = \frac{i_m + i_f}{L_m + L_f}$$

Factors which influence i , L , h^2 , or σ_p also affect the rate of genetic progress that is attainable for breeding objective traits. Age at first mating and flock reproductive rate are two such factors and are both important considerations in breeding program design. Age at first mating directly impacts on generation interval influencing selection response, whilst flock reproductive rate affects the number of selection candidates, which in turn affects selection intensity (Falconer 1989). The age at which replacements are chosen also influences the accuracy of selection and variability in response.

2.3.1 *Impact of age at first mating on breeding programs*

The age at first mating is an important consideration in sheep breeding programs influencing generation interval and selection accuracy. Early selection of flock replacements decreases both generation interval and selection accuracy, although the decrease in generation interval may compensate for the loss of accuracy that is a consequence of early selection. Animals with Best Linear Unbiased Prediction (BLUP) of breeding values have an increased accuracy as they get older (Banks *et al.* 1998) because they accumulate more measurement records and therefore information over time. Hopkins and James (1977) demonstrated that selection across age classes resulted in higher levels of expected genetic gain when compared with a “progeny selection” strategy of culling based on age and selecting replacements from the lamb drop only. This is supported by James (1987) who demonstrated an optimal selection strategy to maximise genetic gain was truncation selection across age classes based on BLUP breeding values, which permits animals of differing ages to have differing levels of information and therefore different accuracies.

A possible downside to selection on BLUP breeding values across ages is that selection is only optimised with respect to genetic gain not overall accuracy. Whilst breeding from younger animals lowers generation interval, as selection accuracy is also lower, variability in outcomes can increase representing increased risk to the breeder. In their simulation of the optimal proportion of young and old rams to use in sheep breeding programs, Banks *et al.* (1998) analysed two age groups: young sires (<18 months old) with own and half-sib records as well as historical relative records, and old sires (>18 months old) with the same records as young sires plus progeny records. They found that, 75% or more of selected sires should be young rams, despite their lower accuracy breeding values. They concluded that it was optimal to use high proportions of young sires whenever selection candidates have their own record, half-sib records and historical family information. Selecting a high proportion of young animals may not be optimal when animals do not have their own phenotypic records prior to selection or for ewes as they have a lower contribution to overall gain compared to rams.

2.3.2 *Impact of ewe fertility rate on flock genetic progress*

Average flock reproductive rate influences the number of selection candidates each year and thus selection intensity, which is an even more complex issue as the reproductive performance of ewes varies with age (Turner and Dolling 1965). Hopkins and James (1977) showed that increasing whole flock fertility level increases flock genetic progress; however, they suggested that a 20% increase in progeny numbers from first parity (2-year-old) ewes would not have a great effect on the estimated rate of genetic progress as these females would represent only a proportion of breeding females. When young ewe fertility is very low, selection intensity is reduced due to fewer selection candidates, which in turn may reduce the rate of genetic progress made for fertility and other traits. Thus the potential advantage offered by early selection and breeding of ewes may not be realised if fertility is low. Ewes joined in the first year have both lower and more variable fertility than older ewes (Fogarty *et al.* 2007), both across flocks and within a flock. Therefore, it is feasible that fertility could be more than 20% lower than in mature ewes and also vary by more than 20% from year to year. In addition to the inability to account for increased variability in response from young selection candidates, BLUP selection over age classes does not consider the lower chance of reproductive success in young ewes.

2.3.3 *Value of genomic information in breeding programs*

The incorporation of genomic information into the estimation of breeding values can increase selection accuracy enabling more accurate selection decisions to be made and the rate of genetic gain to be increased (Meuwissen *et al.* 2013), especially for young candidates. In a study of seven industry Merino flocks, Dominik (2012) found that on average the addition of genomic information would enable breeders to select a ram at 8 months of age with the same level of accuracy as an 18-month-old ram without genomic information. The rate of genetic progress would be expected to increase as the breeding program benefits from a reduction in generation interval without an accompanying loss of accuracy. This is in agreement with Pickering *et al.* (2013) who reported that the combination of genomic information and reducing the generation interval by one year could increase genetic gain by 84% in New Zealand Romney animals.

The benefits of genomic selection are greatest for traits that are not recorded on selection candidates at time of selection (Meuwissen *et al.* 2013) such as sex-limited traits, traits measured later in life, or hard-to-measure traits (van der Werf 2009; Pickering *et al.* 2013). This is particularly relevant for reproduction traits which are both sex-limited and measured late in life. The study by Daetwyler *et al.* (2013) was one of the first genomic prediction studies for reproduction traits in sheep. A cross-validation approach was used to compare genomic BLUP (GBLUP) to BLUP for number of lambs weaned (NLW) in Merino and Border Leicester sheep. Reproduction records of genotyped ewes and daughters of genotyped rams were utilised in the estimation, with ewe and ram records weighted to account for differences in phenotype accuracy. Regardless of which cross-validation method was used, GBLUP accuracies were 14 to 100% higher than conventional BLUP accuracies. For example, the accuracy of BLUP was 0.15 whilst GBLUP accuracy was 0.22 in Border Leicester sheep using a random cross-validation approach. These results generally agreed with the study of Daetwyler *et al.* (2014), in Merino and Border Leicesters, which expanded the previous work to include number of lambs born per ewe mated (NLB) and litter size of ewes lambing (LSIZE). Litter size in Border Leicester sheep did not show an increase in accuracy with the addition of genomic information.

Whilst the addition of genomic information using different analytical approaches mostly increased selection accuracy compared to BLUP, these gains were small (0.01 – 0.03) in this later study (Daetwyler *et al.* 2014). The accuracies obtained are currently not high enough to use to generate GBLUP breeding values for reproduction traits. The accuracy of GEBVs will increase with the continued expansion of the sheep reference population and better estimates across the diverse Australian sheep breeds will be achieved. Whilst genomic selection may offer the opportunity to increase accuracy of early selection, the merit in testing ewes is less than that of rams (van der Werf *et al.* 2014) and the cost of genotyping cannot be justified unless genomic selection is combined with advanced reproductive technologies such as multiple ovulation and embryo transfer or juvenile in vitro fertilisation and embryo transfer programs (Granleese *et al.* 2014).

2.3.4 *Assessing the risk of breeding programs*

It is important to assess the likely benefits and possible negative consequences of a decision before implementing a change on farm. In livestock breeding, risk is best thought of as uncertainty surrounding the consequences of an action (Anderson 1988). A good measure of risk will consider not only average performance but also capture information on uncertainty or variability as well as expected outcomes (Anderson 1974). A key aspect to the risk inherent with the adoption of a particular breeding program strategy is the balance of mean genetic gain and likely variation in response. Other management and cost risk factors contribute to the decision-making process in considering changes to an existing breeding program, but they are not addressed here.

Assessments of risk in livestock breeding have previously been conducted in several ways. Recent literature discussing breeding program design and the use of genomic information does not discuss risk explicitly, though selection accuracy is usually an important consideration (Dekkers 2012; Johnston *et al.* 2012; Daetwyler *et al.* 2014). Selection accuracy is defined as the correlation between estimated and true breeding value (Dekkers 2012), where the true breeding value is approximated from a highly accurate progeny test as an animal's true breeding value cannot be observed. An individual with a low accuracy breeding value has a higher chance that its breeding value will change over time than an individual that has a breeding value with a high accuracy (Falconer 1989); thus, selecting an animal with a low accuracy

breeding value represents a more risky option. Earlier studies have considered more explicit definitions of risk. Schneeberger and Freeman (1980) defined risk as the variation in expected return, using four risk utility functions to evaluate and rank European dual-purpose and beef-cattle breeds based on farmer attitude to the risk of losing money due to difficult calving. Risk was defined as variation in net merit in a utility function to rank dairy sires (Rogers 1990). Rogers (1990) found that the ranking of dairy sires only changed when the weighting given to risk aversion was very high. Similarly, Klieve *et al.* (1993) found that significant animal re-ranking only occurred when a high weighting was placed on risk in a selection index incorporating a weighted value for breeding value accuracy alongside the animal's estimated breeding value to account for risk.

2.4 Puberty and the reproductive cycle in sheep

The ewe is a seasonally polyoestrus animal (Gordon 1997; Goodman and Inskeep 2006) exhibiting two distinct cycles, the oestrus cycle and the annual cycle of ovarian activity. The oestrus cycle is 16 – 17 days long and describes the repetitive sequence of physiological events leading up to ovulation. Anoestrus usually occurs over spring and summer is the period of the year where no ovulation occurs. Considerable breed differences in the duration of the breeding season and anoestrus period have been documented across a number of studies (Hafez 1952; Goodman and Inskeep 2006; Yeates 1949; Rawlings and Bartlewski 2007). It is widely accepted that breeds of European origin, such as the Border Leicester tend to have a more restricted breeding season and longer anoestrus (Hafez 1952; Yeates 1949). In contrast the Australian Merino has a longer breeding season (Goodman and Inskeep 2006).

2.4.1 *Neuroendocrine control of the oestrus cycle*

The oestrus cycle is under complex neuroendocrine control. The cycle can be divided into two phases, the follicular and luteal phases (Clarke 1984). During the follicular phase which lasts for 2 – 3 days, oestradiol levels rise which increases the ovarian signal for gonadotropin-releasing hormone (GnRH). GnRH acts on the pituitary triggering a surge in luteinising hormone (LH). LH surges to 50 to 100 times its basal concentration (Clarke 1984; Gordon 1997; Goodman and Inskeep 2006; De Graaf 2010) triggering ovulation and, if the ram is present, the onset of estrus behaviour. Fertilisation is then possible

over the 24 to 36 hour period following ovulation (Jainudeen *et al.* 2000; Goodman and Inskeep 2006; De Graaf 2010).

Ovulation is seen as the transition into the luteal phase of the cycle and is usually considered as day 0 of a cycle. After ovulation, the collapsed follicle becomes a corpus hemorrhagicum, before becoming a corpus luteum (CL). The CL secretes progesterone so a sharp increase in progesterone concentration is seen from around day 3 (Rawlings and Bartlewski 2007). Through negative feedback, progesterone inhibits GnRH and thus LH and follicle-stimulating hormone secretion. Progesterone levels remain high throughout the luteal phase until luteolysis (De Graaf 2010). During luteolysis the CL regresses, losing the ability to secrete progesterone. Progesterone concentration falls and the ewe enters the follicular phase again. If an egg was fertilised, the CL remains and progesterone plays an important role in maintaining pregnancy (Goodman and Inskeep 2006).

2.4.2 *Neuroendocrine control of the onset of puberty*

The onset of puberty in the ewe is influenced by internal and external factors (Foster and Jackson 2006), and a ewe will only commence cycling under the right photoperiod signals. Before a ewe reaches puberty GnRH secretion is very sensitive to negative feedback from estradiol. As a ewe enters puberty a reduction in GnRH sensitivity to estradiol inhibition occurs. This enables the first high frequency rhythm of GnRH secretion to occur, which is characteristic of the commencement of the follicular phase. Subsequently, the first LH surge occurs (Foster and Olster 1985; Foster *et al.* 1986; Foster and Jackson 2006). As the ewe begins normal oestrus cycles, progesterone produced by the CL acts as a negative feedback agent regulating GnRH secretion during the luteal phase (Foster and Jackson 2006).

The endocrine system of the ewe is well-developed from a young age (Quirke 1981); however, pre-pubertal ewes do not spontaneously have surges of LH (Foster and Jackson 2006). It has been shown, however, that they are capable of doing so from 10 to 16 weeks of age (Foster *et al.* 1975; Foster and Jackson 2006). Similarly, the endocrine system of the ewe is capable of producing the high frequency GnRH required for ovulation from a young age (Quirke 1981; Foster and Jackson 2006). Foster (1984) showed that the pre-pubertal ewe's GnRH/LH surge system responded in the same manner as an adult

ewe's to estradiol. Therefore, the current hypothesis is that the GnRH/LH surge system does not occur before puberty as there is no large sustained estradiol rise (Foster and Jackson 2006).

2.5 Defining puberty in sheep

In this study, we define puberty as the stage of an individual's development whereby they are capable of producing functional gametes (Adams and Steiner 1988). In ewes, this can be interpreted in several ways and puberty has been defined as both detection of "first oestrus" and "first ovulation", which are two separate events (Foster and Jackson 2006). First oestrus is considered to be the first instance in which a ewe exhibits estrus behaviour which is detected by a ram. First ovulation is the first time a CL is detected in the sheep and/or hormonal blood assays indicate the oestrus cycle has commenced. The age at which puberty occurs in ewe lambs is known to be influenced by several internal and external occurrences. Given this, it is not surprising that large variation in the age of onset of puberty in sheep is reported in the literature (Dýrmundsson 1973). There is no universally accepted method for measuring puberty in sheep and various studies have employed different methods to determine the timing of puberty in ewe lambs.

2.6 Methods of measuring puberty in sheep

Methods that have been employed to measure puberty and/or the onset of oestrus include detection using males, hormone profiles, and novel techniques such as laparoscopy. In choosing an appropriate measurement technology, measurement cost, ease of measurement and reliability must be considered.

2.6.1 *The use of males to identify onset of oestrus*

The use of males wearing harnesses with crayons has historically been a relatively cheap way of identifying the onset of oestrus in a large number of ewes. Studies have used entire rams (Mukasa-Mugerwa *et al.* 1991), vasectomised rams (Dickerson and Laster 1975; Foster 1981; Kor *et al.* 2012) or hormone-treated wethers (Fogarty *et al.* 2007; Bird-Gardiner *et al.* 2012), all wearing harnesses with crayons, in order to record when a ewe is first served by the ram. There are several challenges associated with this method. Firstly, the ability of the male to detect the ewe's first cycle which is often shorter and less strong than that of mature ewes (Hafez 1952) might not be reliable and the fact that the introduction

of a ram can advance puberty in pre-pubertal ewes (Al-Mauly *et al.* 1991; Rosa and Bryant 2002). There is also evidence that in the event of a long exposure period to males, as may be the case when ewes are exposed to teasers for several months, the ewe may become adapted to a male presence and take longer to mate than ewes kept isolated from males (Notter 1989). In addition, Oldham and Cognie (1980) demonstrated that it is possible for ewes that have been teased to fall back into anoestrous.

2.6.2 *Measurement of hormones to determine puberty onset*

Of the hormones used in monitoring the onset of ewe oestrus cycles, progesterone concentration appears to have been the most commonly used, though measurement of LH concentration changes have also been used (Ebling and Foster 1988). Progesterone is only produced in significant quantities after a ewe has commenced oestrus cycles making it a useful indicator of whether oestrus cycles are occurring (Goodman and Inskip 2006). Puberty was defined by Bartlewski *et al.* (2006) as an elevation in serum progesterone concentrations of 0.1 ng/ml or greater for at least 7 days in a row. However, Lahlou-Kassi *et al.* (1989) defined ovulation as having occurred in two native Moroccan sheep breeds, the D'Man and Sardi, when progesterone levels first exceeded 1 ng/ml, as did Foster and Olster (1985) in Suffolk lambs. Alcaraz Romero *et al.* (2012) also used the 1 ng/ml threshold. Pittroff *et al.* (2003) trialled thresholds of both 0.5 ng/ml and 1 ng/ml of progesterone as indicators of the commencement of cycling in Targhee ewes but did not discuss the usefulness of either threshold.

2.6.3 *Use of transrectal ultrasonography to determine onset of puberty*

Recent studies have considered transrectal laparoscopic examination of the ewe's ovaries as a method of detecting the commencement of oestrus cycles. This method was first validated in sheep by Schrick *et al.* (1993). After recording images of uterine horns during ultrasonography, ewes were ovariectomised and the same measurements of follicular size and CL were taken. Results from both techniques closely aligned with 15 of 16 CL and 55 of 59 follicles correctly identified. This method offers a clear advantage over the use of rams, namely that it is a direct measure and is very accurate. However; it requires the use of trained operators, usually the same operator for all measurements (Schrick *et al.* 1993; Bartlewski *et al.* 2006), carries additional costs through labour and equipment requirements, and the technique is also somewhat invasive to the ewe. However, Bartlewski *et al.* (2002) found that this technique could be used on the ewe

from as early as 4 weeks of age. Of the studies conducted so far, several possible traits have been identified, such as counting the number of follicles greater than 2 mm in size (Schrick *et al.* 1993; Alcaraz Romero *et al.* 2012), 3 mm in size (Robertson 2011), luteinised follicles (Robertson 2011), and corpus lutea (Schrick *et al.* 1993; Robertson 2011).

The variability in techniques employed and methods used highlights the lack of a clear measurement of puberty in sheep. If we are aiming to make genetic improvement for age at puberty or the attainment of sexual maturity in ewes, a definitive measure that is capable of being conducted on many animals in a short space of time, that has minimal animal handling requirements, and that is not cost prohibitive or invasive to the animal is required.

2.7 Factors influencing puberty and reproductive performance

2.7.1 *The influence of season and month of birth on puberty and reproductive performance*

Photoperiod is the main factor influencing seasonality of reproduction in sheep (Hafez 1952, Rosa and Bryant 2003) with ewe lambs usually only reaching puberty during the autumn and winter months (Hafez 1951, Dýrmundsson 1973) despite the melatonin response to photoperiod being functional by 3 weeks of age (Claypool *et al.* 1989). A detailed account of the proposed neuroendocrine pathways for control of seasonality in sheep can be found in Rosa and Bryant (2003). In summary, the pineal gland converts information from retina photoreceptors into a circadian rhythm of melatonin secretion. As photoperiod changes, this rhythm alters. Melatonin then acts upon the LH-generating system to influence the reproductive cycle.

Photoperiod is more important for initiation of oestrus cycles during puberty than it is for recommencement of oestrus cycles in mature ewes. When housed and subjected to an artificial photoperiod of 16 hours of light, mature Suffolk cross ewes recommenced oestrus cycles and at the normal time in the season (Ebling and Foster 1988). In contrast, only two of six ewe lambs subjected to the same artificial photoperiod showed oestrus activity by 52 weeks of age, whereas their counterparts raised under natural lighting commenced oestrus activity by 28 ± 1 weeks of age. Young ewes also need a signal of increasing day length followed by decreasing day length before they commence cycling (Foster

1981; Foster *et al.* 1986). Spring-born lambs, raised under natural lighting, reached puberty at an average of 30 weeks of age; however, their autumn-born counterparts raised under natural light, failed to reach puberty at the same age. Raising autumn-born lambs under artificial photoperiod to mimic the lighting conditions experienced by spring born lambs resulted on average in puberty occurring at 30 weeks of age (Foster 1981). Another example of the influence of photoperiod on ewe oestrus cycle is the ability of ewes who are transported from the Northern to the Southern hemisphere to change the timing of their anoestrus period to match the opposite light conditions encountered in the Southern hemisphere (Yeates 1949)

Although sheep are all seasonal polyoestus there are considerable breed differences in the length of the anoestrus period in sheep, largely driven by the geographical origin of the breed (Hafez 1952, Yeates 1949). In breeds of tropical origin the influence of photoperiod on puberty attainment is less defined with Lahlou-Kassi *et al.* (1989) reporting D'Man ewes, a subtropical breed, commenced cycling during the summer period. Conversely, British breeds such as the Suffolk have distinct seasonal cycles (Hafez 1952) and only commence cycling in autumn and winter months (Hafez 1951). In their review of seasonal reproduction in sheep, Rosa and Bryant (2003) also concluded that the amount of seasonality exhibited by sheep varies with breed, with the Australian Merino being one of the less seasonal breeds.

2.7.2 *Breed and genotype differences for puberty and early reproductive performance*

Considerable variation in age at puberty has been observed between different breeds of sheep, as summarised by Dýrmundsson (1973). A tendency for more prolific sheep breeds to reach puberty at younger ages has been observed (Dickerson and Laster 1975; Lahlou-Kassi *et al.* 1989). Given the variation in age at puberty reported, and the variation in mature ewe reproductive potential across breeds (Walker *et al.* 2002; Curtis 2014), it stands to reason that breed differences are also observed in ewe reproductive performance at 1 year of age. Genetic parameter estimates for puberty and reproductive performance will be discussed in Section 2.8.

Sire breed was not found to have a significant effect on age of puberty but it was found to have a significant effect ($p < 0.01$) on maiden reproductive performance of cross-bred ewe lambs (Fogarty *et al.* 2007). Fertility ranged from 0.71 ± 0.06 for East Friesian-sired ewes to 0.24 ± 0.07 for Corriedale-sired

ewes. These findings contrast to earlier studies (Dýrmundsson 1973, 1981). Although 91 sires from 20 different breeds were used by Fogarty *et al.* (2007), 12 of the breeds were only represented by one or two sires, which could have prevented the detection of breed differences. Robertson (2011) reported poorest reproductive performance from Corriedale-cross ewe lambs with significantly fewer ewes, 31%, detected in oestrus by teaser wethers compared with cross-bred ewes sired by Border Leicester, Coopworth, Dohne, and South African Meat Merino (SAMM) rams. She also found that Corriedale-cross ewes had the lowest fertility rate, but due to low animal numbers ($n=74$), the majority of observed differences between breeds, although large, were not significant. A recent study by Alcaraz Romero *et al.* (2012) also reported differences in age at puberty in cross-bred lambs born from different sire breeds. First ovulation occurred later in Ill de France-cross ewes, 308.6 ± 11.9 days, whilst Black Face Dorper-cross ewes displayed first ovulation at the earliest age, 240.9 ± 13.0 days.

2.7.3 *The “ram effect” and its’ influence on puberty and early reproductive performance*

The “ram effect”, the ability of pheromones produced by the ram to alter ovarian activity in females, is the most widely used method of manipulating reproductive cycles in anoestrus ewes. There are two types of ram effect, the chronic ram effect and the acute ram effect, with the acute ram effect being the more commonly used. The chronic ram effect refers to changes in the ovarian activity of ewes due to a continuous male presence, while the acute ram effect refers to changes in the ovarian activity of ewes induced by the sudden introduction of rams to anoestrus ewes after a separation period (Rosa and Bryant 2002). The introduction of rams to ewes after a period of isolation induces an increase in luteinising hormone (LH) pulse frequency, which leads to ovulation and oestrus in ewes (Martin *et al.* 1986).

The acute ram effect can also be used to accelerate puberty in young sheep, though comparatively less information is available on this (Dýrmundsson 1981). Kassem *et al.* (1989) showed that exposing pre-pubertal Awassi ewes to rams can reduce both age at first oestrus and age at first conception, by 16 and 19 days, respectively. This is supported by Al-Maully *et al.* (1991), who reported a similar reduction in mean age at first oestrus in Suffolk x Mule lambs after exposure to males. Increases in Suffolk x Western White Face ewe lamb ovarian activity after exposure to rams were reported by Bartlewski *et al.* (2002) with 4 of

14 ewes showing their first luteal structure following first male exposure at 25 to 26 weeks of age with a significant ($p < 0.05$) increase in luteal structure again observed at second male exposure 4 weeks later.

The effect of teasers increasing the proportion of ewe lambs that mate in the first 17 days of joining is well documented in New Zealand flocks (Kenyon *et al.* 2004b; Kenyon *et al.* 2005; Kenyon *et al.* 2006, 2007), though there is some disagreement as to how the use of teasers prior to joining lifts flock reproductive performance. Previous studies have found lambs exposed to teasers on commercial properties had a 4.3% higher lambing percentage (Kenyon *et al.* 2004d) and that significantly more ewes exposed to teasers fell pregnant compared to non-teased ewes when a teasing ratio of 1:32 was used (Kenyon *et al.* 2007). Of the hoggets that were known to be serviced by a ram during the joining period, Kenyon *et al.* (2005) reported that a greater proportion of teased hoggets were pregnant at scanning compared to un-teased animals. This analysis omitted ewes from the same contemporary groups that were not serviced by the ram during joining. When the results from these un-joined ewes were also included no difference in pregnancy rate was detected. Pregnancy rate was not found to differ between ewes that were teased, for either 8 or 17 days, and un-teased ewes by Kenyon *et al.* (2006), though scanning percentage and twinning rate were higher in ewes teased for 17 days.

2.7.4 *Impact of age, liveweight and nutrition on puberty and reproduction.*

Nutrition and body weight influence many aspects of reproductive performance in sheep including age at puberty, oocyte and CL development, ovulation, fertilisation rate, and embryo and lamb survival (Dýrmundsson 1981, 1987; Robinson 1996; Gordon 1997; Zieba *et al.* 2005; Blanc *et al.* 2007; De Graaf 2010). One of the challenges of quantifying the effects of factors which influence reproduction is that they are often confounded. This was demonstrated by Dýrmundsson and Lees (1972) who reported that, ewes born earlier in the lambing period tended to experience their first oestrus earlier in the subsequent breeding season than lambs born towards the end of the lambing period. These ewes were older than their contemporaries but also tended to be heavier. Conversely, ewes that did not commence oestrus activity in the first breeding season tended to have low growth rates and were younger as they were born towards the end of the previous lambing season.

Strong links between high weaning weights and growth rates and earlier onset of puberty have been reported in several studies. A significant relationship between increasing numbers of ewes reaching puberty and increasing weaning weights ($p < 0.01$) was reported by Dickerson and Laster (1975) in spring-born ewe lambs of British and American breed origin. This link between higher liveweights and puberty is supported by the findings of Mukasa-Mugerwa *et al.* (1991) in Menz sheep and Haley *et al.* (1989) in Finn x Dorset ewe lambs. Restriction of nutrition has been shown to reduce the proportion of ewe lambs reaching puberty by 28 weeks of age (Fitzgerald *et al.* 1982) and delay ovulation (Foster and Olster 1985).

Similarly, a positive association has been shown between liveweight and reproductive performance at 12 months of age. Romney ewes that were heavier at joining than their contemporaries were significantly more likely to conceive (Kenyon *et al.* 2005; Cave *et al.* 2012), whilst Kenyon *et al.* (2010) reported heavier ewe lambs were more likely to conceive in the first 17 days of the joining period. Liveweight had a positive impact on the reproductive performance of the Maternal Central Progeny Test ewes that were first mated at 7, 14 or 17 months of age (Afolayan *et al.* 2008). This is further supported in Merino ewes where ewe lambs with high breeding values for post-weaning weight were significantly ($p < 0.001$) more likely to reach puberty by 251 days of age and give birth to a lamb (Rosales Nieto *et al.* 2013).

Ewes reach puberty over a wide range of liveweights and proportions of mature size and there does not appear to be a consistent weight threshold (Dýrmundsson 1973). As discussed by Pittroff *et al.* (2008) it also appears unlikely that Brody's law which states that the inflection point of the growth curve coincides with puberty onset in domestic animals is true for sheep. A study in Targhee ewe lambs by Pittroff *et al.* (2003) found that the experimental group that had the highest initial yearling reproductive performance actually had the lowest average weight. It should be noted that the 107 ewe lambs were drawn from two selection lines, one that had been selected for high growth rates and increased weight of lamb weaned and the other was a random mating control line. The ewes were assigned to one of three different diets, a high protein diet to maximise growth, a low-protein-high-fat diet and a control diet typical of a post-weaning diet in the region. The lambs with lowest body weight and highest pregnancy scanning percentage, 83.3%, came from the random mating line, which were fed the low-protein-high-fat diet. Higher liveweights at

joining did not correspond to increased pregnancy scanning results in Robertson (2011)'s study of cross-bred ewe lambs. When ewes were on average 6 kg heavier than the previous year, only 8% of experimental animals scanned in lamb, compared with 41% the previous year. These two studies highlight the complexity of the relationship between nutrition and body weight, and puberty and reproduction, demonstrating how difficult it is to consider each of these factors in isolation.

2.7.5 *Impact of body condition on reproduction*

Condition score has been shown to be an important tool in managing mature ewes (Graham and Hatcher 2006; van Burgel *et al.* 2011) with higher condition scores associated with fewer dry ewes (Kenyon *et al.* 2004a) and higher litter size (Kenyon *et al.* 2004a; Hatcher *et al.* 2007a). In young ewes higher condition scores have also been shown to increase the likelihood of being mated (Kenyon *et al.* 2009) and increase pregnancy scanning rate (Kenyon *et al.* 2010; Cave *et al.* 2012). However, after adjusting for liveweight the influence of condition score on reproduction was no longer significant in mature ewes (Kenyon *et al.* 2004a) or young ewes (Kenyon *et al.* 2009) of maternal breeds. Condition score was still found to influence reproductive performance in mature Merino ewes, after accounting for liveweight. At a given liveweight, increasing fat score by 1 was associated with an additional 5 foetuses scanned per 100 ewes (Hatcher *et al.* 2007a) with a similar trend seen in maiden Merino ewes first mated at 1.5 years (Hatcher *et al.* 2007b).

The above studies demonstrate that ewes of higher liveweight and condition score are more likely to reach puberty earlier and fall pregnant. It is not clear whether an interaction exists between condition score and liveweight and whether these relationships are present in other major Australian sheep breeds.

2.8 Genetic parameter estimates for reproduction

Whilst ewe management plays an important role in ewe reproductive performance, reproduction is also under genetic influence. Ewe reproduction traits are widely accepted to have a low heritability. A comprehensive range of genetic parameter estimates for sheep production traits, including reproduction, from 165 studies was compiled by Safari and Fogarty (2003). Their report covered genetic analyses from

1992 to 2003 for a wide range of sheep breeds. This literature review will focus on recent studies and studies involving breed types common to Australia.

2.8.1 *Heritability of reproduction.*

2.8.1.1 Reproduction traits as repeated record traits.

Heritability of reproduction traits varies between studies, depending on trait definition, breed, animal numbers and flock phenotypic performance. Low heritabilities for reproduction traits of the ewe were reported by Safari and Fogarty (2003). A subsequent review of the same data (Safari *et al.* 2005) calculated weighted means for genetic parameter estimates using the studies from their earlier paper (Safari and Fogarty 2003). As anticipated these estimates are generally low, ranging from 0.03 ± 0.01 for the ratio of lambs weaned to lambs born (PLSURV) to 0.13 ± 0.01 and 0.13 ± 0.03 for litter size (LSIZE) and weight of lamb weaned per ewe joined (WTWEAN) (Table 2.1) respectively.

Similar estimates have been obtained from more recent studies (Table 2.1), though there are a few interesting observations to note. Two common definitions of lamb survival are seen in literature; the ratio of lambs weaned to lambs born (PLSURV) and the number of lambs weaned per ewe lambing (LSURV). Although the first is represented by a proportion and the second by an actual number, heritability estimates are similar. A large scale analysis of Merino ewes from seven resource flocks (Safari *et al.* 2007a) with an average of 2.76 reproduction records per ewe reported lower heritabilities than those obtained by Safari *et al.* 2005 ranging from 0.05 to 0.07. The maximum heritability estimate was 0.074 ± 0.005 for LSIZE. A study by Herbart *et al.* (2010) of only 8,172 ewes with an average of 2.55 reproduction records per ewe reported heritability estimates of a similar magnitude to Safari *et al.* (2005). The analysis of the Maternal Central Progeny Test Data (Afolayan *et al.* 2008, 2009), which featured predominately cross-bred animals from a number of breeds, had slightly higher heritability estimates than the weighted averages reported by Safari *et al.* (2005), ranging up to 0.19 for LSIZE. As all ewes were cross-bred, hybrid vigour perhaps contributed to these increased estimates (Fogarty 1984). The multi-breed nature of the dataset has also likely increased genetic variance. A recent paper by Bunter *et al.* (2014) showed that heritability estimates, as well as other parameter estimates for reproduction differed between Merino strains.

Table 2.1 Overview of recent studies estimating the heritability of reproductive traits of the ewe as a repeated records trait

Overview includes number of ewes with record (N), number of reproduction records (N_r), average number of lambs born per ewe joined (X_{NLB})

Paper	Breed	N (N _r)	Age (yrs)	X _{NLB} (s.d.)	SFERT	SNLB	FERT	LSIZE	LSURV	Heritability ^A			
										PLSURV	NLB	NLW	WTWEAN
Safari <i>et al.</i> (2005)	Mixed	7 – 49 studies					0.08 ± 0.01 (18) ^B	0.13 ± 0.01 (49)	0.05 ± 0.01 (8)	0.03 ± 0.01 (16)	0.07 ± 0.01 (11)	0.10 ± 0.01 (19)	0.13 ± 0.03 (7)
Hanford <i>et al.</i> (2006)	Polypay	3487 (9081)	1 2 3 4-6 7	1.23 1.81 2.05 2.15 2.08							0.11 ± 0.02	0.02 ± 0.01	
Safari <i>et al.</i> (2007a)	Merino	25 000 (69 000)	Mixed	0.80 (0.40)			0.05 ± 0.01	0.07 ± 0.01			0.05 ± 0.01	0.05 ± 0.01	
Afolayan <i>et al.</i> (2008)	Maternal x Merino	2846 (6824)			0.13 ± 0.04	0.18 ± 0.04	0.11 ± 0.04	0.19 ± 0.05		0.03 ± 0.02	0.17 ± 0.04	0.13 ± 0.04	0.17 ± 0.04
Afolayan <i>et al.</i> (2009)	Maternal x merino	2460 (6824)	Mixed (includes 1 yr olds)	1.34 (0.83)			0.11 ± 0.04	0.18 ± 0.05		0.03 ± 0.02	0.17 ± 0.05	0.14 ± 0.04	0.16 ± 0.05
Hebart <i>et al.</i> (2010)	Merino	8172 (20 816)			0.08 ± 0.01	0.10 ± 0.01	0.08 ± 0.01	0.11 ± 0.01		0.03 ± 0.02	0.10 ± 0.01	0.07 ± 0.01	
Bunter <i>et al.</i> (2014)	Medium wool Merino (FecB gene)	7983	Mixed (includes 1 yr olds)	1.57 (0.69)	0.05 ± 0.02	0.10 ± 0.02	0.03 ± 0.01	0.10 ± 0.02	0.07 ± 0.01		0.07 ± 0.01	0.03 ± 0.01	
	Medium – Strong wool Merino	4287	Mixed	1.11 (0.68)	0.18 ± 0.01	0.16 ± 0.01	0.22 ± 0.01	0.10 ± 0.02	0.04 ± 0.02		0.19 ± 0.01	0.10 ± 0.03	
	Fine wool Merino	6392	Mixed	0.92 (0.54)	0.05 ± 0.01	0.07 ± 0.01	0.07 ± 0.01	0.06 ± 0.01	0.04 ± 0.01			0.09 ± 0.01	0.05 ± 0.01
	Maternal composite	12 749	Mixed (includes 1 yr olds)	1.25 (0.88)	0.05 ± 0.01	0.05 ± 0.01	0.14 ± 0.01	0.08 ± 0.01	0.04 ± 0.01			0.09 ± 0.01	0.06 ± 0.01

^A Pregnancy scanning fertility (SFERT), Pregnancy scanning litter size (SNLB), fertility (FERT), no. lambs born per ewe lambing (LSIZE), no. lambs weaned per ewe lambing (LSURV), ratio of lambs weaned to lambs born (PLSURV), no. lambs born per ewe joined (NLB), no. lambs weaned per ewe joined (NLW), no. lambs weaned per ewe lambing (WTWEAN). ^B No. of studies weighted estimate is derived from.

2.8.1.2 Parity effect on reproduction trait heritability estimates

Over her lifetime, a ewe retained in a pedigree-recorded flock will receive multiple reproduction records. The most common method of analysis is to treat reproduction records from different parities as repeated records (Safari and Fogarty 2003). A limited number of studies have also considered the trait of “average lifetime performance” (Brash *et al.* 1994a) or treated each parity as a separate trait (Bunter and Brown 2013).

The heritability of FERT, NLB, NLW and WTWEAN was found to be higher at first parity than from a combined analysis of three parities in Hyfer Sheep (Fogarty *et al.* 1994), a stabilised composite breed comprised of 50% Dorset, 25% Booroola and 25% Merino. The heritability of FERT, NLB and NLW were all higher at first parity compared to second parity in a dataset featuring a large number of yearling reproductive records (n=12,153) (Bunter and Brown 2013) (Table 2.2). Dominik and Swan (2006) also reported differences in the heritability of pregnancy scanning records across four parities, though they did not find a consistent trend across ages. However, their method of deriving heritability estimates of reproductive performance at earlier and later ages was to fit bivariate mixed animal models in ASReml, which differs from the other two studies where estimates were derived from univariate analysis.

Whilst low trait heritability can limit the amount of genetic gain, reproduction traits have a large phenotypic variance (Safari *et al.* 2007a), which means increased selection differentials can be applied and it should still be possible to achieve good rates of genetic improvement. Reproductive performance at 1 year of age is variable; this is reflected in a much higher phenotypic variance for fertility at 1 year of age, 0.15 compared to 0.07 in 2-year-old ewes (Bunter and Brown 2013). This may mean that the selection differential can be higher and there is potential to increase genetic gain for yearling fertility more rapidly than for adult fertility. Conversely, phenotypic variance of LSIZE tends to be greater for older ewes (Bunter and Brown 2013) as older ewes have more multiple births, so it is likely there is more scope to make genetic improvement for LSIZE in adult ewes.

Table 2.2 Overview of recent studies estimating the heritability of reproductive traits of the ewe treating ewe parity as separate traitsOverview includes number of ewes with record (N), number of reproduction records (N_r), average number of lambs born per ewe joined (X_{NLB})

Paper	Breed	N (N _r)	Age (yrs)	X _{NLB}	SNLB	FERT	LSIZE	LSURV	Heritability ^A			
									PLSURV	NLB	NLW	WTWEAN
Bunter and Brown (2013)	Border	12 153	1	0.75 (0.79)		0.16 ± 0.02	0.05 ± 0.02	0.07 ± 0.02		0.13 ± 0.02	0.08 ± 0.01	
	Leicester,	9315	2	1.47 (0.72)		0.07 ± 0.02	0.10 ± 0.02	0.07 ± 0.02		0.10 ± 0.02	0.08 ± 0.02	
	Coopworth, White Suffolk, Maternal	6657	2+	1.65 (0.73)		0.07 ± 0.02	0.11 ± 0.02	0.06 ± 0.02		0.09 ± 0.02	0.06 ± 0.02	
Fogarty <i>et</i> <i>al.</i> (1994)	Hyfer sheep (½ Dorset, ¼ Booroola, ¼ Merino)	1619 ^B	2	0.793		0.10 ± 0.06	0.20 ± 0.08		0.10 ± 0.06	0.17 ± 0.06	0.08 ± 0.05	0.12 ± 0.06
			2,3 & 4	1.15		0.03 ± 0.02	0.19 ± 0.02		0.07 ± 0.03	0.09 ± 0.03	0.04 ± 0.02	0.06 ± 0.02
Dominik and Swan (2006)	Merino	5851 (17 324)	2	0.78 (0.44)	0.09 ± 0.02			0.01 ± 0.00				
			3	0.89 (0.43)	0.03 ± 0.02			0.11 ± 0.04				
			4	0.98 (0.46)	0.14 ± 0.01			0.09 ± 0.01				
			5	1.03 (0.56)								
			All			0.07 ± 0.02			0.12 ± 0.13		0.03 ± 0.01	

^A Pregnancy scanning litter size (SNLB), fertility (FERT), no. lambs born per ewe lambing (LSIZE), no. lambs weaned per ewe lambing (LSURV), ratio of lambs weaned to lambs born (PLSURV), no. lambs born per ewe joined (NLB), no. lambs weaned per ewe joined (NLW), no. lambs weaned per ewe lambing (WTWEAN). ^B Ewes were in an accelerated joining system.

2.8.1.3 Pubertal traits of the ewe

Few studies have reported heritability estimates for pubertal traits in sheep or other livestock species. Due to the cost and difficulty of obtaining accurate assessments of puberty or the attainment of sexual maturity most published studies on pubertal traits in ewes have a low to moderate number of records. An exception to this is the New Zealand Central Progeny Test Flock (Anonymous 2011) where 7 years of records were collected on date of first oestrus on progeny of dual-purpose rams. In this New Zealand study, heritability estimates were low and liveweight had little influence on the estimates. The heritability of age of first oestrus as detected by teasers was 0.090 ± 0.039 with weight and 0.098 ± 0.039 without weight in the model (Table 2.3). Although higher heritability estimates of 0.16 ± 0.21 and 0.35 ± 0.60 for age at first oestrus were obtained in the Ethiopian bred ewes, Horro and Menz, (Toe *et al.* 2000) and Awassi ewes (Alkass *et al.* 1994), respectively, both these studies had low numbers ($n=450$ and $n=113$, respectively). The number of hogget oestrus cycles was also moderately heritable, 0.31 ± 0.08 , in Romney ewes (Baker *et al.* 1979) and, 0.34 ± 0.08 , in Romney, Perendale and Booroola cross ewes (Meyer *et al.* 1994) (Table 2.3).

Table 2.3 Overview of studies with heritability estimates for pubertal traits in sheep

Overview includes number of ewes (N), trait name, a summary of how the trait was measured (measurement) and heritability (h^2) estimate

Paper	Breed	N	Trait	Measurement	h^2
Anonymous (2011)	Mixed maternal sheep breeds		Date of first oestrus (AFO)	Date first marked by teaser wearing a harness	0.098 ± 0.039
			Date of first oestrus – weight adjusted		0.090 ± 0.039
Toe <i>et al.</i> (2000)	Horro and Menz	450	Age of puberty Age of puberty – with maternal effects	2 consecutive harness marks from a teaser	0.16 ± 0.21 0.14 ± 0.19
Alkass <i>et al.</i> (1994)	Awassi	113	First standing estrus	Date first marked by teaser wearing a harness	0.35 ± 0.06
Meyer <i>et al.</i> (1994)	Romney	387	No. of hogget oestrus cycles	Number of times marked by vasectomised ram wearing a harness	0.26 ± 0.14
	Perendale	400			0.56 ± 0.21
	Booroola cross	544			0.30 ± 0.12
	Overall	1331			0.34 ± 0.08
Baker <i>et al.</i> (1979)	Romney	1050	No. of hogget oestruses	Number of times marked by teaser wearing a harness	0.31 ± 0.08

2.8.2 *Genetic and phenotypic correlations between traits*

A large number of heritability estimates for reproduction traits in sheep were summarised by Safari *et al.* (2005). Estimates for correlations amongst reproduction traits were derived from the results of five or

fewer studies. Studies estimating the relationship between wool, growth, and carcass traits with reproduction were also limited.

2.8.2.1 Correlations within reproduction traits

Genetic correlations within reproduction traits of the ewe are generally high and positive in analyses where reproduction records from different parities are treated as repeated records of the same trait. Some variation existed in the magnitude of these correlations with NLW being highly correlated with NLB, 0.84 whilst genetic correlations between ewe rearing ability and other reproduction traits tended to be lower, 0.14 to 0.63 (Safari *et al.* 2005). Weaker genetic correlations between PLSURV and reproduction were also seen in crossbred ewes (Afolayan *et al.* 2008). Unsurprisingly, PLSURV had a negative genetic correlation with litter size (LSIZE), -0.29 ± 0.26 , indicating that as litter size increased lamb survival decreased (Afolayan *et al.* 2008). Phenotypic correlations with reproduction traits were also moderate to high and positive, with the exception of correlations with lamb survival (Afolayan *et al.* 2008) and ewe-rearing ability (Safari *et al.* 2005). A similar trend was seen for correlations between reproductive performance for a specific ewe parity (Bunter and Brown 2013)

2.8.2.2 Correlations between reproduction traits across parities

Where reproduction records from different parities have been analysed as separate traits, comparisons of correlations across age classes not just within age classes are possible. Bunter and Brown (2013) found that genetic correlations for the same trait measured at different ages were not one. The genetic correlation between fertility (FERT), LSURV, NLB and NLW measured at 1 and 2 years of age were all significantly lower than one. Correlations ranged from 0.33 ± 0.11 for NLB to 0.44 ± 0.12 for FERT. Correlations of a similar magnitude were also reported between reproductive traits at 1 year of age and in ewes older than 2 years. This indicates that reproductive performance at 1 year of age is a genetically different trait than later reproductive performance and they are not affected by the same genes. Genetic correlations for LSIZE between age groups did not differ from one. Genetic correlations between 2-year-old and later performance were higher for LSURV, NLB and NLW, indicating performance at second and later parities were genetically more similar than performance at first and second or first and later parities.

These findings are more conclusive than an earlier study by Dominik and Swan (2006) on Merino ewes with first parity at 2 years of age. The genetic correlation between pregnancy scanning at parity one and later parities was 0.77 ± 0.24 , whilst the correlation between parity two and later parities was higher at 0.91 ± 0.54 . However, this trend was inconsistent for fecundity traits and was not observed in lamb survival to weaning traits. Although their dataset had 17,324 reproduction records across the four parities Dominik and Swan (2006) concluded that a larger volume of data was required for accurate estimates. In contrast Bunter and Brown (2013)'s study had over 28,000 ewe reproduction records across three parities.

2.8.2.3 Correlations between ewe and ram reproduction traits

Ram scrotal circumference and ewe reproductive performance are positively correlated. One of the early studies to estimate this was that of Fossecoea and Notter (1995) in composite sheep. They reported a genetic correlation between 90-day scrotal circumference and yearling ewe fertility of 0.20. Duguma *et al.* (2002) reported that scrotal circumference had a significant effect on ewe fertility in South African Merinos. Using a maximum likelihood analysis they found that lower scrotal circumference was associated with lower ewe fertility rates. A moderate positive genetic correlation, 0.35 ± 0.30 , was found between yearling scrotal circumference and NLW in Merino sheep (Apps *et al.* 2003). The genetic correlation between age of puberty in ewes and male scrotal circumference varied with age in Horro and Menz sheep (Toe *et al.* 2000). It ranged from 0.46 ± 0.32 for scrotal circumference measured at 6 months to -0.78 ± 0.33 for scrotal circumference at 12 months of age.

2.8.2.4 Correlations between reproduction and production traits

There are mixed results from studies which have estimated the relationship between pubertal traits in sheep and other production traits. To the best of the author's knowledge, no studies have reported parameter estimates between pubertal traits and other reproduction traits. Low negative and non-significant genetic correlations, ranging from -0.01 to -0.09, were reported between the number of hogget ewe cycles and weight traits in New Zealand Romney sheep (Baker *et al.* 1979). These estimates were associated with high standard errors, ranging from 0.17 to 0.21, which can largely be attributed to the low record numbers and low trait heritability. This partially agrees with Alkass *et al.* (1994) who reported a negative genetic correlation of -0.65 ± 0.05 between age and weight at puberty but low to moderate

positive genetic correlations with ewe weaning weight and ewe growth rate in Awassi ewes. The genetic relationship between age at puberty in ewes and liveweight in ram lambs was reported as moderate to strong and positive by Toe *et al.* (2000), ranging from 0.85 ± 0.56 to 0.35 ± 0.23 for body weights taken at 6 and 9 months of age respectively. The inconsistent nature of the correlations estimated from these studies coupled with the low number of animals with records highlights the need to gain a better understanding of the relationships between puberty, the attainment of sexual maturity, and reproduction in order to be able to make genetic improvement for young ewe reproduction.

In the last decade, several studies have been undertaken to better quantify the relationship between ewe reproductive performance and wool, growth, and carcass traits. Low to moderate genetic correlations exist between reproduction traits and liveweight, with stronger correlations seen for weaning, post-weaning and adult weights than for birth weight (Safari *et al.* 2005); however, the magnitude of these correlations was variable across studies. Genetic correlations which vary with age were also seen in a study looking at genetic relationships in Australian Merinos (Huisman and Brown 2008). Huisman and Brown (2008) reported positive genetic correlations between reproduction traits and weaning and yearling liveweights. However, they also reported negative genetic correlation between reproduction and birth weight whilst finding negligible correlations between post-weaning, hogget, and adult weight and reproduction. In both studies phenotypic correlations between liveweight and reproduction were accepted to be low and positive. From this it can be concluded that selecting ewes with higher liveweights could induce a correlated increase in ewe reproductive performance.

Low to moderate positive genetic correlations were also found between reproduction and eye muscle and fat depth measured at yearling and hogget ages in a large study of Merino ewes drawn from industry flocks (Huisman and Brown 2009). Fat depth at post-weaning age had a negative correlation with both NLB, -0.34 ± 0.34 , and NLW, -0.17 ± 0.37 . The standard errors associated with these two estimates were higher than for the yearling and hogget stages however, fewer Merino animals had a post-weaning fat depth measurement ($n=5479$) than did yearling fat depth ($n=17,888$). These findings might suggest that ewes with greater fat and eye muscle depth will give birth to and rear more lambs.

Genetic correlations between fleece weight and reproduction traits were generally antagonistic, whilst phenotypic correlations were low to negligible. Again, a big variation in the magnitude of estimates was seen between studies summarised by Safari *et al.* (2005). When parameter estimates originated from a large analysis of seven research resource flocks with over 55,000 reproduction records, the magnitude of standard errors was reduced leading to more robust estimates (Safari *et al.* 2007b). Low negative genetic correlations between fleece weight, clean (CFW) and greasy (GFW), and reproduction ranged from -0.09 ± 0.04 between GFW and NLB to -0.27 ± 0.05 between GFW and NLW. Phenotypic correlations were also negative ranging from -0.07 between LSIZE and GFW to -0.18 between NLW and both GFW and CFW. Genetic correlations between fibre diameter and reproduction although positive were low and not significantly different from zero. Fleece yield and coefficient of variation of fibre diameter both had low negative genetic correlations with reproduction ranging from -0.05 ± 0.05 to -0.13 ± 0.05 .

2.9 Implications of the attainment of sexual maturity and yearling lambing for adult performance and ewe progeny performance

2.9.1 *The relationship between sexual maturity attainment and later reproductive performance*

The early attainment of puberty is linked to improved reproductive performance at later ages. In a New Zealand study of Romney and Romney-cross sheep, ewes that were identified as pubertal through the use of vasectomised rams were more likely to fall pregnant ($p < 0.01$) and gave birth to significantly more lambs ($p < 0.001$) at 2 years of age (Edwards *et al.* 2015). This difference was largely attributed to a higher ovulation rate in ewes which reached puberty earlier and was not seen at 3 or 4 years of age. This contrasts with Hulet *et al.* (1969) who found reaching puberty in the first year was associated with improved lifetime reproductive performance. However, only 11% of the ewes in Hulet *et al.* (1969)'s study reached puberty in the first year compared to 81% of ewes in Edwards *et al.* (2015)'s study. Of note is that ewes were not mated in their first year in either study. A positive association between lifetime reproductive performance and whether oestrus was expressed as a hogget (between 1 and 2 years of age) was also reported by Hight and Jury (1976).

2.9.2 *Impact of yearling lambing on adult performance.*

Although positive genetic relationships have been reported between reproductive performance at 1 and 2 years of age, it is somewhat contested whether mating ewes prior to 1 year of age has negative phenotypic effects on a ewe's future reproductive performance. Across a range of cross-bred ewes that were first mated prior to 12 months of age, Fogarty *et al.* (2007) found that ewes that reared a lamb at 12 months of age reared 12% more lambs at second and third reproductive performance due to improved fertility and lamb survival. Effects on parities later than this could not be determined as ewes were only recorded for 3 reproductive events. This agrees with McCall and Hight (1981) who found lambing performance at 2 years of age was highest in Romney ewes that had reared a lamb the previous year, with previous lambing performance explaining 67% of the variation in second lambing. Lambing at 1 year of age also improved reproductive performance at 2 years of age in Romney ewes and Romney-Border Leicester ewes with McMillan and McDonald (1983) reporting significantly improved lamb survival ($p < 0.05$) in ewes that had previously lambed. They found no significant differences in oestrus, ovarian activity, fertility, fecundity or lamb growth. Knight *et al.* (1995) failed to find any differences in milk yield or composition at 2 years of age between Poll Dorset ewes that had or had not lambed previously.

In contrast, Kenyon *et al.* (2008b) found lambing at 1 year of age had a negative effect on 2-year-old performance, with Romney ewes that lambed at 12 months of age significantly ($p < 0.05$, 6-7kg) lighter with lower condition scores ($p < 0.05$) at joining the following year than those that were not bred or did not lamb at 1 year of age. They also reported significantly lower fecundity in these ewes; however, the overall proportion of ewes that conceived did not differ between the groups. It should be noted that ewes which lambed at 1 year of age did not receive preferential feeding. A later study by Kenyon *et al.* (2011) on the same groups of ewes followed their lifetime performance and concluded that although lambing at 12 months of age may have a negative impact on liveweight at 2 years of age it was not a permanent effect seen in mature ewes. Despite lower reproductive performance at 2 years of age (Kenyon *et al.* 2008b), ewes that lambed at 12 months of age reared significantly ($p < 0.05$) more lambs over their lifetime (Kenyon *et al.* 2011).

A significant reduction in NLB at 2 years of age for ewes that lambed at 1 year of age was also reported by Baker *et al.* (1978) in the Norwegian sheep breeds, Dala and Steigar. However, this reduction was not seen at 3- or 4-year-old lambings. Ewes who lambed at one year of age tended to be culled 6 months earlier than their contemporaries who did not lamb at one year of age. However, their productive life was still longer than ewes who did not lamb in the first year due to their earlier commencement of reproductive cycles. Whilst Baker *et al.* (1978) also reported lower body weights and fleece weights at 2 years of age this was not detected at 3 years of age. Both McCall and Hight (1981) and McMillan and McDonald (1983) reported small decreases in 2-year-old fleece weight for ewes that lambed at 1 year of age compared to those that did not.

2.9.3 *The performance of the progeny of ewe lambs*

Little research has been conducted into how the progeny of ewes that lamb at 1 year of age perform. Late born progeny out of 1-year-old dams were found to have a maternal handicap, with only 18.7% of progeny from 1-year-old dams lambing at 1 year of age compared with 36.7% of progeny from dams 2 years and older (McCall and Hight 1981). This could be due to lower weaning weights in progeny from yearling ewes. Baker *et al.* (1978) reported a 3 kg difference in weaning weight of progeny from 1-year-old versus adult ewes, 40kg compared with 43kg.

2.10 Conclusion

The majority of the literature recommends the practice of joining ewes prior to 1 year of age provided nutritional and management requirements can be met, despite possible negative effects on 2 year old reproductive performance. In addition to considering nutritional and management requirements it is important to evaluate the risks and opportunities mating ewes before they are 12 months of age may represent to flock genetic progress. In the overview of the literature, it was evidenced that yearling reproductive performance is currently evaluated as a separate trait from adult reproduction and a need exists to align this research with the quantification of the relationship between yearling reproduction and other key production traits. The attainment of sexual maturity is an important consideration when mating ewes at younger ages. The development of a novel trait to record the attainment of sexual maturity may be

a useful tool for predicting a ewe's later fertility. If a robust, practical on-farm measure of sexual maturity can be developed it may also be possible to select for earlier maturing ewes and see a correlated response in yearling reproduction outcomes. In order to assess the merit and feasibility of using a sexual maturity trait as part of the breeding program strategy, accurate heritability estimates and genetic correlations with yearling reproduction and other key production traits will need to be estimated.

Chapter 3. Impact of young ewe fertility rate on risk and genetic gain in sheep breeding programs using genomic selection²

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3.1 Summary

The impact of young ewe fertility rate, selection age and genomic information on genetic gain in sheep breeding programs was evaluated using stochastic simulation. Ewe fertility level at yearling age, ram and ewe age and the availability of genomic information all significantly ($p < 0.05$) influenced genetic gain. On average, at fertility levels of 10% and above in yearling ewes flock genetic progress is unlikely to be adversely impacted and there is no increase in breeding program risk.

Key words: stochastic simulation, Merino, maternal

² Submitted to Animal Production Science

Chapter 4. Genetic and phenotypic parameters between yearling, hogget and adult reproductive performance and age of first oestrus in sheep³

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4.1 Summary

Reproductive rate is an important profit driver in sheep enterprises. The aims of this study were to quantify the relationships between age at first oestrus and yearling reproductive performance, and reproduction performance across age classes in sheep. Our results support the current practice of analysing yearling reproductive performance as a separate trait from later reproductive performance in Australia's genetic evaluation system and indicate that age at first oestrus is not a reliable measure of sexual maturity in sheep.

Keywords: ewes, Merino, puberty, reproduction.

³ Newton, J. E., Brown, D. J. *et al.* (2014). Genetic and phenotypic parameters between yearling, hogget and adult reproductive performance and age of first oestrus in sheep. *Animal Production Science* **54**(6): 753-761.

Chapter 5. Progesterone levels as an indicator for young ewe sexual maturity and early reproductive performance.

I) Progesterone levels during joining are moderately heritable.⁴

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5.1 Summary

Identifying new indicator traits for sexual maturity may enable us to improve reproductive performance of ewes at 1 year of age. Field data collected on the novel trait, circulating blood progesterone level at time of joining, was found to be moderately heritable and positively associated with reproductive performance in young ewes. Should further work establish that progesterone levels are genetically correlated with reproductive traits, circulating progesterone at joining could be used to increase rates of genetic gain for reproduction.

Key words: ewe lambs, reproduction, heritability

⁴ Prepared for Animal Production Science.

Chapter 6. Progesterone levels as an indicator for young ewe sexual maturity and early reproductive performance.

II) Correlations with yearling and hogget reproduction and production traits⁵

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6.1 Summary

Factors influencing the variable reproductive success rates of ewes joined prior to 12 months of age need to be quantified. This study's aim was to quantify the relationships between progesterone levels measured at first year joining with yearling and hogget reproduction traits and with other production traits.

Progesterone level, liveweight and condition score measured at first year joining are genetically and phenotypically correlated with yearling reproduction and may be useful to increase the rate of gain for yearling reproduction.

Key words: ewe lambs, hogget, reproduction, heritability, correlation, puberty

⁵ Prepared for Animal Production Science.

Chapter 7. General Discussion

Focusing on yearling reproductive performance in ewes, this thesis has several overarching aims explored over four experimental chapters: to assess the impact of joining ewes to lamb as yearlings on flock genetic progress, to better understand the role of pubertal traits and how they relate to yearling reproductive performance, to gain a better understanding of the factors influencing yearling reproduction by quantifying relationships between yearling reproductive performance and key production traits, and to quantify the relationship between reproduction traits recorded at different ages.

Chapter 3 focused on the first aim, to consider the impact early selection of ewes and young ewe fertility rate has on genetic progress and breeding program risk when coupled with, and compared to, the other breeding program changes of early mating of rams and genomic information availability. Chapters 4, 5 and 6 met the other components of the aims. Two methods of assessing whether young ewes were cycling were evaluated from a genetic perspective in this thesis; age at first oestrus (AFO) recorded using teaser wethers and progesterone concentration (PROG) measured during joining. Chapter 5 evaluated the novel trait PROG, looking at influential factors and considering how best to analyse the trait. The relationship between yearling reproduction traits and AFO and PROG was quantified in Chapters 4 and 6, respectively. In these two chapters the relationship between reproduction traits across parities was also estimated. In Chapter 4, this occurred between yearling and hogget ages in maternal-cross ewes and between hogget and adult age in Merino ewes from the Sheep CRC Information Nucleus Flock (INF), whilst in Chapter 6 the relationship between yearling and hogget age was estimated in a large multi-breed population from industry ram-breeding flocks. Chapter 6 also quantified relationships between yearling reproductive performance and other key liveweight and carcass traits.

The major findings from each of these four chapters will be considered in this general discussion. Chapter 3 identified that higher young ewe fertility levels correspond to significantly more genetic progress without increasing breeding program risk provided fertility levels of at least 10% were achieved. This is discussed in Section 7.1. The advantages and disadvantages of AFO and PROG as indicator traits for

sexual maturity and reproductive success are discussed in Section 7.2. The other associations identified between yearling reproduction outcomes and key production traits are discussed in Section 7.3. The relationship between reproductive performance at yearling and later ages from both genetic and phenotypic viewpoints is considered in Section 7.4. The implications for future research are considered in Section 7.5, before a series of recommendations to industry are made in Section 7.6 prior to the conclusion.

7.1 The impact of young ewe fertility rate on rate of genetic progress and breeding program risk

Provided fertility levels of at least 10% are achieved in yearling ewes, the adoption of early mating in ewes does not increase breeding program risk or result in less genetic gain, based on the results from the simulation study in Chapter 3. Breeding programs with early selection of ewes, with medium or high fertility rates, achieved significantly ($p < 0.001$) higher genetic gain than breeding programs where ewes were selected at 18 months of age. Although breeding programs with low fertility in young ewes did not, on average, achieve greater genetic gain than breeding programs where ewes were selected at 18 months of age, they were also no more risky. This is because the probability of obtaining a value below the distribution of solutions from the breeding programs where ewes were selected late was zero for both Merino and maternal programs. At this low young ewe fertility level, there are fewer selection candidates, which reduces selection intensity, meaning the potential advantage offered through reducing the generation interval is not realised.

This study differed from other breeding program simulations published to date in that it considered the impact of young ewe fertility rate and developed a new method of assessing breeding program risk. By assuming the range of possible responses in a breeding program was normally distributed, a measure of breeding program risk was developed using probability distribution methodology (Inman and Bradley 1989; Bradley 2006). This measure could account for both changes to the breeding program mean response and variability in response, an important consideration in comparing early and late selection

strategies. This enabled a range of parameter changes to be easily evaluated based on whether they carried greater risk than the “base breeding program.”

Although a 20% change in average ewe fertility rate at first parity does not have a big influence on flock genetic progress (Hopkins and James 1977), changes larger than this have been seen in yearling maternal ewe average fertility rates. In this research, a large variation was seen in yearling fertility across sites and years both in the INF and in industry ram-breeding flocks. Yearling fertility in the maternal-cross ewes from Information Nucleus Flock ranged from 0% to 89% across the sites and years studied (Chapter 4). Similarly, in Chapter 5, average fertility across the maternal breed flocks ranged from 28% to 61% in 2013. These differences in yearling fertility levels observed in Chapters 4, 5 and 6 are much larger than the 20% change in average fertility rate modelled by Hopkins and James (1977). Given that changes to yearling fertility rate of greater than 20% are probable in Australian maternal flocks, we can conclude that variable fertility levels of yearling ewes will significantly impact flock genetic progress.

It does not appear to be feasible to reach fertility levels of 10% at yearling age in all Merino flocks, which may mean early joining could have negative impacts on some flocks if such fertility levels cannot be achieved. Merino fertility rates at 1 year of age tend to be lower than those of maternal breeds (Rosales Nieto *et al.* 2013; Corner-Thomas *et al.* 2014). These lower fertility rates were evident in the INF data analysed in Chapter 4, where the small number of Merino ewes with yearling records had an average YNLB of 22% compared with 43% in maternal breeds. The industry data analysed in Chapter 5 showed that, overall, Merinos ewe had lower fertility than maternal and terminal ewes and no ewes in the Superfine wool Merino flock conceived. This implies that a 10% fertility rate may not always be attainable in young Merino ewes and perhaps explains the low rate of adoption (3%) of yearling lambing by Merino producers (Curtis and Croker 2005). Although the simulation study did not consider fertility levels below 10%, we can deduce that as fertility continues to decrease flock genetic progress will also continue to decrease as the number of selection candidates continues to fall.

Overall, the results obtained in this research suggest that provided a fertility rate of at least 10% can be achieved, without major additional feed expenses or other costs, the joining of young ewes should result

in more genetic gain and be considered for adoption by more producers, in particular those with maternal breeds. The selection and breeding of ewes at younger ages requires the consideration of other risk factors such as additional costs, feed, management and labour requirements (Kenyon *et al.* 2004c; Whale 2013; Kenyon *et al.* 2014) which were not considered in the context of this thesis. It is likely there will be additional costs associated with the management of young ewes to join at 7 months, particularly if supplementary feeding is required. Whale (2013) found that pasture type, pasture quantity, stocking rate and reproductive performance achieved had a large impact on whether early mating was a profitable practice for producers. Any additional costs associated with joining young ewes must be recouped by the producer through additional lambs on the ground. At low fertility rates these costs may not be recouped; hence, the added risk from joining young ewes. These additional management costs need to be factored into breeding program considerations and perhaps represents an area for further research.

7.2 Measuring the attainment of sexual maturity in ewes and its relationship with reproductive performance at 1 year of age

Based on these preliminary results, progesterone concentration measured early in the joining period (PROG) has more merit than the use of teaser wethers to record age at first oestrus (AFO) as an indicator for sexual maturity and subsequent reproduction. The reasons for this conclusion are threefold: 1) PROG has a higher heritability than AFO, 2) PROG has more favourable correlations with reproduction and 3) measurement of PROG can be undertaken at a single time point. Data on the two traits come from different sources. Historical data from Sheep CRC INF which included AFO was evaluated. Secondly, an experimental protocol was designed and data collection conducted to measure PROG in industry flocks. The genetic and phenotypic correlations calculated in Chapters 4 and 6 represent the first instance of quantifying genetic and phenotypic correlations between pubertal traits and other reproduction traits in sheep.

Although PROG had higher heritability estimates than AFO, both align with limited published estimates of pubertal traits in sheep. The heritability of AFO was 0.02, while the heritability of PROG ranged from 0.09 when PROG was analysed as a binary trait to 0.26 when PROG was analysed as a continuous trait.

Although considerable phenotypic variation exists for both traits, the higher heritability of PROG means it will be possible to make more rapid changes through selection. The magnitude of these estimates is in general agreement with previous estimates recorded in sheep (Alkass *et al.* 1994; Toe *et al.* 2000; Anonymous 2011) and cattle (Morris *et al.* 2000; Johnston *et al.* 2009). A key difference between the data used in this thesis and previous sheep studies was the volume of records, with 910 AFO and 1896 PROG records being much greater than the 113 and 450 record in Alkass *et al.* (1994) and Toe *et al.* (2000), respectively. This larger sample size gives greater confidence to the estimates in this thesis in comparison to those earlier studies.

Genetic correlations between PROG and yearling reproductive traits were favourable, and PROG may have potential as an indirect selection criterion for yearling reproduction. The genetic correlations estimated between PROG and yearling reproductive performance in Chapter 6 were positive, though generally of low to moderate magnitude. They indicated that whilst animals with higher PROG were more likely to lamb and have a higher litter size, reproductive performance at 1 year of age is not strongly genetically associated with PROG. Although the relationship between PROG and hogget reproductive performance was weak in this study, Edwards *et al.* (2015) found that ewes that were identified as cycling by vasectomised rams had a significantly ($p < 0.05$) higher litter size at 2 years of age. In addition Hulet *et al.* (1969) found that earlier onset of oestrus cycles was associated with improved lifetime reproductive performance.

Although the genetic relationship between PROG and yearling reproductive performance was low, PROG may have potential to be used as an indirect selection criterion alongside reproduction traits to lift rate of genetic gain for reproduction. The use of physiological traits to improve selection response for litter size in sheep was explored by Walkley and Smith (1980). They found gains were greatest when physiological traits were used in addition to direct recording of litter size in a combined selection strategy. A genetic correlation of at least 0.3 between the traits was recommended by Walkley and Smith (1980) in order to achieve additional genetic gain. Genetic correlations between yearling fertility and litter size traits and PROG traits ranged from 0.33 ± 0.21 to 0.42 ± 0.22 , so based on Walkley and Smith (1980) recommendations, PROG has potential as an indirect selection criterion. However, more accurate

estimates of the genetic correlation between PROG, reproduction and other traits are required to better determine PROG's usefulness as the magnitude of the correlations will have a significant impact on the correlated response.

Genetic correlations between AFO and yearling reproduction traits were unfavourable, being positive with high standard errors and contradicting the hypothesis. The direction of the correlation suggests that animals that reach sexual maturity later and have higher AFO values are more likely to conceive, give birth to and rear a lamb. However, record numbers and trait heritability were low and there was a variable length of teaser exposure, ranging from 5 weeks to 4 months prior to joining. These factors all resulted in large standard errors of the estimate of genetic correlations. It was anticipated that animals with a younger AFO would be more likely to fall pregnant; however, as earlier maturing ewes would have had a longer exposure period to the teasers prior to joining this may have adversely impacted their subsequent reproductive performance. Ewes that have experienced extended exposure to teasers have previously been shown to take longer to mate to entire rams (Notter 1989) or fall into anoestrous after teaser exposure (Oldham and Cognie 1980). The undesirable nature of the genetic correlations and possible negative effects on subsequent reproductive performance suggest that the use of teasers for an extended period to record AFO does not result in a reliable measure of sexual maturity in young ewes and is not a useful indicator of reproductive success.

PROG was also more strongly phenotypically associated with yearling reproduction than AFO. However, the phenotypic association between PROG and YFERT, found in Chapters 5 and 6, is not strong enough to make PROG a useful phenotypic predictor of reproductive success. The phenotypic correlations between PROG and yearling reproduction traits were less than 0.20 (Chapter 6). In Chapter 5 fertility rate was found to be significantly ($p < 0.05$) higher in ewes with progesterone concentrations greater than 1 ng/ml, 59%, compared with ewes with progesterone concentrations less than 1 ng/ml, 35%. These two results indicate that animals with higher progesterone tended to have higher yearling reproductive outcomes, but a high progesterone concentration did not necessarily mean the ewe would fall pregnant. A similar trend was seen by Rosales Nieto *et al.* (2013) who found that only one third of Merino ewes who

showed evidence of having commenced oestrus cycles, as evidenced by raddle marks from teasers, conceived across two mating opportunities prior to 1 year of age.

Measurement of PROG can be adopted on-farm with fewer additional animal handling or labour requirements than AFO. One of the challenges in developing an indicator trait for sexual maturity is that to be suitable for adoption by industry it needs to be measurable with minimal additional animal handling or labour requirements and have low measurement cost. In reality this means a suitable trait needs to be accurate enough to require only one measurement. Due to the intensive nature of data recording associated with using teasers to collect AFO information and the need for frequent monitoring of ewes, it is highly unlikely the practice of using teasers to detect oestrus will be adopted by industry flocks. PROG, on the other hand, was measured in this thesis using only one sampling, which required only one additional yarding of ewes. Measuring progesterone concentration of young ewes is labour intensive on the day of measurement. However, collecting samples only requires one additional yarding and handling of the ewes which is less than that required to record AFO, giving it better potential for adoption on-farm. Opportunities also exist to consider cost-effective methods of collecting and analysing samples, such as through the use of blood cards (Bunter *et al.* 2005) or salivary ELISAs (Demeditec 2015), and the suitability of using on-farm assays as are used in the dairy industry (Allen and Foote 1988; Bajema *et al.* 1994).

Relying on one sampling time point is a possible criticism of the protocol used for measuring progesterone concentration as previous hormonal assays tended to utilise more than one sampling event (Lahlou-Kassi *et al.* 1989; Alcaraz Romero *et al.* 2012). This study is the first to consider using progesterone concentrations for genetic analysis. These results indicate that one sample is sufficient for genetic analysis. It is acknowledged that relying on one sampling point means that individual ewes may have been at different physiological stages in their cycles on the day of sampling. However, these differences are spread randomly across each sire family. This means a ewe with a false negative record would still receive a good breeding value based on information from her half siblings. In Chapter 5 the average number of daughters per sire was 15. Also, if the sampling error rate was too high data would have been noisy and no heritability would have been found for PROG and the standard errors would have

been large. Looking to the future, there may be merit in sampling ewes over a range of time points to see whether there is a better time point to measure progesterone concentration than the 14 days into joining at approximately 8.5 months of age used here. It is also possible that obtaining greater accuracy of genomic breeding values for reproduction traits will mean that genomic breeding values will represent an alternative predictor of yearling reproductive success in sheep (Daetwyler *et al.* 2014; van der Werf *et al.* 2014).

7.3 Other factors influencing reproductive performance at 1 year of age

Condition score at joining may be more strongly genetically correlated to yearling reproduction than either PJWT or PROG (Chapter 6) and thus have more potential as an indirect selection criterion for yearling reproduction. In addition, PJCS is cheap and quick to measure and is not sex-limited as PROG is. The genetic correlation estimate of 0.60 ± 0.18 between PJCS and YFERT, easily meets Walkley and Smith (1980)'s recommendation of a genetic correlation of least 0.3 between trait of interest and indirect selection traits, and the heritability of PJCS, 0.19 ± 0.05 , is higher than the heritabilities of yearling reproduction traits. This means it may be feasible to increase the rate of genetic gain for yearling fertility through indirect selection on PJCS in conjunction with direct reproduction recording. Few genetic parameter estimates exist between condition score and reproduction in sheep. When reproductive performance was analysed by parity in Scottish Blackface ewes, body condition score at joining was also positively genetically correlated to reproductive performance at second and third parity, 0.45 ± 0.18 and 0.24 ± 0.21 , respectively, but not first parity, -0.03 ± 0.16 (Walkom, 2013). In addition, the genetic relationship between condition score and reproduction was stronger than the relationship with liveweight at second and third parity. However, Walkom (2013) also found low negative genetic correlations between adult condition score at joining and adult NLW in the Maternal Central Progeny Test Ewes and a composite industry ram-breeding flock. Walkom (2013) suggested that the higher average condition score recorded in the Maternal Central Progeny Test Ewes and the composite industry flock relative to that of the Scottish Blackface ewes could have influenced the relationship found between the two traits. The existence of a positive genetic relationship between yearling reproduction and ewe condition is supported

by the genetic relationship estimated by Huisman and Brown (2009) between PCF and PEMD, and reproduction.

Although no other study has estimated the relationship between pre-joining condition score and yearling reproductive performance, the existence of a positive genetic relationship between yearling reproduction and condition score is further supported by the positive association found between condition score and yearling reproduction in smaller studies of young ewes (Kenyon *et al.* 2009; Kenyon *et al.* 2010; Cave *et al.* 2012). In this thesis, PROG and PJCS measurements were only recorded on one third of animals with yearling reproduction records and also represented different population subsets. In particular, PJCS records mainly came from maternal breed ewes. Before the merit of PJCS or PROG as an indirect selection criterion for yearling reproduction can be accurately assessed, more accurate correlation estimates are required, only possible through further data collection. This is challenging for reproduction traits that are sex limited and where numbers are also restricted through unsuccessful reproductive events.

Ewes which were older at joining, had higher PCF, condition scores and liveweights were more likely to fall pregnant and weaned more lambs at yearling age. PJWT and PCF were positively genetically correlated with yearling reproductive performance, although not as strongly correlated as PJCS was (Chapter 6). A significant genetic correlation of 0.52 ± 0.17 was found between PJWT and YWTLW, indicating ewes that were heavier at joining weaned more kilograms of lamb. Age at joining and its quadratic were also highly significant ($p < 0.01$) for yearling reproduction traits, when fitted as a covariate. Genetic correlations between production traits and reproduction traits tended to be low to moderate which indicates that yearling reproductive performance is largely influenced by different genes to those that influence the production traits studied here.

7.4 The relationship between reproductive performance at 1 year of age and later parities

This thesis shows that parameters for the same reproduction trait measured at 1 and 2 years of age in ewes are different in both research (Chapter 4) and industry (Chapter 6) flocks in several ways. Reproduction traits were more heritable at yearling age than at hogget age, as reported in both Chapters 4 and 6, though

LSIZE was a notable exception to this. With the exception of LSIZE, reproduction traits recorded at yearling age also had higher phenotypic variance than at hogget age. This means increased selection differentials can be applied and it might be possible to achieve more rapid genetic improvement for fertility at yearling age as opposed to hogget age. The reverse may be true at hogget age. The other obvious difference was that fertility at hogget age was nearly double that achieved at yearling age in both the research and industry flocks, supporting existing literature that the reproductive performance of ewes at their first parity is lower than that of mature ewes (Dýrmondsson 1981; Corner et al. 2013; Kenyon et al. 2014). Finally, genetic correlations between reproduction measured at yearling and hogget age differed in maternal-cross ewes (Chapter 4). A similar trend was seen in reproductive traits for Merino ewes between hogget and adult ages in Chapter 4, which also generally represented first and second parity. These findings are in agreement with the hypothesis and the earlier conclusions of Bunter and Brown (2013) that reproductive performance recorded at yearling and later ages are related but genetically different traits. The genetic correlations across age classes were not as consistent for the different reproduction traits reported in Chapter 6 and, due to high standard errors, could not be said to differ from one. Low sample size was likely a contributing factor. Genetic correlations estimated by Bunter and Brown (2013) between yearling and 2-year-old were lower than the estimates from Chapters 4 and 6. Overall, the two studies described in this thesis and the study by Bunter and Brown (2013) are more conclusive than an earlier study by Dominik and Swan (2006) on Merino ewes where genetic correlations between reproductive performance at parity one and two differed only for pregnancy scanning results. These studies support the separate analysis of yearling reproductive performance from other parities and also indicate that different genes influence reproductive performance at yearling and adult ages.

Ewes that did not lamb as yearlings weaned significantly fewer lambs at 2 years of age and had lower fertility as hoggets than ewes that did lamb as yearlings in industry flocks (Chapter 6). This is in general agreement with earlier studies in New Zealand (McCall and Hight 1981; McMillan and McDonald 1983) and Australia (Fogarty *et al.* 2007). Whilst there is some contention in the literature about whether mating ewes in the first year has a positive effect on subsequent reproduction performance or not, it is generally accepted that, provided ewes are well managed, there are minimal detrimental effects on liveweight at

next joining and reproductive performance is not negatively affected (Kenyon *et al.* 2014). Although Kenyon *et al.* (2008b) found that Romney ewes that lambed at 1 year of age had significantly ($p < 0.05$) lower fecundity at 2 years of age than their contemporaries who were not mated, a later study (Kenyon *et al.* 2011) of the same ewes found that this was not a permanent effect. Ewes that lambed at 12 months of age reared significantly more ewes over their lifetime (Kenyon *et al.* 2011). This also agrees with earlier published work by Dýrmondsson (1973). To date, most analysis of the effect of yearling reproductive performance on later reproductive performance has come from research flocks. The finding that there were no detrimental effects of lambing as a yearling on hogget reproductive performance in ewes raised under commercial Australian conditions (Chapter 6) is encouraging.

A potential negative aspect of early mating as perceived by farmers (Kenyon *et al.* 2004c) and seen in several research flocks (Baker *et al.* 1978; McCall and Hight 1981) is that the future performance of ewe progeny is reduced. The structure of the industry data was not explicitly designed to test this, though some inferences can be made from the results presented in Chapter 6. There was only a 1.2 kg difference in weight of lambs weaned at yearling and hogget ages in the industry data set, smaller than the 3kg difference reported by Baker *et al.* (1978). Also supporting this was the fact that the genetic correlation between yearling and hogget WTLW did not differ from one. From the data collected in this thesis, it not clear whether the progeny of yearling ewes have a maternal handicap throughout their lives; for instance, being less likely to conceive as yearling dams themselves, as reported by McCall and Hight (1981). It would be interesting to further compare the performance of progeny from yearling ewes to mature ewes to ascertain whether these effects need to be accounted for in genetic evaluation.

7.5 Implications for future research

Yearling and later reproductive performance are currently analysed as separate traits in the national genetic evaluation for sheep, Sheep Genetics (Brown *et al.* 2007), however none of Sheep Genetics current indexes include yearling reproduction traits. As yearling and later reproductive performance are genetically different traits this makes using indexes impractical for breeders wishing to place more focus on improving yearling reproductive performance. An important next step for future research will be to

explore how best to incorporate information on yearling reproduction traits and sexual maturity traits into industry selection indexes. From this thesis it is already apparent that it is unlikely that NLW, the net reproduction trait currently used in indexes, is the best selection criteria to improve reproductive performance across ages. The majority of the differences in reproductive performance seen at yearling and hogget ages in Chapter 6 were driven by differences in fertility rate. Incorporating component reproduction traits like FERT and LSIZE into the national genetic evaluation database for sheep would enable breeders to place greater focus on improving the fertility rate of young ewes. A knowledge gap exists as it is not yet clear which yearling reproduction traits and sexual maturity traits should be included in an index that would place emphasis on improving yearling reproduction. Further simulation studies will assist in estimating the likely genetic gain from including these traits in an index and assist in the calculation of appropriate economic weights.

A valuable assessment that can be made from the findings of Chapters 5 and 6 is that it is possible, through collaboration with industry flocks, to obtain large volumes of data which are suitable for genetic analysis. Estimates for previously recorded traits in Chapter 6 were consistent with heritability estimates from Chapter 4 and with other studies (Safari and Fogarty 2003; Safari *et al.* 2005). This demonstrates that the models used were able to accurately account for the complex multi-breed nature of the data and industry flocks represent a suitable source of data for future genetic research. A challenge when working with industry data is that weather conditions can contribute to unexpected changes in management, as in this study where there was widespread drought across Eastern Australia during data collection in 2013 and 2014. The effects of seasonal conditions are likely to be greater in industry flocks as research flocks often maintain greater levels of supplementary feeding during such periods. However, industry data collections can have higher relevance because the animals were subjected to commercial conditions. Future collaborations in a similar manner represent a valuable opportunity to collect large quantities of data without the expense of setting up and maintaining large resource flocks. Such data could also be used as a reference population for fertility traits for the purpose of genomic selection. Industry data collections also encourage the development of stronger relationships between researchers and the wider sheep industry which should aid in dissemination of research outcomes.

7.6 Industry recommendations

- The joining of young ewes can be adopted by breeders without increasing risk to the breeding program in terms of genetic gain provided fertility levels of at least 10% can be achieved. Significant improvement genetic gain will only be achieved at fertility levels above 10%.
- Measuring progesterone concentration has more merit than using teasers to record age at first oestrus as an indicator trait for sexual maturity and as an indirect selection criterion to improve yearling reproductive performance due to higher heritabilities and more favourable correlations.
- Ewes with higher progesterone concentration, liveweights and condition score and that were older at the start of joining were more likely to conceive and rear a lamb at 1 year of age. Selecting ewes with these attributes will result in improved reproductive performance at 1 year of age.
- Genetic correlations between yearling reproduction traits and the production traits studied were low to moderate indicating yearling reproductive performance is largely governed by different genes. In order to make genetic gain for reproduction, reproduction needs to be measured directly and breeders interested in yearling reproduction need to measure it.
- Ewes which lamb at 1 year of age are more likely to be fertile and will wean more lambs at 2 years of age.
- Further measurements of PJCS and PROG are required to obtain more accurate correlation estimates before their merit as an indirect selection criterion can be accurately assessed.

7.7 Conclusion

Although fertility at yearling age is currently lower and more variable than fertility recorded at later ages, potential exists to make more rapid genetic gain for yearling fertility relative to fertility in older ewes. Production traits like liveweight, condition score and progesterone concentration at joining are genetically and phenotypically associated with yearling reproductive traits; however, to maximise the rate of improvement for yearling reproduction breeders need to measure and record it directly. A need exists to develop new Sheep Genetics Indexes that incorporate yearling reproduction trait/s in addition to adult NLW. There may also be merit in incorporating condition score and/or progesterone concentration into a selection index focusing on improving yearling reproduction. Condition score is the obvious candidate as it is easy and cheap to measure and is not sex-limited. The addition of more data for condition score and progesterone concentration at joining will enable more accurate estimates of their relationship with yearling reproduction so their potential as indirect selection criteria can be accurately assessed. Furthermore, reproductive performance at yearling and hogget ages are genetically and phenotypically different traits and should continue to be treated as such in genetic evaluation. It is possible to manage ewes first mated prior to 1 year of age in a commercial environment to ensure that reproductive performance at 2 years of age is not compromised by the rearing of a lamb at yearling age. Another aspect of yearling reproduction not addressed in this thesis that should be explored is how the progeny of ewe lambs perform over their lifetime.

Chapter 8. References

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