Reproductive consequences of genetic improvement in clean fleece production in ultrafine Merino ewes

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Abstract

To date, genetic improvement of Uruguayan Merino sheep has focused on selection for reduced fibre diameter (FD) and increased clean fleece weight (CFW) and live weight (LW). The effects of selection for these traits on ewe productive and reproductive performance have not been studied in Uruguay. The aim of this thesis was to evaluate the impact of a long-term selection program applied in an Uruguayan Merino flock between 1999 and 2018. Phenotypic responses of yearling lambs and adult ewes across 20 years of selection demonstrated that selection strategies applied in the flock resulted in heavier animals that produced heavier and finer fleeces. These phenotypic responses were accompanied by a decrease in body condition score (BCS) at mating, with a small positive change in ewe reproductive performance. Strong positive genetic correlations were found between yearling and adult expressions of FD, CFW, and LW. The genetic relationships between FD and reproduction traits were negligible. There were generally favorable genetic correlations between LW and reproduction traits. The genetic relationships between adult CFW and ewe reproductive performance were unfavorable. Genetic trends indicated that the breeding strategies applied during the study period were effective in improving genetic merit in the traits under selection (FD, CFW, and LW) and caused only marginal genetic changes in BCS at mating and ewe reproductive performance. A total of 13, 22, 42, 22, 24 and 29 genomic regions were significantly associated with FD, CFW, LW at mating, BCS at mating, pregnancy rate, and lambing potential, respectively. The results obtained in this thesis will be used to refine the breeding programmes for Merino sheep in Uruguay in the future.

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List of Abbreviations

A_CFW	Adult clean fleece weight
2-yo_BCSM	2-year-old ewe body condition score at mating
2-yo_LWM	2-year-old ewe live weight and mating
A_FD	Ault fibre diameter
A_GFW	Adult greasy fleece weight
A_SL	Adult staple length
BCS	Body condition score
BCSM	Body condition score at mating
BCSPL	Body condition score pre-lambing
BCSW	Body condition score at weaning
CFW	Clean fleece weight
CVfd	Coefficient of variation of FD
EBV	Estimated breeding value
EMA	Eye muscle area
ERA	Ewe rearing ability
FAT	Fat thickness
FD	Fibre diameter
FMP	Fine Merino project
GWAS	Genome-wide association studies
JWAS	Whole-genome analyses software
LP	Lambing potential
LW	Live weight
LWM	Live weight at mating
LWPL	Live weight pre-lambing
LWW	Live weight at weaning
MCMC	Markov chain Monte Carlo
NLWEJ	Number of lambs weaned per ewe joined
PR	Pregnancy rate
SNP	Single nucleotide polymorphisms
SSD	Standardised selection differentials
TLW	Total number of lambs weaned
TLWW	Total lamb live weight at weaning
UPG	Unknown parent groups
Y_BCS	Yearling body condition score
Y_CFW	Yearling clean fleece weight
Y_EMA	Yearling eye muscle area
Y_FAT	Yearling fat thickness
Y_FD	Yearling fibre diameter
Y_GFW	Yearling greasy fleece weigh
Y_LW	Yearling live weight at shearing
Y_SL	Yearling staple length
W_LW	Lamb live weight at weaning

Chapter I

Introduction and Thesis Objectives

Uruguay is located between 30 and 35° latitude south and presents a temperate to subtropical climate. The total productive area is 16.35 million ha and the agricultural activity is mostly on native pastures. Most extensive livestock farms include both beef cattle and sheep. The beef population was 11.9 million in 2021, while the sheep population was 6.2 million (DIEA, 2022). The Corriedale breed represents 42% of the national flock, followed by Australian Merino (27%), with other breeds contributing less than 10% each (Bottaro et al., 2019). Mid-micron wools (25.1 - 32.0 µm) are the most abundant wool type (approximately 65%) with the remainder (35%) being lower than 25.0 µm (Cardellino et al., 2018).

Since the 1990s, the Uruguayan wool Industry has undergone changes in wool micron profile (Cardellino, 2020). During the late 1990s, the mean fibre diameter (FD) of Merino wool was approximately 22 µm, with insignificant amounts of fine wool (Cardellino, 2020; Montossi et al., 2007). Since this time, the demand for coarser Merino wool has declined which led to a reduction in the number of sheep. This reduction has been accompanied by increases in fine-micron Merino sheep (Montossi et al., 2013). From 1997 to 2019, fine-micron wool (≤ 22.5 µm) production increased by approximately 150% (3.0 to 7.5 million kg; greasy basis). Currently, fine-micron wool accounts for approximately 32% of the total wool production in Uruguay (Cardellino, 2020).

Genetic evaluation for fine-wool Merino sheep has been undertaken since 1995 in Uruguay (Ciappesoni et al., 2013). This evaluation provides selection indices that cover a range of breeding objectives with varying emphases on FD, clean fleece weight (CFW), and live weight (LW). According to the genetic trends of the Uruguayan sheep industry, the Merino breeding program has been successful in reducing FD and increasing CFW and LW (https://www.geneticaovina.com.uy/evaluaciones.php). Some studies to date have reported that breeding objectives based on reduced FD and increased CFW have undesirable consequences for ewe reproductive performance (Bunter and Swan, 2021). In addition, moderate to high negative genetic correlations between CFW and the number of lambs weaned per ewe joined (NLWEJ) suggests that selection for increased CFW could reduce ewe reproductive performance (Dominik and Swan, 2018; Safari et al., 2007). On the other hand, a negligible genetic correlation between adult CFW and NLWEJ has been observed by Chapman et al. (2021). Phenotypically, there is no information on the effects of the current Uruguayan breeding program on ewe productive and reproductive performance. More importantly, there is a lack of information on genetic parameters involving reproduction and other production traits in Uruguayan Merino sheep.

Between 1999 and 2018, two long-term research projects entitled Fine Merino project (FMP) and Regional Consortium for Innovation in Ultrafine Wool (CRILU) were developed in Uruguay. The overall breeding objective of the FMP project (1999 - 2010) was to reduce FD while allowing for only a slight loss in CFW. During the CRILU phase (2011 - 2018), the selection objective was altered to focus on maintaining FD (less than 15.5 µm), while increasing both CFW and LW. The aim of this thesis was to evaluate the impact of the selection strategies utilized in these two research projects (1999 to 2018) on ewe productive and reproductive performance. The specific aims were to evaluate the phenotypic trends for wool and growth traits in both, yearling and adult animals over a twenty-year period (Chapters III and IV), estimate heritability and genetic and phenotypic correlations among and between wool and growth traits, including ewe reproductive performance (Chapter V), estimate the genetic trends for production and reproduction traits over the study period (Chapter VI), and identify potential genomic regions associated with wool, growth, and reproduction traits in an Uruguayan Merino flock (Chapter VII). This thesis will advance the knowledge for the optimization of future Merino selection programs in Uruguay.

Chapter II

Literature review

Introduction

Global sheep population has increased in the last 10 years. In 2021, world sheep numbers were approximately 1,26 billion (IWTO, 2022). Products from sheep include meat, wool, and milk for both national and international markets. The total annual world sheep meat production was 16.4 million tonnes in 2021, which represents approximately 4.5% of global meat production (FAO, 2022). Total clean wool production was approximately 1,033 million kg in 2021, with major contributions from Australia (22.1%), China (13.5%), and New Zealand (9.4%) (IWTO, 2022). Wool represents around 1% of global fibre production (IWTO, 2022). While sheep milk production is approximately 2% of the global milk production (Balthazar et al., 2017).

There are three major sheep management systems used, namely, extensive production for wool and meat, intensive dairy production, and traditional pastoralism (Kilgour et al., 2008). Additionally, some countries utilize housed lamb production systems where ewes and lambs are indoors and there are also outdoor feedlots systems (Morris et al., 2017). In South America, sheep production occurs mainly in Argentina, Uruguay, Chile and in southern Brazil, where the climate is more temperate. These countries contain approximately 60% of the South American sheep population and produce more than 80% its wool production (Morris, 2017). In general terms, this region presents two types of production systems, small holder production systems, characterized by low input and productivity, and larger commercial systems, where even if the main objective is wool production, meat production is also relevant (Morris et al., 2017).

This literature review will include firstly a background on sheep production in Uruguay and drivers of productivity, secondly, a summary of heritability for economically relevant wool traits, thirdly, a background on genetic correlations between sheep production and reproduction traits, and finally a summary of genome-wide association studies (GWAS) for wool, growth, and reproduction traits in sheep.

Sheep production in Uruguay

Uruguay is located between 30 and 35° latitude south and presents a temperate to subtropical climate. Average annual rainfall oscillates between 1,000 to 1,300 mm, with autumn and spring being the wettest seasons (Berretta et al., 2000). The total productive area is 16.35 million ha and the agricultural activity is mostly on native pastures. Most extensive livestock farms include both beef cattle and sheep. The beef population has ranged between 10 and 12 million in the last two decades (DIEA, 2022). In contrast, the sheep population has decreased drastically from 25.2 to 6.2 million between 1990 and 2021 (Montossi et al, 2013; DIEA, 2022). This sheep number reduction has also been accompanied by changes in the sheep population's distribution, which currently is mostly limited to the northern and eastern regions (Figure 2.1; Montossi et al., 2013). The Corriedale breed represents 42% of the national flock, followed by Australian Merino (27%), with other breeds (Ideal, Merilin, Texel, Romney and Merino Dhone) contributing less than 10% each (Bottaro, 2019).

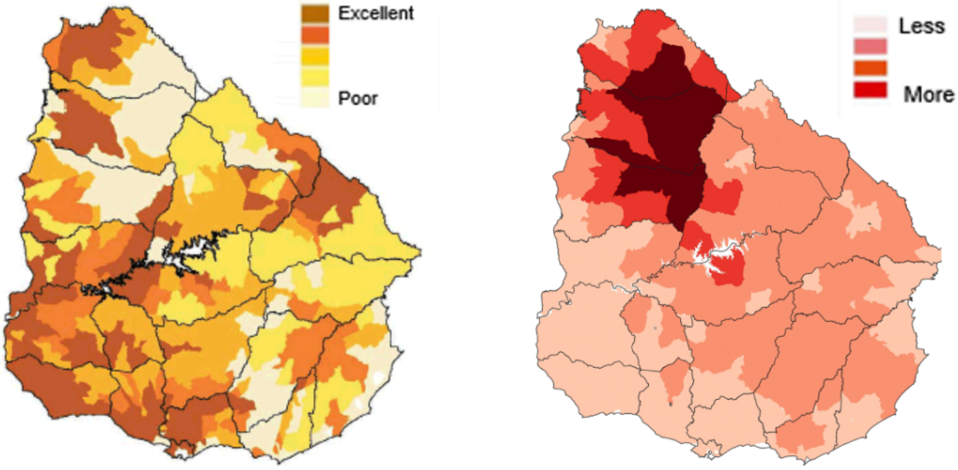

Figure 2.1 Map of Uruguay. Soil pastoral aptitude (Left), Sheep population distribution (Right). DIEA, 2022.

According to a recent sheep ultrasound reproductive report (Sheep pregnancy scanner workshop, 2022), the average pregnancy rate (pregnant ewes/joined ewes) and lambing potential (ultrasound-scanned fetuses/ewe joined) of the national flock was approximately 93% and 115%, respectively. However, there is a wide difference between lamb weaning potential number and those finally weaned. The average percentage of lambs weaned per ewe joined ranges between 70 and 85% with a high variation between years (Wool of Uruguay, 2023). Mid-micron wools (25.1 - 32.0 µm) are the most abundant wool type (approximately 65%) with the remainder (35%) being lower than 25.0 µm (Cardellino et al., 2018). Annual exports of wool and wool products were 19.0 million kg (greasy basis) in 2020 (Wool of Uruguay, 2023). Of the total wool products exported, 54% was in the form of Tops, followed by scoured and greasy wool accounting for 24 and 22%, respectively (Wool of Uruguay, 2023). In 2021, the number of sheep slaughtered was approximately 1.37 million. The average carcass weight was 19.6 and 16.5 kg for adults and lambs, respectively (INAC, 2021). The total carcass weight export was 24,074 tons (INAC, 2021).

Sheep production systems in Uruguay and drivers of profitability

There are three main sheep production systems, aligned to ecological regions of Uruguay (Table 2.1; Montossi et al., 2013). The three systems are *Intensive meat production, Semi-extensive production*, and *Extensive wool production.*

The *Intensive meat production* system is promoted for use on high forage production potential soils. A 100-ha farm model (90% highly productive pastures) producing fattening lambs slaughtered at 10 months (Corriedale) or 6 to 8 months of age (prolific and meat crossed breeds) was evaluated (Montossi et al., 2013). The Corriedale scenario analysed produced approximately 40 kg of wool/ha and 190 kg live weight/ha, generating an income of approximately US$ 390/ha (Montossi et al., 2013). While the scenario with more prolific breeds and terminal sires, achieving weaning rates of 150%, at stocking rates of 9 - 10 ewes/ha, producing 236 to 370 kg/ha of lamb meat and approximately 50 kg of wool/ha, which resulted in an income of US$ 500 to US$ 850/ha.

Table 2.1 Conceptual model proposed to develop a more competitive sheep industry in Uruguay.

Facts	**Extensive systems**	**Semi-extensive systems**	**Intensive systems**
Production orientation	Mainly breeding operations	Breeding operations with or without the use of terminal sires for lamb fattening	Specialized breeding operations with the use of terminal sires for lamb fattening
Type of soil	Shallow	Shallow-Medium	Medium-Deep
Products	Fine and superfine wool and sheep meat as sub-product	Fine wool and lamb meat	Lamb meat and wool as sub-product
Breed	Merino	Dual-purpose	Prolific sheep, high lamb growth and heavy carcass weight

Adapted from Montossi et al., 2013.

The *Semi-extensive production* system is suggested for use on shallow - medium soils, where improved pastures represent approximately 25% of the total (Montossi, 2016). A semi-extensive production system model was evaluated for a 1,000-ha farm, utilising a dual-purpose system (lamb meat and wool), producing wool of 28 µm and the combination of differing lambs weaning percentages (65, 75 and 85%) and two type of lambs (light lambs sold at weaning at 25 kg *vs.* heavy lambs slaughtered at 35 to 38 kg) (Montossi et al., 2013). In this system, sheep meat represents between 55 to 65% of total income. In this model scenario, increasing reproductive efficiency from 65 to 85%, plus lamb 35 to 38 kg live weight would allow an increase of up to 170% in producer income compared with the traditional system, with a weaning percentage of 65%, weaning 25 kg lambs (US$ 29 to US$ 80/ha; Montossi et al., 2013).

The *Extensive wool production* system is proposed for use on shallow soils, where improved pastures do not exceed 10% of the total (Monotssi et al., 2016). In these wool production systems the highest economic efficiency of sheep production is driven by wool income (Chalkling et al., 2019). The economic impact of reducing wool fibre diameter (FD) on Extensive wool production systems was evaluated (Montossi et al., 2013). The scenario modelled was based on a 1,000-ha farm, on shallow soils (less than 10% improved pastures). The impacts of differing lamb weaning percentages (60, 70 *vs.* 80%) and FD (22, 20 *vs.* 18 µm) were simulated. Regardless of weaning percentage, reducing FD from 22 to 18 µm represented an increase in producer's income of at least 120%. Changes in weaning percentage had only a minor impact. Additionally, in scenarios evaluated, the majority of the producer income (60 - 70%) came from wool production, rather than meat sheep production (Montossi et al., 2013) reinforcing the findings of Chalkling et al. (2019).

Another simulation study reported an increase of 70% in the farmer's income (US$ 60 *vs.* US$104/ha) when FD was reduced from 21 to 17µm (Buffa et al., 2017). Uruguayan commercial farms located in extensive production regions and producing wool of approximately 17µm reach an income exceeding US$ 100/ha (De Barbieri, personal communication). These combined findings support why producing fine wool is an aim for many of these farmers to increase profitability.

Merino production in Uruguay

Most Merino production in Uruguay is concentrated in the Basaltic region, in the north of the country and predominantly on shallow soils. In this region, annual pastures production ranged between 2,885 and 4,580 kg of dry matter/ha (Berretta, 1997). The highest annual forage production is during the summer and spring periods, while winter production only represents 15% of the total (Figure 2.2; Berretta et al., 2000). Dry matter digestibility, metabolizable energy and crude protein content vary between 50 - 61%, 1.8 - 2.2 Mcal/kg of dry matter and 6 - 15%, respectively (Ramos et al., 2019; Berretta et al., 2000). The winter and summer present the highest and lowest crude protein levels, respectively (Berretta et al., 2000).

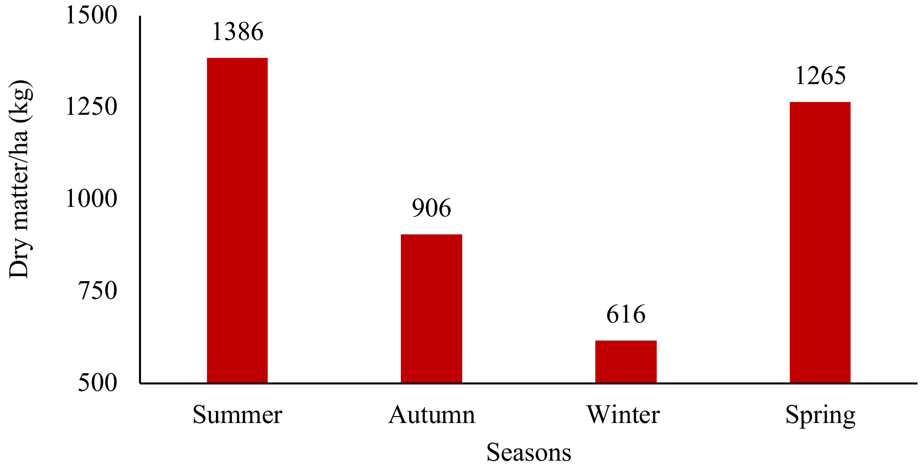

Figure 2.2 Average seasonal native pastures production (Kg dry matter/ha) in the Basalic region (Berretta et al., 2000).

Of the approximately 122,297 ha utilized by forty Merino sheep farmers, 83% corresponded to native pastures (Ramos, personal communication). On most Merino sheep farms (approximately 80%), ewe conception (breeding) occurred in autumn, and ewes were first mated at approximately 18 months of age. Reproductive ultrasounds performed for three years on approximately 20,000 Uruguayan Merino ewes, reported an average of 90 and 104% of pregnancy rate and lambing potential (ultrasound-scanned fetuses/ewe joined), respectively (Ramos, personal communication). In this study, lambs marking percentage (approximately one-month post-birth) ranged between 57 and 88% (Ramos, personal communication). In Merino sheep production systems, a castrated male lamb's potential role in the system varies between years and, it depends on several factors such as wool prices and other agricultural activities scenarios. There are commercial farms where castrated male lambs are utilized as wethers for three or more years, producing mainly wool (between 3.5 to 3.9 kg/animal/year), and in other cases, all castrated lambs are slaughtered after the first shearing (at approximately one year of age; Abella et al., 2018).

In Uruguay, national genetic evaluation for Merino sheep has been developed and undertaken since 1995 (Ciappesoni et al., 2013). This evaluation is conducted by the Uruguayan Secretariat of Wool (SUL) and the National Institute of Agricultural Research (INIA). Currently, genetic evaluation for Merinos produces estimated breeding values (EBVs) for FD, clean fleece weight (CFW), greasy fleece weight (GFW), staple length (SL), coefficient of variation of FD (CVfd), LW, faecal worm egg count, and visual traits (face cover and pigmentation score). This evaluation offers three selection indices that cover a range of breeding objectives with varying emphases on FD, CFW, and LW. According to the genetic trends of Uruguayan Merino sheep, there has been substantial improvement in the traits included into selection indices (https://www.geneticaovina.com.uy/evaluaciones.php).

Genetic and phenotypic parameters for production traits

Genetic improvement programs applied to different species have increased the profitability of agricultural production systems (Rauw et al., 1998). The design of breeding plans requires a breeding objective, appropriate and sufficient production and environmental records and an efficient method to identify genetically superior parents. Knowledge of the genetic (co) variation within and between traits is also needed to develop effective sheep breeding programs and to predict genetic progress (Safari and Fogarty, 2003). The estimation accuracy of genetic parameters requires large data sets for each population (Safari et al., 2005). Additionally, parameter estimation generated from several stable populations may be more reliable than those obtained from a single population (Safari et al., 2005).

Phenotypic variation in a population is explained by environmental factors, genetic factors, and interactions between genetic and environmental factors (Wray and Visscher, 2008). The genotypic value for a trait comprises the combined effect of all loci, including possible allelic interaction within loci (dominance) and between loci (epistasis) (Wray and Visscher, 2008). The genotypic value for a trait is estimated through breeding value, which is the sum of the alleles an animal carries at the loci that affect this particular trait. The heritability is the proportion of phenotypic variation (V_P) that is due to variation in genetic values (V_G) (Visscher et al., 2008; Masters and Ferguson, 2019). The variation in genetic values depends on segregation of the alleles that influence the trait, the allele frequency, the effect sizes of the variants and the mode of gene actions (Visscher et al., 2008). Genetic and environmental factors vary across populations therefore, genetic parameters such as heritability can also vary between populations within species (Visscher et al., 2008). Genetic parameters can be classified as high (≥ 0.45), moderate (from 0.2 to 0.45), or low (< 0.2) (Wuliji et al., 2001).

Fibre diameter and CFW largely explain the value of a Merino fleece (Taylor et al., 2007a). Therefore, these two traits should be prioritised within Merino breeding programs for improving economic returns of the sheep industry and are the focus of the following sections.

Fibre diameter heritability

Safari and Fogarty (2003) undertook a substantial review of the scientific literature on estimating the heritability for FD in the Australian Merino breed. Table 2.2 summarizes estimated heritability for FD for Merino sheep from various countries (Australia, New Zealand, South Africa, and Uruguay) and a wide range of wool FD (14.2 to 24.8 µm).

Estimated FD heritabilities reported across twenty-three studies ranged between 0.42 and 0.81, with a focus around a heritability of approximately 0.60 (Table 2.2), which is consistent with Safari et al. (2005) who reported FD heritabilities of 0.59 and 0.57 for wool-breeds and dual-purpose breeds, respectively. The mean heritability for FD in Uruguayan Merino sheep has been reported to be relatively high (0.73, Ciappesoni et al., 2013) and similar to Huisman et al. (2008) for Australian and

New Zealand Merinos (Table 2.2). These two studies used similar wool breeds with the traits of FD, GFW, and SL varying within a narrow range (17 to 18 µm, 3.0 to 3.8 kg, and 7.5 to 8.0 cm) only (Huisman et al., 2008; Ciappesoni et al., 2013).

Fibre diameter in Merino sheep is expressed on multiple occasions in an animal's lifetime (Fozi et al., 2012). A genetic correlation of 0.9 for FD measured at different ages has been reported (Mortimer and Atkins, 2003). This indicates that one measurement of FD is a good predictor of genetic merit for this trait later in life. However, the FD genetic correlations at different ages become weaker as the age difference increases and varies with wool genotype (fine or medium) (Fozi et al., 2012). FD heritability tends to increase as animals aged (0.62 and 0.72 at 18 and 28 months, respectively, Lee et al., 2002). While there were some differences between estimated FD heritabilities at different ages, all cases are considered high values.

Fibre diameter is one of the most economically relevant traits for Uruguayan Merino sheep farms (Buffa et al., 2017). A significant proportion of FD differences between animals is explained by genetic factors (see Table 2.2). In addition, high correlations between FD measured at different ages allows for the use of one measurement, as an indicator of an animal's genetic merit for this trait (Huisman and Brown, 2009b). Combined these data support using FD in yearling lambs as a component of breeding objective for Uruguayan Merino sheep farmers.

Table 2.2 Published estimates heritability for fibre diameter (FD) for Merino sheep, numbers of records, age of animals, mean value, number of years covered, country and reference of the publication.

Heritability	Records	Age (approx.)	Mean (µm)	Year	Country	Reference
0.58 ± 0.12	1,527	15m	-	6	Australia	Lewer et al., 1994
0.59 ± 0.09	2,084	15m	-	6		
0.62 ± 0.07	3,830	15m	-	7	Australia	Mortimer and Atkins, 1994
0.44 ± 0.05	2,862	12m	-	18	Australia	Swan and Hickson, 1994
0.45	2,200	10m	21.3	4	Australia	Ponzoni et al., 1995
0.59	2,200	16m	22.6	4		
0.60 ± 0.04	7,396	18m	19.5	22	South Africa	Snyman et al., 1996
0.58 ± 0.10	1,284	10m	20.1	2	Australia	Brash et al., 1997
0.55 ± 0.10	1,211	16m	22.7	2		
0.68	5,100	9m	16.9	5	Australia	Purvis and Swan, 1997
0.52 ± 0.08	2,286	10m	21.5	4	Australia	Hill, 2001
0.62 ± 0.08	2,239	16m	22.8	4		
0.72 ± 0.06	2,134	16m	22.2	4		
0.73 ± 0.06	2,087	28m	24.0	4		
0.68 ± 0.06	2.000	40m	24.8	4		
0.59 ± 0.06	1,790	10m	-	5	New Zealand	Wuliji et al., 2001
0.67 ± 0.23	758	12m	17.2	-	Australia	Brown et al., 2002
0.66 ± 0.03	10,731	18m	19.2	-		
0.62 ± 0.10	1,729	18m	18.2	2	Australia	Lee et al., 2002
0.72 ± 0.12	1,292	28m	19.8	3		
0.76 ± 0.02	1,199	Adult	22.5	6	South Africa	Cloete et al., 2003
0.57 ± 0.06	2,182	16m	22.6	4	Australia	Ingham, 2003
0.42 ± 0.03	85,782	12, 17m, adult	14.2	15	New Zealand	Sherlock et al, 2003

Heritability	Records	Age (approx.)	Mean (µm)	Year	Country	Reference
0.68 ± 0.01	116025	-	21.3	30	Australia	Safari et al., 2007a
0.77 ± 0.02	94,049	12m	18.1	18	Australia and New Zealand	Huisman et al., 2008
0.62 ± 0.02	68,429	17m	19.0	18		
0.67 ± 0.04	11,273	28m	18.5	17		
0.65	4823	12m	16.6	7	Australia	Fozi et al., 2012
0.66	3686	24m	18.4	7		
0.63	2985	36m	18.2	7		
0.66	2781	48m	18.4	7		
0.60	2166	60m	18.5	7		
0.70 ± 0.03	3891	10m	16.7	10	Australia	Dominik and Swan, 2018
0.69 ± 0.03	3891	22m		10		
0.67	13,497	13m	17.9	11	Uruguay	Ciappesoni et al., 2006
0.73	10,978	12m	17.2	15		Ciappesoni et al., 2010
0.67	3,110	12m	-	-		Ciappesoni et al., 2011
0.81	430	adult	-	-		Ciappesoni et al., 2011
0.73 ± 0.03	29,998	13m	16.9	15		Ciappesoni et al., 2013
0.74 ± 0.04	5,796	12m	16.9	5	Australia	Mortimer et al., 2017

(Adapted from Safari and Fogarty 2003; Safari et al., 2007a; Huisman et al., 2008; Ciappesoni et al., 2006, 2010, 2011 and 2013; Mortimer et al., 2017; Dominik and Swan, 2018)

Clean fleece weight heritability

The majority of the literature which has published estimates of FD heritability have also included the heritability estimates for other relevant wool traits such as CFW (Table 2.3).

Estimated CFW heritabilities reported by eighteen studies ranged between 0.25 and 0.59, with the majority being greater than 0.35 (Table 2.3). The lowest (0.32) and highest (0.50) direct heritability for CFW was reported at hogget and adult stage, respectively (Huisman et al., 2008), which is consistent with Hill (2001) who reported heritabilities of 0.42 and 0.51 at 16 and 40 months of age, respectively (Table 2.3). For the Uruguayan Merino sheep population, the heritability for CFW was estimated in animals at 12 to 13 months of age, these ranged from 0.30 to 0.46 (Tables 2.3; Ciappesoni et al., 2006; 2010; 2011; 2013). According to the authors, the highest estimated heritability obtained in one of their studies (0.46), could be explained by maternal effects not being included in the statistic model (Ciappesoni et al., 2013). Estimated CFW heritabilities were moderate to high, indicating that genetic improvement in this trait is possible through selection.

As with FD, CFW in Merino sheep is expressed several times throughout the life of an animal (Murray et al., 2001; Fozi et al., 2012). The estimated genetic correlation between yearling CFW and adult CFW has been reported to be high (0.57; Huisman et al., 2008). This suggests that genetic merit for CFW at yearling age can be used as a good predictor of genetic merit for this trait at adult age.

Table 2.3 Published estimates heritability for clean fleece weight (CFW) for Merino sheep, numbers of records, age of animals, number of years covered, country and reference of the publication.

Heritability	Records	Age (approx.)	Year	Country	Reference
0.44 ± 0.11	1,527	15m	6	Australia	Lewer et al., 1994
0.27 ± 0.07	2,084	15m	6		
0.35 ± 0.05	3,830	15m	7	Australia	Mortimer and Atkins, 1994
0.59	2,200	10m	4	Australia	Ponzoni et al., 1995
0.51	2,200	16m	4		
0.26 ± 0.04	7,371	18m	22	South Africa	Snyman et al., 1996
0.39 ± 0.09	1,284	10m	2	Australia	Brash et al., 1997
0.34 ± 0.08	1,209	16m	2		
0.29	5,100	9m	5	Australia	Purvis and Swan 1997
0.48 ± 0.08	2,286	10m	4	Australia	Hill, 2001
0.57 ± 0.08	2,239	16m	4		
0.42 ± 0.06	2,134	16m	4		
0.39 ± 0.06	2,087	28m	4		
0.51 ± 0.06	2,000	40m	4		
0.28 ± 0.07	1,785	10m	5	New Zealand	Wuliji et al., 2001
0.38 ± 0.08	1,729	12m	2	Australia	Lee et al., 2002
0.52 ± 0.11	1,292	28m	3		
0.25 ± 0.02	27,445	13m, adult	15	New Zealand	Sherlock et al., 2003
0.42 ± 0.01	115244	-	30	Australia	Safari et al., 2007a
0.36 ± 0.02	69,496	12m	18	Australia and New Zealand	Huisman et al., 2008
0.32 ± 0.02	44,163	17m	18		
0.50 ± 0.07	3,642	25m	14		

Heritability	Records	Age (approx.)	Year	Country	Reference
0.43 ± 0.03	3891	10m	10	Australia	Dominik and Swan, 2018
0.42 ± 0.04	3891	22m	10		
0.39 ± 0.02	12,955	13m	11	Uruguay	Ciappesoni et al., 2006
0.46	10,848	12m	15		Ciappesoni et al., 2010
0.39	3110	12m	-		Ciappesoni et al., 2011
0.38	430	adult	-		Ciappesoni et al., 2011
0.30	29,771	13m	15		Ciappesoni et al., 2013
0.52 ± 0.05	5,599	12m	5	Australia	Mortimer et al., 2017

(Adapted from Safari and Fogarty 2003; Safari et al., 2007a; Huisman et al., 2008; Ciappesoni et al., 2006, 2010, 2011, and 2013; Mortimer et al., 2017; Dominik and Swan, 2018)

Greasy fleece weight components

The components of GFW are shown in Figure 2.3. GFW is a result of CFW and other non-fibre components (wax, suint, vegetable matter, dirt, and dust) (Turner and Young, 1969; Schlink, 2009). CFW is a composite trait that includes wool-bearing skin area and wool per unit skin area. Skin area comprises smooth body surface area, which is related to LW, and a wrinkling factor, associated with the folding degree. Wool per unit skin is the result of the number of fibres per unit skin area (fibre density) and fibre weight, the latter dependent on the fibre volume and the specific gravity of wool. Fibre diameter and fibre length define the fibre volume. Changes in one or more of these components can arise from selection for CFW and/or FD, with different responses according to the strains (Turner and Young, 1969; Adams and Cronje, 2003; Schlink, 2009).

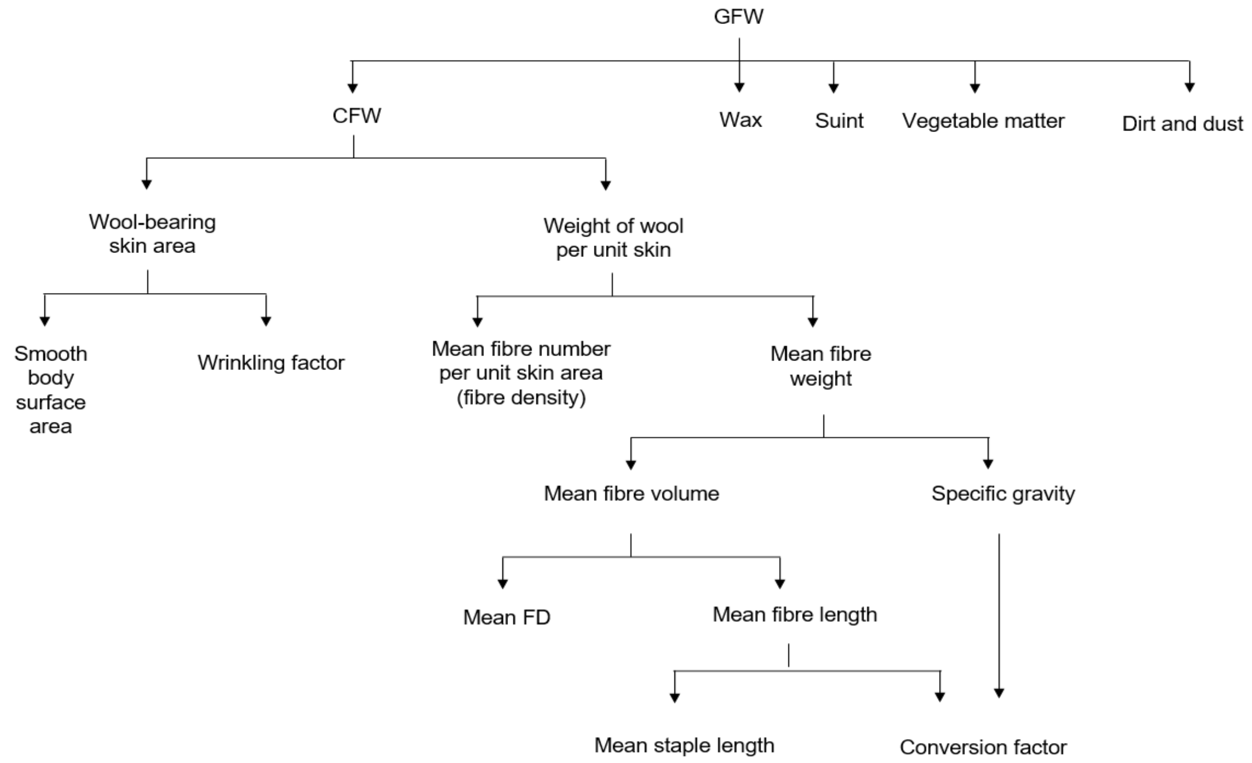

Figure 2.3 The components of greasy and clean fleece weight (Turner and Young, 1969).

Maternal effects

Body and wool growth are a result of combination of genes an animal has (direct additive effects), and environmental effects (Lewis and Beatson, 1999; Ciappesoni et al., 2013). Maternal effects have three components, (1) *maternal additive effect* (explained by dam's genotype), (2) *permanent environmental effect* (it is dependent on each lambing of a dam) and (3) *temporary environmental effects* (associated to one litter of dams) (Lewis and Beatson, 1999). The maternal effect is highly associated with the milking ability of the dams and is more important in early life, declining with increasing age, especially after weaning (Safari et al., 2007c). For different wool-breeds, maternal heritability was 32% and 21% of the magnitude of the direct heritability for GFW and CFW, respectively (Safari et al., 2005). For superfine Merino sheep (17.0 µm on average), most wool traits (GFW, CFW, FD and SL) were influenced by maternal effects (Ciappesoni et al., 2013).

Together, this section indicates that FD and CFW are strongly inherited and inexpensive to measure, resulting in ideal selection criteria for Merino breeding programs focused on maximising genetic improvement in wool revenue (Taylor et al., 2007a). To avoid potential unintentional responses, it is necessary to know the genetic relationship between wool traits and other traits of relevance. These relationships between traits will be discussed in following sections.

Genetic correlations

Breeding objectives for sheep production can be complex, considering not only body and wool traits but also those associated with health and reproduction (Safari et al., 2005). When selecting for two or more traits, it is necessary to consider whether they are independent of each other, or if they are correlated, either positively or negatively (Rae, 1982). The phenotypic correlation is the association between two traits, measured on the same animal, and has both genetic and environmental components (Turner and Young, 1969). The genetic fraction can arise from link genes affecting two or more traits or from the action of one gene on more than one trait (pleiotropy). The environmental component results from an environment shared by the two traits. For example, lambs reared under poor nutritional conditions, will likely have both low fleece weight and live weight (Searle, 1961; Rae, 1982). However, the environmental factor will not affect the correlation between the two traits in the next generation. On the other hand, the genetic component means that selection on one trait can result in a correlated change in another genetically correlated trait (Turner and Young, 1969; Rae, 1982; Sajjad, 2012).

Correlations can be classified in three ways: strength, sign (positive or negative), and whether they are favourable or unfavourable (Sajjad, 2012). Strength of correlation is indicated by its value, being either high ($|r| \geq 0.45$), moderate ($0.2 \geq |r| < 0.45$) or low (Wuliji et al., 2001; Sajjad, 2012). The sign indicates the direction of change. A positive correlation implies that the two traits tend to change in the same direction. As an example, increases in GFW will be associated with an increase in LW, as these traits are positively correlated (0.27, Ciappesoni et al., 2013). On the other hand, a negative correlation implies that as one-trait increases the other decreases, for example, GFW and wool yield are negatively genetically correlated (-0.14), which indicates that selection for increased GFW is associated with decreased wool yield (Safari et al., 2005). A favourable correlation means selection for one trait favourably improves another trait (Sajjad, 2012). The sign of the genetic correlation does not indicate if the relationship between traits is favourable or unfavourable. For example, GFW and FD are positively genetically correlated, which implies that heavier fleeces are associated with coarser fibres, but this association is considered unfavourable for fine wools, because finer wool are associated with higher per kg value.

Genetic correlations also enable for the selection of a trait that is difficult to measure, expensive to record or expressed at older ages, by using a correlated trait (Greeff et al., 2010). The prediction of breeding values for a trait based on the records of that trait itself, is named direct selection (Rae, 1982). On the other hand, indirect selection occurs when breeding value estimation for a given trait is made from a characteristic (trait) genetically correlated with it (Rae, 1982). If 'Y' is an easily observed trait which is favourably highly correlated with 'X', it is possible to improve 'Y' and to obtain desirable progress in ‘X’ (Sajjad, 2012). As an example, the genetic correlation between GFW and CFW is positive and high (0.86), indicating that selection for increased GFW will increase CFW (Safari et al., 2005). Given the difficulty (cost and time) a farmer would have to select based on CFW they can use GFW as an approximation.

The correlated response between various traits is very relevant for sheep breeding programs (Safari et al., 2006; Refshauge, 2011). Selection for increased production traits can have unintentional consequences, which may vary across environments and breeds (Greeff, 2020; Dominik et al., 2001, Safari et al., 2005; Masters and Ferguson, 2019). For example, selection for increased CFW may lead to economically undesirable correlated changes in scanning percentage, little size and number of lambs weaned per ewe joined (NLWEJ) (Safari et al., 2007b; Dominik and Swan, 2018). For 3 breeding objectives (fine wool, dual-purpose wool/meat and meat), the efficiency of selection is sensitive to the genetic correlations between lambs weaned and both CFW and FD (Safari et al., 2006). Genetic correlations may change under selection, and re-estimates should be carried out at intervals of every few years (Turner and Young, 1969).

Fleece weight and FD are the two most important wool production traits affecting farmers income (Atkins, 1997). Reducing FD, while not allowing for loss in CFW, can involve changes in fibre density (Adams and Cronjé, 2003). A negative genetic correlation (-0.52) between FD and follicle density was reported for fine Merino sheep (Mortimer and Atkins, 1993). Therefore, selection for decreased FD is accompanied by increases in follicle density. Follicle density was negatively genetically correlated (-0.74) with skin weight (Hill et al., 1997), suggesting that selection for decreased FD can indirectly reduce the weight of the skin. The weight of the skin per unit area showed similar trends to that of LW (Williams and Morley, 1994). Therefore, reducing FD, while either maintaining or increasing CFW, may have undesirable effects on LW, which may have unfavourable effects on ewe reproductive performance. The present review will include the genetic correlations between CFW, FD and LW, and the possibility of achieving genetic improvements in these productive traits.

Genetic correlations between clean fleece weight and the production traits of greasy fleece weight, fibre diameter, live weight at weaning and yearling live weight for Merino sheep

Figure 2.4 summarizes genetic correlations between CFW and GFW and FD estimated mostly at yearling age. Genetic correlations between CFW and GFW were positive and high, ranging between 0.71 and 0.90 (Figure 2.4), which implies that selection for increased GFW will increase CFW. Positive genetic correlations between CFW and FD ranged between 0.19 to 0.45, with many being classified as moderate, although some studies were low or high (Figure 2.4). The lowest (0.19) and highest (0.45) genetic correlations between CFW and FD were reported for superfine (16.9 µm on average) and medium-woolled Merinos (22.7 µm on average), respectively. Wuliji et al. (2001) suggested that genetic correlations between CFW and FD are no stronger in fine than coarser Merino sheep, although, in their study, the genetic correlation between these two traits was imprecise (0.12 ± 0.15).

Approximately 90% of Merino wool value is determined by FD and CFW (Taylor et al., 2007a; Refshauge, 2011), therefore, ideally both traits need to be improved together. Reducing FD without considering CFW may reduce the overall value of the wool clip, due to their unfavourable genetic correlation (Figure 2.4). Using an appropriate selection Index to rank sheep on their combined performance, will achieve simultaneous improvement in both traits (Taylor et al., 2007a; Safari et al., 2007b). As an example, between 2001 and 2011, the Uruguayan Merino sheep population achieved annual genetic gains of -0.64% and 0.54% for FD and CFW, respectively (Ciappesoni et al., 2014). This demonstrates that, genetic progress can be achieved in both FD and CFW, despite being unfavorably genetically correlated.

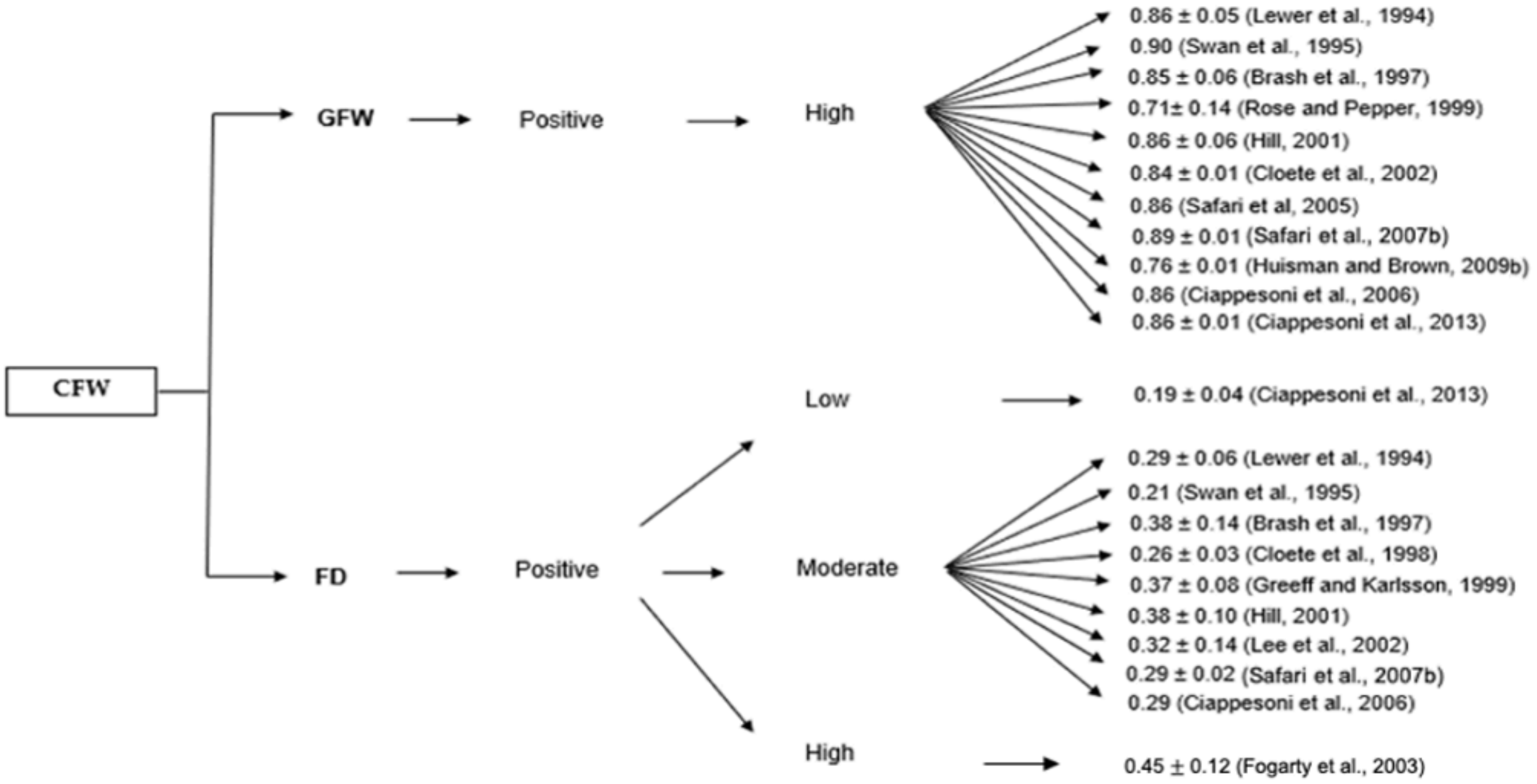

Figure 2.4 Sign (positive or negative; in this case only positive relationships have been reported) and magnitude (high: ≥ 0.45, moderate: $0.2 \geq |r| < 0.45$, or low: < 0.20) of genetic correlations between clean fleece weight (CFW) and: greasy fleece weight (GFW) and fibre diameter (FD) for Merino sheep.

Figure 2.5 summarizes genetic correlations between CFW and LW at weaning (W_LW) and yearling LW (Y_LW), with most animals aged between 7 to 16 months. Genetic correlations between CFW and W_LW and Y_LW were positive, with most being classified as moderate (Figure 2.5). The highest genetic correlation between CFW and LW was reported by Mortimer et al. (2017) for superfine Merino sheep (16.9 µm on average). According to the author, this high correlation could be explained by an underestimation of the maternal effects affecting CFW, which was lower (0.03) than reported in other studies (Ciappesoni et al., 2013; Huisman et al., 2008). This argument seems reasonable given this study utilized younger animals (7 months of age). Combined Figure 2.5 indicates that genetic correlations between CFW and LW are positive and moderate, although the magnitude has varied across studies.

Selection for more than one trait can be made efficiently by selecting for the traits simultaneously. Selection index combines EBVs for several traits with an economic weighting (based on costs of production and returns on outputs), to give a single economic value, making it possible to rank the animals in the most accurate manner (Taylor et al., 2007a; Ciappesoni et al., 2012). Depending on a breeder's predictions of future premiums for FD, it is possible to vary the relative selection emphasis and resultant rate of improvement in FD relative to CFW or LW (Taylor et al., 2007a; Ciappesoni et al., 2012). In Uruguay, the national genetic evaluation for Merinos provides three selection indices that cover a range of breeding objectives with varying emphases on FD, CFW, and LW (Ciappesoni et al., 2012).

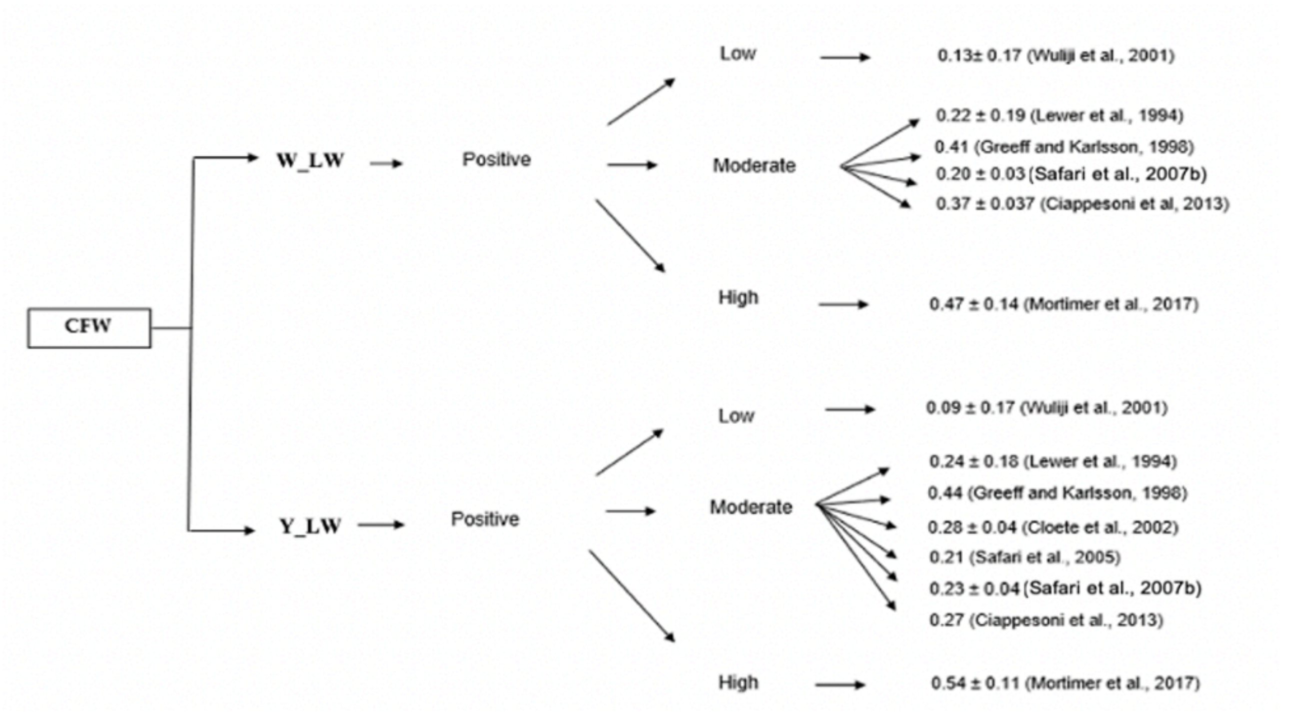

Figure 2.5 Sign (positive or negative; in this case only positive relationships have been reported) and magnitude (high: ≥ 0.45, moderate: $0.2 \geq |r| < 0.45$, or low: < 0.20) of genetic correlations between clean fleece weight (CFW) and: live weight at weaning (W_LW) and yearling live weight (Y_LW) for Merino sheep.

Genetic correlations between clean fleece weight and fat thickness and number of lambs weaned per ewe joined for Merino and crossbred breeds

Genetic correlations between CFW at different ages and yearling fat depth (FAT) are illustrated in Figure 2.6. The genetic relationships between CFW and FAT are mostly not significant (Figure 2.6). Considerable variation between genetic correlations between studies could be explained by the breed used (Dominik and Swan, 2018). For example, the mean FD for sheep utilized in these studies varied substantially (17.1 to 22.7 µm). Additionally, genetic correlations between CFW and FAT reported by Safari et al. (2005) included wool-, dual-purpose and meat-breeds, which also could have led to the differences in correlations. Genetic correlations reported by Lee et al. (2002) were imprecise (standard error of 0.81) due to the relatively low number of records (approximately 900 young sheep).

Genetic correlations between FAT and production traits may change across environments (Pollott and Greeff, 2004). Therefore, some of the variation in correlations may be explained by different selection programs in the flocks (Greeff et al., 2008). Further research is warranted before firm conclusions can be drawn for Merino regarding the relationship between CFW and FAT.

Genetic correlations between CFW and NLWEJ are presented in Figure 2.6. Negative genetic correlations between CFW and NLWEJ have been reported indicating that selection for increased CFW may reduce ewe reproductive performance. The lowest genetic correlation between CFW and NLWEJ (-0.08, Ingham and Ponzoni, 2002, Figure 2.6) was estimated from approximately 1170 ewes (25.5 µm on average) and had a large standard error (0.25). The highest negative genetic correlation between CFW and NLWEJ (-0.65) were reported for superfine Merino sheep (16.7 µm on average) (Figure 2.6; Dominik and Swan, 2018). This latter study also reported a moderate negative genetic correlation between CFW and the number of foetuses at pregnancy scanning (-0.43). Ignoring these correlations, while selecting for increased CFW will potentially result in the deterioration of reproduction rate.

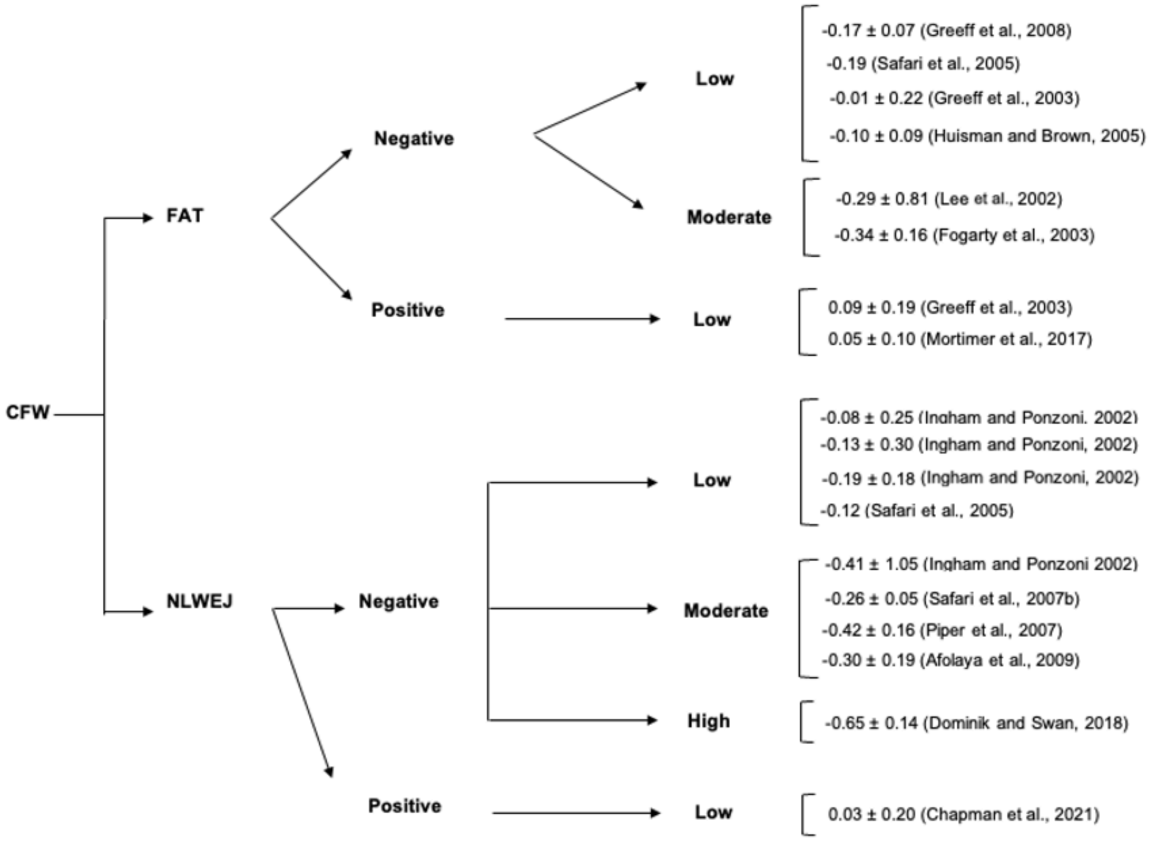

Figure 2.6 Sign (positive or negative) and magnitude (high: ≥ 0.45, moderate: 0.2 ≥ $|r|$ < 0.45, or low: < 0.20) of genetic correlations between clean fleece weight (CFW) and: fat depth (FAT) and number of lambs weaned per ewe joined (NLWEJ) for Merino sheep and crossbred breeds.

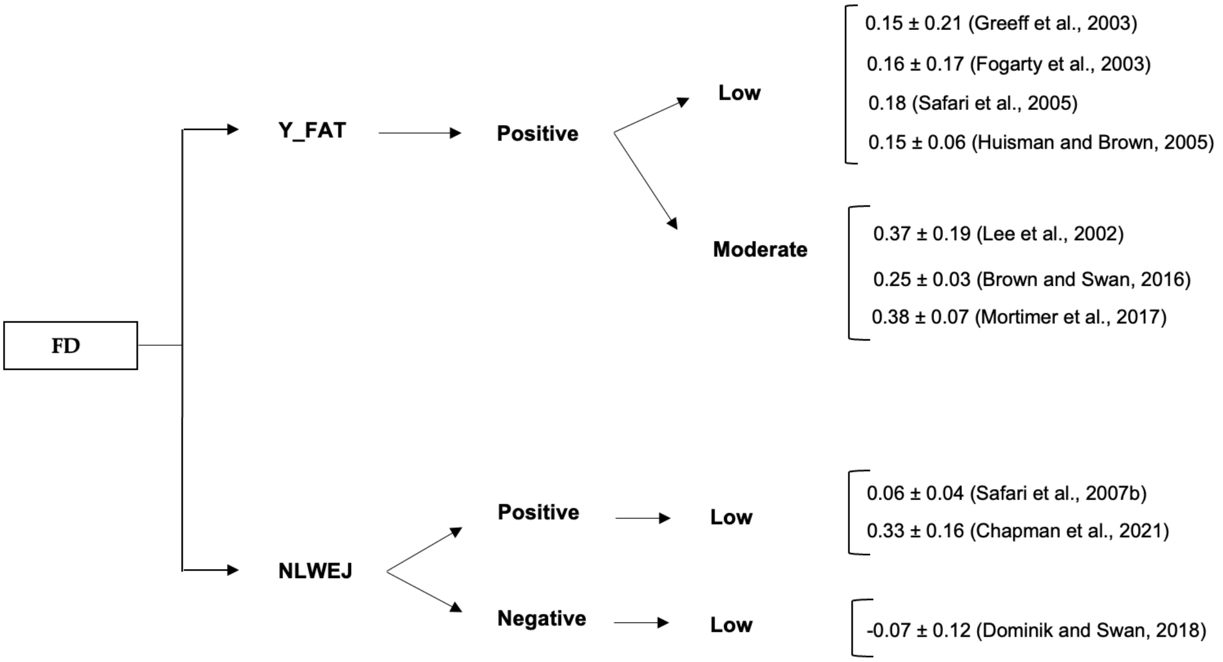

Figure 2.7 Sign (positive or negative) and magnitude (high: ≥ 0.45, moderate: $0.2 \geq |r| < 0.45$, or low: < 0.20) of genetic correlations between fibre diameter (FD) and: fat depth (FAT) and number of lambs weaned per ewe joined (NLWEJ) for Merino sheep and crossbred breeds.

Genetic correlations between fibre diameter *and* fat thickness*, and* number of lambs weaned per ewe joined *for Merino and crossbred breeds*

Genetic correlations between FD and FAT, and NLWEJ are presented in Figure 2.7. Low to moderate positive genetic correlations between FD and FAT have been reported, indicating that selection for decreased FD may reduce FAT (Figure 2.7). However, some of the reported correlations had large standard errors, resulting in either non-significant associations (Fogarty et al., 2003) or imprecise genetic estimations (Lee et al., 2002). Moderate unfavourable genetic associations between FD and FAT (0.25 and 0.38) have been reported for superfine Merino sheep (17.5 and 16.9 µm on average, Figure 2.7; Brown and Swan, 2016; Mortimer et al., 2017). These findings suggest that selection for reduced FD in fine-wool Merinos may be at the cost of FAT (reduced body reserves).

Genetic relationships between FD and NLWEJ were not different from zero, indicating that selection for reduced FD will not necessarily affect ewe reproductive performance. On the other hand, a moderate unfavorable genetic correlation between adult FD and NLWEJ has been observed by Chapman et al. (2021). Phenotypically, no relationships between FD and NLWEJ were observed by Dominik and Swan (2018).

Together, this section indicates that selection for increased CFW will negatively impact on FAT and likely NLWEJ. Selection for reduced FD will not adversary impact ewe reproductive performance. Selection for decreased FD will negatively impact on body fat levels. This information suggests that placing too much emphasis on major wool traits, whilst neglecting other relevant traits, may result in undesirable consequences on overall animal performance. However, simultaneous improvements in wool traits, FAT, and NLWEJ would occur using appropriately designed selection indices (Brown and Swan, 2016).

Genome-wide association studies

The identification of genes or genomic regions associated with economically relevant traits would become an important tool for genetic improvement of Merino sheep. Genome-wide association studies (GWAS) are utilized to identify genes that are associated with phenotypic traits, using single nucleotide polymorphisms (SNPs) as genetic markers. A SNP is a single base change in a DNA sequence, with a usual alternation of two possible nucleotides at a given position (Vignal et al., 2002). A number of statistical models, including Bayesian regression approach, have been used to simultaneously fit thousands of SNPs to determine the proportion of genetic variance explained by the markers (Fernando and Garrick, 2013). Bayesian regression analyses have been implemented in the JWAS package (Cheng et al., 2018). The software tool JWAS is an open-source package for single-trait and multiple-trait genome-enabled prediction and analysis. JWAS is a single-language software that is easy for community members to use. The documentation and examples of JWAS can be found at https://reworkhow.github.io/JWAS.jl/latest/theory/theory accessed on 1 July 2022.

There are currently many GWAS for economically relevant traits in the Australian, Chinese, and New Zealand sheep populations (Wang et al., 2014; Hess et al., 2019; Zhao et al., 2021a and 2021b; Bolormaa et al., 2021). However, there have been no GWAS for production and reproduction traits in Uruguayan Merino sheep.

Summary of literature review

Many studies have reported genetic parameters for wool, growth, and reproduction traits in Australian and New Zealand fine-wool Merinos. Overall, the information suggests that selection for reduced FD will not impact on ewe reproductive performance. However, placing too much emphasis on CFW may result in undesirable consequences on ewe reproductive performance. To date, there is no information on genetic parameters involving reproduction and other production traits in Uruguayan Merino sheep. Also, there is no research on the genomic regions associated with production and reproduction traits in Uruguayan Merino sheep

Chapter III

Phenotypic responses to selection for ultrafine wool in Uruguayan yearling lambs

This chapter has been published as:

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Abstract

This study evaluated the phenotypic trends for wool and growth traits of the fine Merino genetic nucleus flock in Uruguay. Data were collected from one-year-old lambs over a twenty-year period (1999–2018). The overall aim of the selection flock was to reduce fibre diameter with concomitant increases in fleece and live weights. Traits analysed included fibre diameter (FD), greasy fleece weight (GFW), coefficient of variation of FD (CVfd), staple length (SL), scoured yield (SY), live weight post-shearing (LW), eye muscle area (EMA) and fat thickness (FAT). Data from approximately 5,300 one-year-old male and female lambs were analysed. During the study period, FD decreased by approximately 3 µm, whereas GFW and LW increased by at least 0.5 and 3.0 kg, respectively. There were interactions between the sex of the individual and the year for all wool traits. Except for FAT, all other traits were affected by the dam age. This study indicates that the selection program applied in the fine Merino genetic nucleus over a twenty-year period resulted in reductions in FD and increases in GFW and LW. Therefore, the results indicate it is possible to produce ultrafine wool in semi-extensive grazing systems without compromising other economically relevant wool traits in one-year-old lambs.

Keywords: sheep; ultrafine; selection; wool; live weight

Introduction

During the early 1990s, the Uruguayan sheep industry was focused on wool production, with less emphasis on lamb meat production (Cardellino et al., 1994). At this time, revenue from wool accounted for approximately 70% of total sheep farmer income (Cardellino et al., 1994). The Corriedale breed represented 70.5% of the national flock, followed by Polwarth (11.6%), Australian Merino (8.4%), Merilin (3.2%), Romney (1.0%) and crossbreeds (5.3%) (Cardellino et al., 1994). Due to the national sheep breed composition, mid-micron wool (25.0–30.0 μm) was the most abundant wool type (approximately 70%) (Cardellino et al., 1994). Lambing occurred predominantly over the winter–early spring (July–September) period, with lamb marking percentage ((number of lambs at approximately one-month of age/number of ewes joined) × 100)) ranging between 65% and 85% (Cardellino and Salgado, 1990). During the early 1990s, the wool price was the main factor influencing sheep farmer decision-making (Cardellino et al., 1994).

In parallel, the world textile industry faced changing consumer preference trends (Champion, and Fearne, 2001; Trewin, 2002). The demand for mid-micron wool (25.0–30.0 μm) declined significantly to the point where its production became uneconomical (Cardellino and Salgado, 1990; Banks and Brown, 2009; Australian Wool Innovation Ltd. 2018). Since the early 1990s, the Australian Merino wool industry has undergone significant changes, resulting in an increase in finer wool production (18.6 to 19.5 μm) at the expense of medium diameter (19.6 to 22.5 μm) Merino wool (Pattinson et al., 2015). This was driven primarily by wool value on a per kg basis, with superfine (15.6–18.5 μm) wool obtaining the highest value (Pattinson et al., 2015, MLA, 2004, Nolan et al., 2013). Uruguayan wool prices were dependent on international market trends, especially those registered in Australia (Cardellino et al., 2018), and therefore changes were needed.

During the late 1990s, the mean fibre diameter of Uruguayan Merino wool was approximately 22 μm, with insignificant amounts of fine and superfine wool (Montossi et al., 2007). To differentiate and add value to Uruguayan Merino wools, by producing finer, more valuable wool, in 1998, the

Uruguayan Wool Secretariat (SUL), Association of the Uruguayan Merino Breeders of Uruguay (SCMAU), National Institute for Agriculture Research (INIA) and 36 Merino sheep farmers developed the fine Merino Project (FMP, 1999–2010) (Montossi et al., 2005). One of the objectives of the FMP was to develop a fine Merino genetic nucleus, located at Glencoe Experimental Unit of INIA Tacuarembó Research Station, specialized in producing fine wool (less than 19.5 µm), generating genetically superior rams to be distributed to commercial farms throughout Uruguay. At the end of the FMP in 2010, the market price trends favored the ultrafine wool type (15.5 µm or finer) (Nolan et al., 2013). In response to those wool price trends and market scenarios, the fine Merino genetic nucleus continued as part of a new project entitled Uruguayan Regional Consortium for Innovation in Ultrafine Wool (CRILU, 2011–2021) (Montossi et al., 2014). This consortium has been run by an increased number of farmers (42), INIA, and wool top makers of Uruguay.

The overall breeding objective of the FMP project (1999–2010) was to reduce fibre diameter while allowing for only a slight loss in fleece weight. During the CRILU phase (2011–2018), the selection objective was to continue to reduce fibre diameter (to produce 15.5 µm or finer wool) while improving both fleece weight and animal live weight. This chapter aims to evaluate the phenotypic trends observed over the period 1999 to 2018 in economically relevant fleece and growth traits of the fine Merino genetic nucleus offspring to one-year-old of age.

Materials and Methods

Background, period, and location

The foundation fine Merino genetic nucleus was established at the Glencoe Experimental Unit of National Institute for Agriculture Research of Uruguay (INIA) (32◦00′21″ S and 57◦08′06″ W) in 1999. In this region, the average annual rainfall ranges between 1,000 to 1,300 mm, with high variability between years (Berretta, 1998). Annual pasture production fluctuates between 2,885 and 4,580 kg of dry matter (DM)/ha, being the highest production in summer and spring, while winter production accounts for only 15% of the total DM production (Berretta et al., 2000).

This study combined data from two research projects carried out in the fine Merino genetic nucleus between 1999 to 2018. To evaluate the information corresponding to each project, the entire study period was classified into three phases: Establishment (1999–2001), FMP (2002–2010), and CRILU (2011–2018). In this study, we analysed the information from one-year-old lambs only.

Selection of original fine Merino genetic nucleus' animals

The selection of the original ewes occurred in two stages. In the winter of 1998 (first phase), approximately 742 ewes were preselected from 5171 ewes (18 to 30 months of age) provided by 36 Merino stud breeders and/or commercial farmers. Subjective criteria, including conformation traits (i.e., leg, feet, shoulder, back, jaw, size and face cover) and wool quality traits (i.e., fleece rot, wool color and character, staple structure, black wool and skin spots, fibre pigmentation and non-fibre pigmentation) were utilized for preselection of the fine Merino genetic nucleus (Australian Wool Innovation Ltd, 2013, SUL, 2018). In the spring shearing of 1998 (second phase), a wool sample was obtained from the preselected ewes (742) and tested by a wool testing laboratory (Uruguayan Wool Secretariat, Montevideo, Uruguay) for fibre diameter (FD). Additionally, greasy fleece weight (GFW) and live weight (LW) were recorded. These three objective criteria (FD, GFW and LW) were used to select 475 ewes, which then finally formed the fine Merino genetic nucleus (Montossi et al., 2007).

To source rams for the formation of the fine Merino genetic nucleus, approximately 40 Merino stud breeders across Australia and New Zealand were visited. Rams were preselected according to visual inspection in situ, their genetic merit for most relevant economic production traits (FD, clean fleece weight and LW), the genetic trends of stud flocks and the technical advice undertaken by the Australian genetic evaluation staff. Later, frozen semen from the selected rams were imported into Uruguay and utilized (Table 3.1). Uruguayan rams were also utilized to connect the fine Merino genetic nucleus with the Merino Progeny Testing Centers of Uruguay (Table 3.1).

Table 3.1 Total annual number of ewes, percentage of ewe replacement by ewe hoggets and number of sires utilized in the fine Merino genetic nucleus over the entire study period (1999–2018).

Phase	**Year**	**N° of ewes**[1]	**Replacement ewes hoggets (%)**[2]	**N° of sires**[3]		
				Imp.[4]	**Nucleus**[5]	**Nat.**[6]
Establishment	1999	456	-	6	-	3
	2000	434	-	6	-	2
	2001	488	28	6	2	-
FMP	2002	484	18	8	5	-
	2003	465	20	8	5	-
	2004	460	18	4	6	-
	2005	478	25	3	6	-
	2006	394	31	6	7	-
	2007	392	31	2	7	-
	2008	362	35	3	7	-
	2009	409	29	3	5	-
	2010	477	27	1	6	-
CRILU	2011	403	21	1	6	-
	2012	398	27	1	6	-
	2013	382	29	2	6	-
	2014	327	27	2	9	-
	2015	358	25	4	5	-
	2016	349	17	-	6	-
	2017	319	20	2	8	-
	2018	369	33	3	9	-

[1] N° of ewes: total ewes of the nucleus (including ewe hoggets and ewes), [2] Replacement ewe hoggets selected (%) = the number of ewe hoggets at 18 months of age/total ewes in the nucleus flock × 100. [3] N° of sires: total sires of the nucleus per year. Total sires of the nucleus = 78 rams (some sires were used for more than one year), [4] Imp: number of rams utilized as imported semen. [5] Nucleus: number of rams utilized and born within the nucleus. [6] Nat: number of rams utilized from local Merino stud breeders.

Fine Merino genetic nucleus: genetic selection

At approximately one year of age, male and female offspring born in the fine Merino genetic nucleus were evaluated to determine if they would be subsequently selected as replacement animals. The animal selection process included phenotypic and genetic criteria. First, prior to shearing (early September, at approximately 11 months of age), all lambs were phenotypically evaluated and classified in one of the three global scores (1–3) based on the animal's conformation and wool traits as previously reported (Australian Wool Innovation Ltd. 2013). The scores 1 and 3 corresponded to the top individuals and cull animals, respectively, while a score of 2 was a phenotypically acceptable animal to use in commercial flocks.

Since 1995, estimated breeding values (EBVs) for several productive traits for Merino sheep have been generated by the Uruguayan national genetic evaluation scheme (Ciappesoni et al., 2013) and were utilized to calculate EBVs for the fine Merino genetic nucleus. Additionally, at the beginning of the FMP, the EBVs for CFW and FD were combined to generate two selection indices for the Uruguayan Merino genetic evaluation. Index II emphasized FD-reduction while allowing for a slight loss in CFW, which in turn was applied as selection criteria across the establishment and FMP periods (1999–2010). In response to new wool and meat price scenarios, in 2011, the EBVs for FD, CFW and LW were combined into three new selection indices (fine wool, wool and dual-purpose alternative options), representing different breeding objectives (Ciappesoni, 2014). The fine wool index aimed to decrease FD and increase both CFW and LW (Ciappesoni et al., 2012) and was utilized as the selection criteria during the CRILU development phase (2011–2018). At this period, there was increased priority in sheep host resistance to gastrointestinal nematodes thus, EBVs for fecal worm egg count were utilized as a complementary selection criterion.

In addition to phenotypic and genetic criteria, potential male and female animal replacements were clinically examined to detect anatomic anomalies that could potentially compromise reproductive performance (e.g., teeth, mouth, foot and reproductive organs). In males, bloodlines of their parents were also considered to help avoid inbreeding. This selection tool became more relevant as more parents from the nucleus were utilized for breeding. Each year approximately three phenotypically acceptable rams (phenotypic global score 1 or 2), with the highest genetic merit (based on high index II or fine wool index), were selected to be utilized as rams in the fine Merino genetic nucleus. The culling decisions on the ewes was based on health-related traits (e.g., foot diseases, udder injuries), mouth and teeth.

During the establishment phase (1999–2001), ewes were inseminated mostly with imported frozen semen (Table 3.1), using six Australian rams each year. In 2001, two nucleus- born rams were utilized as sires. As more rams from the nucleus became available, the use of imported semen was gradually reduced and substituted by nucleus-born rams. During the CRILU phase (2011–2018), most of the rams utilized were born in the fine Merino genetic nucleus. From 2001 to 2018, the percentage of ewe hoggets selected ((number of ewe hoggets at 18 months of age/total ewes of the nucleus) × 100) each year as female replacements ranged between 18 and 35% of the nucleus. In addition, from 2004 to 2014, superovulation reproductive treatments were applied on a maximum of 14 ewes per year.

Fine Merino genetic nucleus: nutrition and animal management

Ewe nutrition was based on native pastures with restricted access to improved pastures (a mix of white clover, annual ryegrass or oats and lotus corniculatus) or supplementation (sorghum, soybean, corn, commercial rations, among others) during the highest dam nutrition requirement phases, such as the last third of gestation and in early lactation. Lambing occurred in spring, predominantly over the September and October period. Ewes in late pregnancy were monitored 24 h a day by qualified field staff (which rotated at eight-hour intervals). Lambing was outdoors on improved pastures. After the mother–lamb(s) bond was established, lambs and their dams were placed indoors into individual pens with ad libitum access to water and lucerne hay (Ramos and Montossi, 2014). Lambs and ewes remained in the indoor pens for a period of 12 to 24 h, depending on environmental conditions, their health status and the mother–lamb(s) bond. When environmental conditions were suitable, both the ewes and their lambs were moved back outdoors into improved pastures with other ewes lambed.

New-born lambs were ear-tagged with an identification number and weighed within 12 h of birth. Additional information collected included: dam identification, lamb status (anomalies or dead), sex of the lamb and birth rank (single, twin or triplet). At approximately one month of age, lambs were marked (notch in the ear with the owner mark), tattooed (print of the individual identification number on the inside of the ear), weighed and immunized with the first Clostridium vaccine dose (Sintoxan® 9TH or Ultravac®, Merial, Montevideo, Uruguay), receiving a second Clostridium vaccine dose approximately 30 days later. Additionally, at approximately one month of age, the tail of each lamb was removed using mostly the hot knife and rubber ring methods according to the procedure described by others (Sheep Standards and Guidelines Writing Group, 2013). In 2018, at approximately 48 h post-birth, the tail was docked using rubber rings.

Weaning occurred at approximately 3.5 months of age (during the December–February period). During summer, when improved pasture availability and quality were limited, lambs grazing native pasture had access to supplementation (at a rate of 1 to 1.5% LW) using a commercial grain-based ration, which was approximately 18–21% crude protein. During autumn, winter and spring, male lambs were managed mostly on improved pastures (a mix of white clover, annual ryegrass or oats and lotus corniculatus) plus supplement (rice bran, soybean, corn and commercial rations) as required. Replacement female lambs were managed with the main target of achieving a LW at first mating (at approximately 18 months of age) greater than 80% of mature LW (SUL, 2018). Their nutrition was mostly based on native pasture with the complementary use of a supplement, if necessary.

Internal parasite control was done by oral drench with an effective anthelmintic complemented by different prevention strategies (safe pastures, rotative grazing, grazing with beef cattle). All lambs were drenched orally at weaning (December–February). Subsequently, fecal samples of ten random lambs were collected monthly for gastrointestinal nematode egg count. Whenever the average number of eggs was greater than 800 per gram of feces, all animals were drenched. All lambs were reimmunized with a clostridial vaccine (Sintoxan® 9TH or Ultravac®, Merial, Montevideo, Uruguay) every six months, and annually treated for external parasites (Mixan®, La Buena Estrella or Elimix®, Nutritec, Montevideo, Uruguay).

Measurements

Data were collected on one-year-old lambs over a twenty-year period (1999–2018). Prior to shearing (early September) at approximately 12 months of age, a patch of approximately 10 × 10 cm was clipped on the mid-flank position of each lamb (Langlands and Wheeler, 1968). Clipped wool was individually bagged, identified and weighed. All samples were sent to a wool testing laboratory (Uruguayan Wool Secretariat, Montevideo, Uruguay), where FD, SL and scoured yield (SY) were assessed (Table 3.2). SL and SY were estimated utilizing the methods described by others (Ramos et al., 2019). FD was measured following norms IWTO 52 (IWTO, 2006) and 12 (IWTO, 2012b). Shearing occurred in spring, predominantly over the September and October period using the Tally-Hi method and green label protocol (Abella et al., 2010). At shearing, the GFW of each lamb was recorded, and approximately within one-week post-shearing, all lambs were weighed (LW). From 2010, at approximately 13 months of age (October), eye muscle area (EMA) and fat thickness (FAT) of each lamb were measured at the Longissimus thoracis et lumborum muscle by ultrasound technique as previously described by Ramos et al., 2019. The wool and growth traits analysed in the present study are summarized in Table 3.2.

Table 3.2 Age of the animal, time of the measurements and data recorded in one-year-old female and male lambs (1999–2018).

Traits	**Age (months)**	**Time**
Wool traits		
Fibre diameter (FD, μm)	12	Shearing (Sept–Oct)
Greasy fleece weight (GFW, kg)		
Coefficient of variation of FD (CVfd, %)		
Staple length (SL, cm)		
Scoured yield (SY, %)		
Growth traits		
Live weight (LW, kg)	13	Post-shearing (Sept–Oct)
Eye muscle area (EMA, cm^2)		
Fat thickness (FAT, mm)		

Statistical analysis

Data were analysed utilizing a general linear model (Proc GLM) in SAS (version 9.4, SAS Institute Inc., Cary, NC, USA). Outliers were detected using a robust regression model (PROC ROBUSTREG) for each trait. This procedure computes a robust version of the Mahalanobis distance by using a generalized minimum covariance determinant method. The model for one-year-old lamb wool traits included “birth year”, “sex”, “birth-rearing rank” (born as single and weaned as single -S/S- or born as multiple and either weaned as single -M/S- or multiple -M/M-), and “dam age” (2-year-old, 3 to 6 years old and aged 7 or older) as fixed effects and “age at shearing” (298 to 432 days of age) as a covariate. Two-way interactions between sex of the lamb and year and birth-rearing rank and sex of the lamb were also included in the model even if they were not significant ($p > 0.05$).

The model for one-year-old lamb live weight post-shearing was as described for wool traits but replacing “age at shearing” with “age at LW” (321 to 438 days of age). This model was then repeated, adding the sex of the individual nested within year. EMA and FAT data were recorded in 2010, 2011 and from 2013 to 2018. The model for ultrasound measurements was as described for live weight but replacing “age at LW” with “age at ultrasound measurements” (355 to 435 days of age). Live weight at the ultrasound measurements time was also tested as a covariate. Means were compared using the Tukey–Kramer test, which was considered significantly different when $p < 0.05$. Non-significant interactions are not shown in the results section.

FD, GFW and LW post-shearing (321 to 438 days of age) trends were evaluated utilizing an orthogonal polynomial regressions model (Proc ORTHOREG) in SAS (version 9.4, SAS Institute Inc., Cary, NC). The order of the polynomial regression utilized was based on the coefficient of determination value (R^2) (results not shown). The regression model for FD, GFW and LW included the same fixed effects described above. For FD, a second–degree polynomial regression model was applied in “birth year” whereas all other effects were treated as first-degree terms. For GFW and LW post-shearing (321 to 438 days), a third-degree polynomial was applied in “birth year”. The polynomial regressions model was performed for all progeny (i.e., males and females together) and for each sex separately, and a 95% confidence interval (CI) calculated.

Results

Summary statistics for wool and growth traits are presented in Table 3.3. Over the period 1999 to 2018, mean FD, GFW and LW ranged between 14.4 to 18.9 µm, 1.9 to 4.2 kg and 40.1 to 53.3 kg, respectively (Table 3.4). The standard deviation values fluctuated between 0.8 to 1.2 µm, 0.3 to 0.9 kg and 6.2 to 13.2 kg for FD, GFW and LW, respectively.

Table 3.3 Descriptive statistics for the combined one-year-old female and male wool and growth traits (1999–2018).

Traits	**Mean**	**Min**[1]	**Max**[2]	**SD**[3]	**CV**	**N**[4]
Wool traits						
Fibre diameter (FD, µm)	15.8	12.4	21.2	1.5	0.09	5,361
Greasy fleece weight (GFW, kg)	3.1	1.2	6.2	0.9	0.29	5,367
Coef. of variation of FD (CVfd, %)	17.6	11.3	24.6	2.2	0.13	5,052
Staple length (SL, cm)	8.4	3.5	14.0	1.8	0.21	5,405
Scoured yield (SY, %)	75.5	61.7	88.7	4.5	0.06	5,390
Growth traits						
Live weight post-shearing (LW, kg)	45.0	18.5	75.5	10.5	0.23	5,402
Eye muscle area (EMA, cm^2)	10.0	3.7	17.2	2.6	0.26	2,042
Fat thickness (FAT, mm)	2.8	1.0	6.0	0.9	0.32	2,019

[1,2,3] Min, Max, SD and CV correspond to minimum, maximum, standard deviation and coefficient of variation values for each trait. [4] N: number of records.

Table 3.4 Annual mean, standard deviation and number of records of fibre diameter, greasy fleece weight at shearing (298 to 432 days of age), and live weight post-shearing (321 to 438 days of age) for the combined one-year-old female and male lambs (1999–2018).

Phase	Year	Fibre diameter (µm)			Greasy fleece weight (kg)			Live weight (kg)		
		Mean	**SD[1]**	**N[2]**	**Mean**	**SD[1]**	**N[2]**	**Mean**	**SD[1]**	**N[2]**
Establishment	1999	17.9	1.2	328	3.1	0.5	327	40.1	6.7	332
	2000	17.4	1.2	242	2.3	0.4	247	40.9	8.4	248
	2001	18.2	1.2	207	2.8	0.6	219	47.3	10.3	219
FMP	2002	18.9	1.1	160	3.4	0.7	178	53.3	10.2	186
	2003	16.6	1.1	334	2.2	0.4	334	48.3	9.5	329
	2004	15.9	1.2	286	1.9	0.3	290	43.1	6.2	292
	2005	16.0	1.2	344	2.6	0.5	345	42.6	7.2	345
	2006	15.4	1.1	309	2.8	0.6	309	41.1	7.8	298
	2007	15.5	1.0	256	3.0	0.5	256	44.0	10.1	254
	2008	15.3	1.1	306	3.2	0.7	300	42.2	7.9	309
	2009	14.4	0.9	269	2.5	0.5	270	40.1	8.2	269
	2010	15.6	1.0	303	3.9	0.7	295	51.0	10.8	304
CRILU	2011	15.1	1.0	364	3.6	0.9	344	46.0	13.2	368
	2012	15.6	1.0	268	4.1	0.8	266	48.8	10.3	268
	2013	14.8	1.0	279	3.2	0.7	281	41.3	11.7	282
	2014	15.0	0.8	151	3.1	0.5	150	43.9	7.7	151
	2015	14.6	0.8	196	3.2	0.6	197	45.2	12.6	196
	2016	15.1	1.0	243	3.7	0.8	246	49.6	12.9	243
	2017	15.3	0.9	231	3.7	0.8	230	46.2	11.6	229
	2018	15.0	0.9	285	4.2	0.7	283	48.4	10.4	280

[1,2] SD and N correspond to standard deviation value and number of records for each trait each year, respectively. FMP = Fine Merino project (1999 - 2010), CRILU = Regional Consortium for Innovation in Ultrafine Wool (2011 - 2018).

Effects of sex of individual on wool and growth traits

There were interactions between the sex of the lamb and the year for all wool traits (p < 0.05, Table 3.5). In 2004, 2005 and 2018, mean FD did not differ ($p > 0.05$) between the sexes, but in 1999 females had coarser fibres than males, whereas, in all other years, males had coarser (0.5 µm extra) fibres than females ($p < 0.05$). In 1999 and 2004, GFW was not affected by the sex of the individual ($p > 0.05$), but in all other years, males produced heavier ($p < 0.05$) fleeces than females. In 1999, 2001, and from 2003 to 2007, and 2010 to 2012 and in 2014, sex of the lamb had no effect ($p > 0.05$) on SL, whereas, in 2017, the females had longer fibres (3% extra, $p < 0.05$) than males, but in all other years, fibres were longer ($p < 0.05$) in males than females. In 2004, 2007, 2008, and from 2010 to 2012, and 2014 to 2017, CVfd was not affected by the sex of the individual ($p > 0.05$), but in 2001 and 2013, females had greater (4 and 3% extra, respectively, $p < 0.05$) CVfd than males, whereas in all other years CVfd was greater ($p < 0.05$) in males. In 2001, 2005, 2007, 2008 and 2016, SY did not differ ($p > 0.05$) between the sexes, whereas in 2006, 2014 and 2018 males had higher (2.0, 2.2 and 3.5% extra, respectively, $p < 0.05$) SY than females, and in all other years, females had higher ($p < 0.05$) SY.

Table 3.5 One-year-old lamb means (±SEM) fibre diameter (FD, µm), greasy fleece weight (GFW, kg), coefficient of variation of fibre diameter (CVfd, %), staple length (SL, cm), scoured yield (SY, %), live weight post-shearing (LW, kg), eye muscle area (EMA, cm^2) and fat thickness (FAT, mm) by sex of the lamb, birth-rearing rank, dam age and the interactions between sex of the lamb and either year or birth-rearing rank (1999–2018).

Traits	**Sex of the lamb**		**SEM**	**Birth-rearing rank**[1]			**SEM**	**Dam age (years)**			**SEM**	**P-value**	
	Male	**Female**		**S/S**	**M/S**	**M/M**		**2**	**3 to 6**	**≥ 7**		**Y/S**[2]	**BRR/S**[3]
Fibre diameter (FD, µm)	16.1^{a}	15.6^{b}	0.05	15.9	15.8	15.9	0.06	15.6^{c}	15.9^{b}	16.1^{a}	0.05	<0.001	0.32
Greasy fleece weight (GFW, kg)	3.3^{a}	2.6^{b}	0.02	3.2^{a}	2.9^{b}	2.8^{c}	0.03	2.9^{b}	3.0^{a}	3.0^{ab}	0.02	<0.001	0.001
Coef. of variation of FD (CVfd, %)	17.8^{a}	17.5^{b}	0.08	17.4^{b}	17.6^{b}	17.9^{a}	0.10	17.5^{b}	17.6^{b}	17.9^{a}	0.09	0.002	0.44
Staple length (SL, cm)	8.5^{a}	8.3^{b}	0.05	8.4	8.5	8.4	0.06	8.7^{a}	8.3^{b}	8.3^{b}	0.06	0.003	0.31
Scoured yield (SY, %)	74.3^{b}	75.8^{a}	0.17	75.5^{a}	75.0^{b}	74.6^{b}	0.20	75.3^{a}	75.4^{a}	74.4^{b}	0.19	0.007	0.13
Live weight post shearing (LW, kg)	52.5^{a}	36.4^{b}	0.22	46.0^{a}	44.5^{b}	43.0^{c}	0.27	43.4^{b}	44.8^{a}	45.3^{a}	0.26	-	<0.001
Eye muscle area (EMA, cm^2)	11.9^{a}	8.1^{b}	0.09	10.1^{a}	10.2^{a}	9.9^{b}	0.10	9.9^{b}	10.0^{b}	10.3^{a}	0.10	-	<0.001
Eye muscle area (EMA, cm^2)^{LW}	10.7^{a}	9.6^{b}	0.13	10.0^{b}	10.1^{b}	10.2^{a}	0.10	10.1^{ab}	10.1^{b}	10.3^{a}	0.09	<0.001	0.06
Fat thickness (FAT, mm)	3.2^{a}	2.2^{b}	0.05	2.8^{a}	2.7^{b}	2.7^{b}	0.05	2.6	2.7	2.7	0.05	<0.001	<0.001
Fat thickness (FAT, mm)^{LW}	2.7	2.8	0.07	2.7	2.7	2.8	0.05	2.7	2.7	2.8	0.05	<0.001	0.21

[1] S/S, M/S and M/M correspond to single-born lambs weaned as single, multiple-born lambs weaned as single and multiple-born lambs weaned as multiple, respectively. [2] Y/S: interaction ($p < 0.05$) between year and sex of the individual, [3] BRR/S: interaction ($p < 0.05$) between birth-rearing rank and sex of the individual, ^{LW}: indicates that live weight was included as a covariate in the model. Different letters within a row (a, b, c) within category indicate statistical significance ($p < 0.05$). SEM = standard error of the mean.

Within each year, lamb LW post-shearing (321 to 438 days of age), EMA and FAT were affected by the sex of the individual ($p < 0.05$, Table 3.5). Males had greater ($p < 0.05$) LW post-shearing, EMA and FAT than females. Ultrasound measurements were affected ($p < 0.05$) by LW at the measurements time, with interactions ($p < 0.05$) between the sex of the individual and year for both EMA and FAT. In 2010 and 2014, EMA did not differ ($p > 0.05$) between the sexes, but in all other years, males had greater EMA (5 to 23% extra, $p < 0.05$) than females. In 2010, 2014, 2016 and 2017 FAT did not differ ($p > 0.05$) between the sexes, but in 2015 females had greater (12% extra, $p < 0.05$) FAT than males, whereas in all other years, males had greater (10 to 15% extra, $p < 0.05$) FAT than females.

Effects of birth-rearing rank on wool and growth traits

One-year-old lamb FD was not affected by birth-rearing rank ($p > 0.05$, Table 3.5). There were interactions ($p < 0.05$) between birth-rearing rank and sex of the individual for GFW. Multiple-born males weaned as single had greater (17% extra, $p < 0.05$) GFW than single- born females. Within multiple-born lambs, males weaned as a multiple produced a greater (19% extra, $p < 0.05$) GFW than females weaned as single.

CVfd and SY were affected by birth-rearing rank ($p < 0.05$, Table 3.5). Multiple-born lambs weaned as multiple had the greatest ($p < 0.05$) CVfd, with no differences ($p > 0.05$) between single-born and multiple-born lambs weaned as single. Single-born lambs had 0.6% and 1.2% greater ($p < 0.05$) SY than multiple-born lambs weaned as single and multiple-born lambs weaned as multiple, respectively. Within multiple-born lambs, SY was not affected ($p > 0.05$) by birth-rearing rank. Staple length was unaffected ($p > 0.05$) by birth-rearing rank.

There were interactions between birth-rearing rank and sex of the individual ($p < 0.05$) for lamb LW post-shearing (321–438 days of age). Multiple-born males weaned as a single had greater (42% extra, $p < 0.05$) LW post-shearing than single-born females. Multiple-born males weaned as a multiple had greater ($p < 0.05$) LW post-shearing than multiple-born females weaned as a single (39%

extra) or multiple (45% extra). Additionally, for female LW post-shearing, there was no difference ($p > 0.05$) between single-born and those born as multiple and weaned as a single.

There was an interaction ($p < 0.05$) between the sex of the individual and birth-rearing rank for EMA. Multiple-born females weaned as single had greater (0.4 cm^2 extra, $p < 0.05$) EMA than single-born females, with no differences between single-born females and those weaned as multiple (8.1 ± 0.05 vs. 7.9 ± 0.08 cm^2 for S/S and M/M females, respectively). Within multiple-born males, EMA was not affected ($p > 0.05$) by birth-rearing rank. When live weight at the time of measurements was included in the model, multiple-born lambs weaned as multiple had the greatest ($p < 0.05$, Table 3.5) EMA, with no differences ($p > 0.05$) between single-born and multiple-born lambs weaned as single. There was an interaction ($p < 0.05$) between the sex of the lamb and birth-rearing rank for FAT. Multiple-born males either weaned as single or multiple had greater (0.7 and 0.9 mm extra, respectively, $p < 0.05$) FAT than single-born females. When live weight at the time of measurements was included in the model, FAT was unaffected ($p > 0.05$) by birth-rearing rank.

Effects of age of dam on wool and growth traits

One-year-old lamb wool traits were affected by dam age ($p < 0.05$, Table 3.5). Lambs born from 2-year-old ewes had the finest ($p < 0.05$), and those born from ewes aged 7 or older the coarsest ($p < 0.05$) fibres. Lambs born from 2-year-old ewes had lighter ($p < 0.05$) fleeces than those from 3 to 6 year-old-ewes. SL was longer ($p < 0.05$) for lambs born from 2-year-old ewes compared with those from all adult ewe groups (≥3 years old). Lambs born from ewes aged 7 and older had lower ($p < 0.05$) SY and higher ($p < 0.05$) CVfd compared to the other two age groups.

Lamb LW post-shearing (321 to 438 days of age) was affected by dam age ($p < 0.05$, Table 3.5). Lambs born from 2-year-old ewes had lighter ($p < 0.05$) LW than those from all adult ewe groups (≥3 years old). EMA was affected ($p < 0.05$) by dam age. Lambs born from ewes aged 7 or older had greater ($p < 0.05$) EMA compared to the other two age groups. When LW at the measurement time was included in the model, lamb born from ewes aged 7 or older had greater EMA than those from 3 to 6 year-old-ewes. FAT was unaffected ($p > 0.05$) by dam age.

Wool and growth traits trends

Over the entire study period (1999–2018), for combined male and female data, 49% (R^2) of the phenotypic changes in one-year-old lamb FD were explained by the second degree polynomial regression model. The coefficient of determination for FD was greater in females ($R^2 = 0.57$) than males ($R^2 = 0.39$). During the establishment and FMP phases (1999–2010), FD decreased approximately 3 µm, whereas, in the CRILU period (2011–2018), this trait changed little (Figure 3.1).

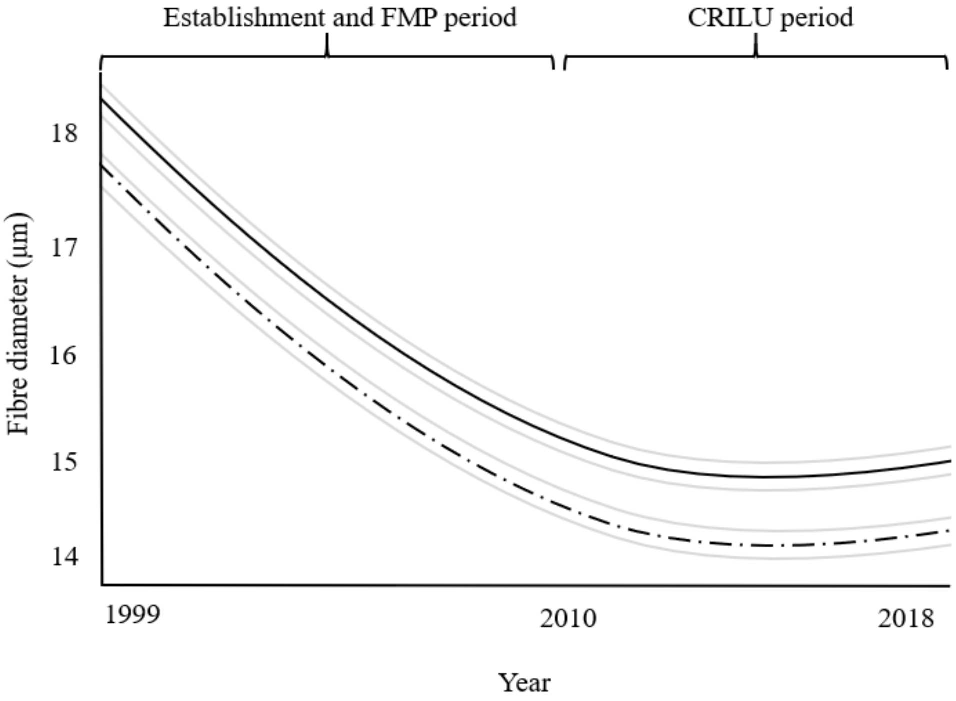

Figure 3.1 Male (solid line) and female (non-solid line) phenotype trends using a second-degree polynomial regression model for fibre diameter at shearing (298 to 432 days of age) across the entire study period (1999–2018). The light gray lines represent the 95% confidence limits. R^2 for the combined (male and female), and individual male and female models were 0.49, 0.39 and 0.57, respectively.

The third-degree polynomial regression model for the combined male and female data explained 61% (R^2) of the phenotypic changes in one-year-old lamb GFW. The coefficient of determination (R^2) for males and females were 0.55 and 0.54, respectively. Male and female GFW was higher at the end of the study period compared to the establishment phase (1999–2001, Figure 3.2).

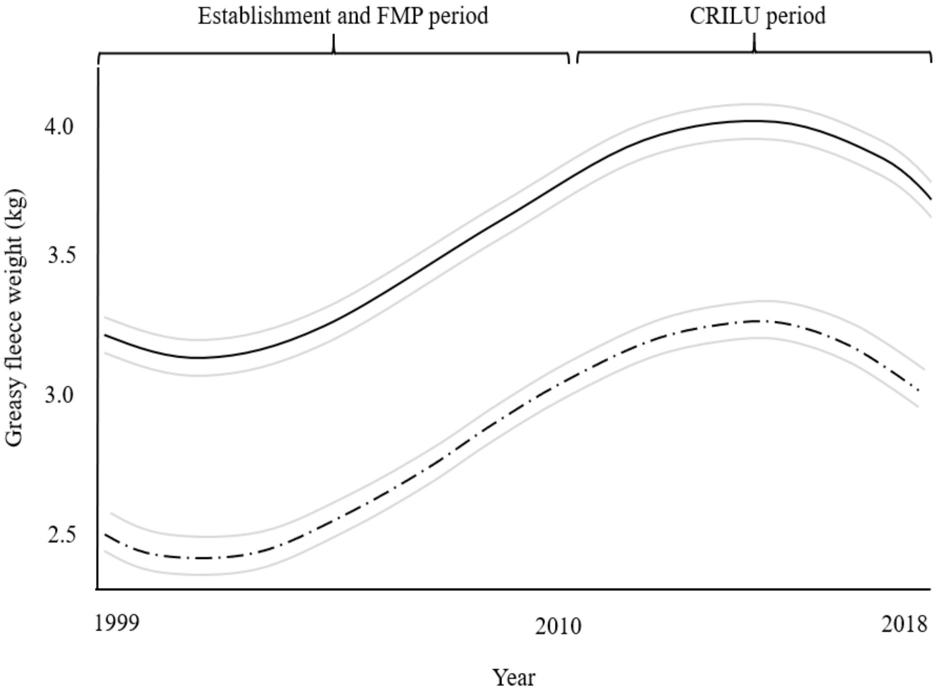

Figure 3.2 Male (solid line) and female (non-solid line) phenotype trends using a third-degree polynomial regression model for greasy fleece weight at shearing (298 to 432 days of age) across the entire study period (1999–2018). The light gray lines represent the 95% confidence limits. R^2 for the combined (male and female), male and female models were 0.61, 0.55 and 0.54, respectively.

Across the entire study period, for the combined male and female data, 69% (R^2) of the phenotypic changes in one-year-old lamb LW post-shearing was explained by the third-degree polynomial regression model. The R^2 for males and females was 0.23 and 0.25, respectively. In both sexes, LW post-shearing at the end of the study period (2018) was heavier than the starting year (1999, Figure 3.3).

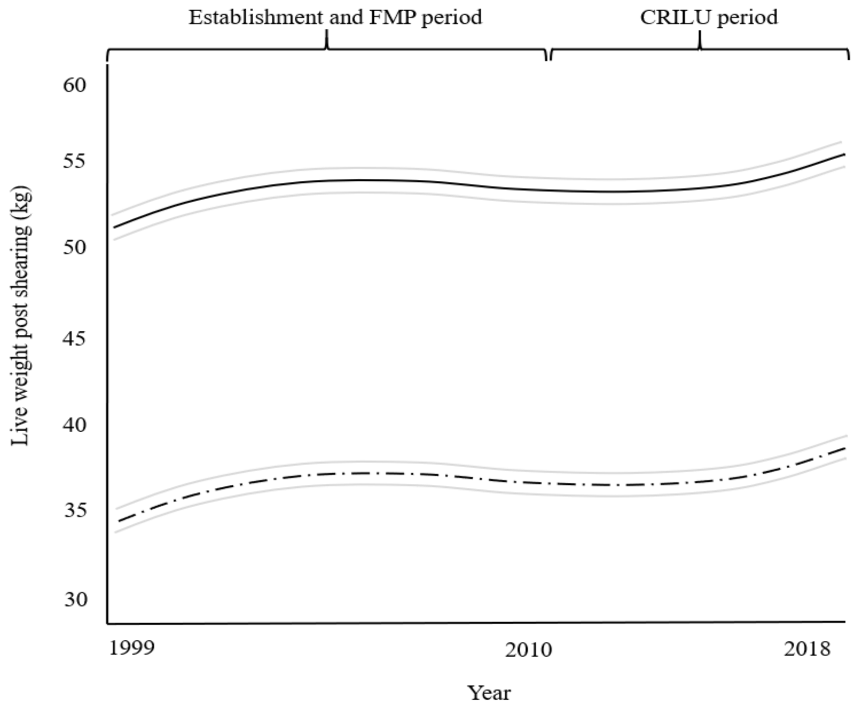

Figure 3.3 Male (solid line) and female (non-solid line) phenotype trends using a third-degree polynomial regression model for live weight post-shearing (321 to 438 days) across the entire study period (1999–2018). The light gray lines represent the 95% confidence limits. R^2 for the combined (male and female), male and female models were 0.69, 0.23 and 0.25, respectively.

Discussion

The current study combined data over the period 1999 to 2018 for the fine Merino genetic nucleus in Uruguay. The entire study period (1999–2018) was classified into three phases: Establishment (1999–2001), FMP (2002–2010), and CRILU (2011–2018). During the Establishment and FMP periods (1999–2010), the breeding objective was to reduce fibre diameter while allowing for only a slight loss in fleece weight. During the CRILU phase (2011–2018), the selection objective was to continue to reduce fibre diameter (to produce 15.5 µm or finer wool) while improving both fleece weight and live weight. Overall, the objectives of the FMP and CRILU were successful.

During the Establishment and FMP periods (1999–2010), one-year-old female and male FD decreased by approximately 3 µm, from 18 to 15 µm, which is consistent with previously reported reductions in FD in other Merino selection flocks (Swan and Purvis, 2005; Greeff and Cox, 2006;

Taylor, et al., 2007b). This phenotypic progress in FD can be partially explained by the application of the selection index (Taylor, et al., 2007b; Safari et al., 2006), the high heritability (0.73) of FD (Ciappesoni et al., 2013) and the inclusion of overseas genetic material. In Uruguay, reducing FD from 21 to 17 µm could increase sheep farmer income by approximately 70% (Buffa et al., 2017) Combined, these data indicate selection for reduced FD should increase farmer income in less than 10 years.

Improvement in animal economic worth generally requires selection for several traits simultaneously (Hazel et al., 1994; Safari et al., 2005). During the CRILU phase (2011–2018), the selection index utilized combined EBVs for FD, CFW and LW. In this period, one-year-old female and male phenotypic FD remained below 16 µm, with little apparent change in FD occurring over time. This outcome is likely due to the unfavorable genetic correlations between FD and both CFW and LW, making it harder to improve these traits jointly (Van der Werf, 2009; Masters and Ferguson, 2019). Despite this, the breeding objective for FD of the fine Merino genetic nucleus (to produce 15.5 µm or finer wool) was still achieved. This finding is supported by others (Taylor 2007a and 2007b; Fogarty, 2006), who have reported that the maintenance or reduction in phenotypic FD can be made when animals are also selected for increased CFW and LW, as the unfavorable correlations between FD and both traits are only moderate (0.19 and 0.22, respectively) (Ciappesoni et al., 2013). Little apparent change in FD towards the end of the study period was expected, given that the breeding objective for this trait had already been achieved.

Fibre diameter, greasy fleece weight, and live weight are the most important production traits in Merino flocks (Safari et al., 2006). In the current study, reductions in lamb phenotypic FD were accompanied by increases of more than 0.5 kg in phenotypic GFW, which is consistent with that previously reported in Merino sheep after 10 years of selection (Taylor et al., 2007b). Across the entire study period, phenotypic LW post-shearing increased by approximately 3 kg, which likely contributed to increased GFW (Mortimer et al., 2017). The change in the selection objective in the

CRILU period, including LW in the selection index, as well as changes in the emphases in FD and GFW, is reflected in the phenotypic trends of these traits. The findings show, therefore, that by using suitable selection indices, farmers can obtain favorable phenotypic changes in the desired economic wool and growth traits.

Phenotypic changes in FD can also occur through non-genetic factors, such as nutritional conditions (Greeff et al., 2010; McGregor and Butler, 2016). In this study, a better nutrition status in males was associated with coarse fibres, which is consistent with a positive relationship between nutrition and FD reported by others (Ramos et al., 2019; McGregor, 2010; Khan, 2012). Interactions between the sex of the lamb and the year for this trait could potentially be explained by fluctuations in annual rainfall, which influences pasture growth in Uruguay (Berretta, 1998), as well as differences in the proportion of males/females by a given sire. In addition, a higher FD in males in the present study can also likely be explained by testosterone (Rather et al., 2019; Nazari-Zonouz et al., 2018).

Factors, such as birth type and dam age, also influence phenotypic lamb FD (Greeff et al., 2010), although the effect of birth rank on this trait is unclear (Kenyon and Blair, 2014). Some studies have shown that multiple-born animals tend to produce coarser wool than singletons (Safari et al., 2007c; Ciappesoni et al., 2014). However, in the present study, as previously reported (Eltawil et al., 1965), birth-rearing rank did not show any significant effect on lamb FD. A potential poorer prenatal nutrition of the fetus(es)/lamb(s) from young dams maybe result in coarser fibres (Thompson et al., 2011a; Kelly et al., 2006). However, earlier findings (Wuliji et al., 1999) reported no effect of the dam age on lamb FD. In the present study, lambs from 2-year-old ewes had finer wool than those from adult ewes (≥3 years old), which is consistent with others (Thompson and Young, 2018), who reported finer wool in ewe lamb offspring. The between studies differences related to the effect of the dam age and birth-rearing rank on lamb FD could potentially be associated with variation in ewe LW at mating and ewe LW gain during gestation, including nutritional status all, of which can affect progeny FD (Thompson et al., 2011a; McGregor et al., 2016). In addition, in the present study, the effect of the dam age on lamb FD may be influenced by differences in genetic merit for FD between young and older dams, where younger dams are expected to be finer.

A lamb's wool production depends on maternal nutrition (Ciappesoni, et al., 2013; Lewis and Beatson, 1999). Insufficient supply of nutrients during the fetal and pre-weaning phases can reduce the number of secondary follicles resulting in lighter fleeces (Thompson et al., 2011a; Kelly et al., 2006). In the present study, lambs from two-year-old ewes had 3.5% lighter fleece than those from three-to-six-year-old ewes, which is consistent with those reported by others (Safari et al., 2007c; Wuliji et al., 1999) in Merino sheep. This result can be explained by the young dam using nutrients for her own growth, resulting in reduced fetal and secondary follicle development (Di et al., 2011). It can also be explained by lower milk production in a young dam (Geenty, 2010). Unsurprisingly, in the present study, multiple weaned lambs had lower phenotypic GFW than single-born lambs, which is consistent with earlier findings (Safari et al., 2007c). This result is likely explained by low birth weight and lower growth rates pre-weaning in multiple weaned lambs, which result in lighter fleeces (Kenyon and Blair, 2014; Thompson et al., 2011a).

The wool and body growth of grazing sheep depends largely on their genetic potential and nutritional status (Ramos et al., 2019; Masters and Ferguson, 2019; Khan et al., 2012). In the present study, males had heavier phenotypic GFW than females, which is coincident with earlier findings (Wuliji et al., 1999; Di et al., 2011). The males in this study were managed on improved pasture plus supplement feeding as required, whereas, in females, the nutrition was mostly based on native pasture. Therefore, higher wool productivity in males compared to females in this study is most likely explained by their better nutritional status during the post-weaning phase (from weaning to shearing) (Ramos et al., 2019; Khan et al., 2012). Increased phenotypic GFW in males in the present study was accompanied by heavier LW, which is consistent with a positive phenotypic relationship between these two traits (Mortimer et al., 2017). In addition to nutritional conditions, differences in GFW, LW and post-mortem EMA between sexes are hormonally driven (Di et al., 2011; Schanbacher et al., 1980; Mahmood et al., 2019). These findings indicate the importance of considering both sexes of the lamb and management group when animals are phenotypically compared.

Greater income through increased meat production is becoming more important in many Merino sheep production systems (Rowe, 2010). Live weight and ultrasound measurements of muscle and subcutaneous fat are key indicator traits of meat yield and fat content (Greeff et al., 2008). In the present study, heavier phenotypic LW in males was associated with greater phenotypic FAT and EMA, agreeing with others (Ramos et al., 2019; Romdhani and Djemali, 2006). Under nutrition during early fetal life influences muscle development (Daniel et al., 2007). In addition, during early life, multiple-born lambs receive less milk than their singleton-born counterparts, which in turn also limits their growth rates (Moffatt, 2002). In the present study, multiple weaned lambs had lower phenotypic EMA than single weaned lambs, which was explained by differences in LW at the time of measurements. This agrees with earlier findings (McCoard, 2010), who reported lower carcass weights in twins than singletons. In addition, the age of the dam influences adipose tissue growth in offspring, with the lowest fat deposition being for lambs from young ewes (Symonds et al., 2004). However, in the present study, as previously reported (Romdhani and Djemali, 2006), there was no effect of dam age on lamb fat content. In the current study, lambs from 2-year-old ewes were lighter and had lower phenotypic EMA than those from ewes aged seven and older, which is coincident with others (Loureiro et al., 2011). This result can be explained by the lighter birth weight of the lamb and the lower lactational performance of the young dam (Kenyon and Blair, 2014; Geenty, 2010).

Conclusions

In conclusion, this study demonstrates that the genetic selection process applied in the fine Merino genetic nucleus over the 1999 to 2018 period resulted in phenotypic improvements in one-year-old female and male wool and growth traits. The results indicate that by using suitable selection indices, reductions of approximately 3 µm in phenotypic FD (from 18 to 15 µm) and increases in both greasy fleece weight (at least 0.5 kg) and live weight (approximately 3 kg) can be obtained. Therefore, this chapter demonstrates it is possible to produce ultrafine wool without compromising other economically relevant traits in Uruguayan yearling lambs. These results, if transferred to the Uruguayan sheep industry, will increase farmer income.

Chapter IV

Productivity and reproductive performance of mixed-age ewes across 20 years of selection for ultrafine wool in Uruguay

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Abstract

This study reports the phenotypic trends for wool, growth, and reproductive traits in mixed-age ewes after twenty years of genetic selection. Data were obtained from the Merino nucleus flock in Uruguay between 1999 and 2020. Overall, the aim of this selection flock was to reduce the fibre diameter (FD) and increase both the clean fleece weight (CFW) and live weight (LW). Data on ewe wool traits, LW and body condition score (BCS) at mating, pre-lamb and weaning, the total number of lambs weaned (TLW), and the total LW of lambs weaned (TLWW) across all lambing opportunities (1–8 mating seasons) were analysed. Between 1,292 and 2,063 ewes were measured across the study period, depending on the trait considered. Ewe FD decreased by approximately 3 μm (19–16 μm), whereas greasy fleece weight (GFW) increased by 0.2 kg. This improvement in wool traits was accompanied by increases in LW at mating (3 kg), decreases in BCS at mating (approximately by 1 unit), and a small positive change in TLWW across years. This study demonstrated that increasing farmer income by selecting for finer wool, heavier fleeces, and heavier animals can be obtained without compromising ewe lifetime reproduction.

Keywords: sheep; wool; selection; live weight; body condition score; lifetime reproduction

Introduction

During the 1990s, the Uruguayan wool industry processed mainly mid-micron wool (25.0–30.0 µm, Cardellino et al., 2018). A decrease in demand for this wool type led to a reduction in the overall number of sheep in Uruguay, but at the same time an increase in the number of fine-micron Merinos (Cardellino, 2020). Between 1997 and 2019, the Uruguayan sheep population decreased from 18.2 to 6.6 million (DIEA, 2022; INAC, 2021), while, fine-micron wool (≤22.5 µm) production increased by approximately 135% (3.2–7.5 million kg). Currently, fine-micron wool (≤22.5 µm) accounts for 32% of the total wool production (Cardellino, 2020) and superfine wool (15.6–18.0 µm) represents 37% of the total wool finer than 20 µm (Cardellino, 2020). Over the last two decades, superfine wool has obtained the highest values, although the price differentials between finer and coarser wool types have varied (Rowe, 2010; Pattinson et al., 2015; Wei et al., 2020).

Sheep production systems focused on either wool or meat production are both interested in improving reproduction performance (Huisman et al., 2008; Walkom et al., 2014). Some studies have reported that the reduced fibre diameter (FD) can be associated with poorer reproduction performance, such as the number of fetuses identified at pregnancy scanning (Dominik and Swan, 2018). Although the effect of selection for reduced FD on lamb survival is inconsistent (Dominik and Swan, 2018; Walkom et al., 2019). Positive genetic correlations between FD and ewe body condition score (BCS) at mating (Walkom and Brown, 2017; Tait et al., 2018; Tait, 2020) indicate that selection for reduced FD will result in lower BCS, which could negatively influence reproduction performance (Kleemann and Walker, 2005; Yilmaz et al., 2011; Kenyon et al., 2014). In addition, selection for increased clean fleece weight (CFW) can have unintentional consequences, which varies across environments and breeds (Masters and Ferguson, 2019). A high negative genetic correlation (−0.65 ± 0.14) between yearling CFW and the number of lambs weaned per ewe joined in superfine Merino sheep also suggests that selection for increased CFW could reduce reproductive performance (Dominik and Swan, 2018). Safari et al. (2007b) reported negative genetic correlations between yearling CFW and the number of lambs weaned per ewe joined (−0.26 ± 0.05). Furthermore, adult CFW expressed as a proportion of live weight at mating appears to be negatively associated with ewe reproduction (Greeff, 2020). By contrast, other studies have shown that selection for increased CFW as a component of a multitrait breeding program can be achieved without compromising the reproduction rate (Piper et al., 2007, 2009, 2013). Most of these studies have been conducted in Australia and the inconsistencies in research findings may be associated with the breed type, amount and structure of the data, and nutritional conditions (Dominik and Swan, 2018; Masters and Ferguson, 2019). There is currently no scientific information focused on the potential effects of selection for reduced FD and increased CFW on ewe growth and reproductive traits in the Uruguayan Merino population.

Between 1999 and 2020, two combined research projects entitled the Fine Merino Project (FMP) and the Regional Consortium for Innovation in Ultrafine Wool (CRILU) were developed in Uruguay, as described in Chapter III. Briefly, the FMP (1999–2010) focused on FD reduction (19 µm or finer), whereas during the CRILU period (2011–2020), the selection objective was to reduce FD (15.5 µm or finer) and to increase both CFW and live weight (LW). In the context of these breeding goals, it is of interest to know if selection for reduced FD and increased CFW influenced other economically relevant traits in adult ewes. This study aimed to evaluate the phenotypic responses in mixed-age ewes to these two combined selection programs (FMP and CRILU) over the period 1999–2020.

Materials and Methods

Period and location

Data were obtained from the Merino nucleus flock, which was run between 1999 and 2020 at the Glencoe Experimental Unit of National Institute of Agricultural Research of Uruguay (INIA) (32°00′21” S and 57°08′06” W). In this region, annual pasture production varies from 2,885 to 4,580 kg of dry matter (DM)/ha (Berretta, 1998). During the study period (1999–2020), total annual rainfall ranged between 830 and 2,800 mm (Banco de datos agroclim.tico, INIA Uruguay, 2021). This study analysed data from mixed-age ewes over the period 1999–2020. All procedures were approved by INIA Animal Ethics Committee (INIA_2018.2).

Animals, nutrition, and management

Data from ewes (2–10 years of age) born in the Merino nucleus flock between 1999 and 2018 were recorded. The animal selection process applied in this nucleus flock has been described in Chapter III. Each year, ewes were managed as a single flock under the same health and nutritional conditions, as recommended for commercial flocks (Bonino and Casaretto, 2012; Ramos and Montossi, 2014). Ewes grazed on native pastures (6–15% of crude protein and 7.5–9.2 MJ/kg metabolizable energy; Berretta et al., 2000), with access to improved pastures or supplements as described in Chapter III.

Each year, ewes were inseminated with either imported frozen semen or fresh semen from nucleus-born rams (Chapter III). Estrus was synchronized using intravaginal sponges impregnated with progesterone (Intervet®, Montevideo, Uruguay, SFGA 40 mg) for 12–14 days followed by a single intramuscular injection of equine chorionic gonadotropin (Folligon®, Intervet, Montevideo, Uruguay, 200–300 UI/a) at the time of sponge removal. At 56–60 h after sponge removal, intrauterine insemination (IUAI) was performed. If a second spontaneous estrus occurred, which is an indicator of the failure of conception, ewes were bred with Uruguayan Merino rams using either cervical insemination (CAI) or natural mating (NM). This breeding protocol was applied each year between 2001 and 2016.

In 2017, for the first estrus cycle, IUAI was utilized on 23% of the flock, with the remaining ewes being covered by CAI. For this insemination method, estrus was synchronized utilizing two injections of Delprostenate (Glandinex®, Universal, Uruguay) or D-Cloprostenol (Enzaperost®, Biogenesis Bagó, Uruguay) 9 days apart. Fourteen days after the last injection, estrus was detected in all ewes every 12 h, using vasectomized rams, and cervical insemination was performed 12–24 h after onset of estrus. If the second estrus occurred, ewes were naturally mated. In 2018, the breeding protocol was as described for 2017, but in this case, for the first estrus cycle, 21, 25, and 54% of the flock was covered by IUAI, CAI, and NM, respectively. In 2019, ewes were single-sire mated over 5 weeks, whereas in 2020, all ewes were bred with multiple rams in teams for 35 days.

Pregnancy diagnosis via transabdominal ultrasonography (Aloka SSD 500VW/2X real-time scanner, Tokyo, Japan) occurred each year at approximately 45 days after ram removal or the end of the second artificial insemination. Pregnancy rate (pregnant ewes/treated ewes), lambing potential (number of fetuses/ewes treated) and estimated lambing date were identified. Between one and two months before lambing (July–August), all ewes were shorn using the Tally-Hi method (http://www.shearingworld.com/training.htm). Prior to the last third of pregnancy, ewes were separated into two groups according to the number of fetuses carried (single- or multiple- bearing). Generally, multiple-bearing ewes were assigned to improved pastures whereas those carrying a single fetus grazed on native pastures. Additionally, approximately one month prior to lambing, all pregnant ewes were group fed 400 g of grain/ewe/day (sorghum or commercial rations). Ewe and newborn lamb management at lambing time is described in Chapter III.

All ewes were annually immunized (August) with a clostridial vaccine (Sintoxan® 9TH Merial, or Ultravac®, Boehringer Ingelheim, Montevideo, Uruguay) and treated for external parasites (Mixan®, La Buena Estrella or Elimix®, Nutritec, Montevideo, Uruguay) (January or February). Internal parasite control was done by oral drench with an effective anthelmintic prior to mating (March to April), lambing (July to August), at lamb marking (September to November) and weaning (December to February). In addition to these internal parasite control treatments, fecal egg counts were monitored as described in Chapter III.

Measurements

Each year, ewe unfasted LW and BCS (according to a five-point scale, from 1= skinny to 5 = fat; Jefferies, 1961) were recorded prior to breeding (March–April), pre-lambing (approximately one month before estimated lambing date), and at weaning (December– February). At shearing (July–

August), greasy fleece weight (GFW) was recorded, and a mid-side wool sample was taken from each ewe. The sample was sent to a commercial wool laboratory (Uruguayan Wool Secretariat, Montevideo, Uruguay) and analysed for FD, coefficient of variation of FD (CVfd), staple length (SL), and scoured yield (SY) utilizing the procedures described by Ramos et al. (2019) and Chapter III.

Total wool and reproductive traits calculations

Data on fleece weight, number of lambs weaned, and lamb live weight at weaning per lambing opportunity across each ewe's reproductive lifetime (2–10 years of age) were collected. In this study, lambing opportunities corresponded to the number of mating seasons each ewe had over her lifetime. Total wool production (TWool), which did not include one-year-old fleece, was calculated as the sum of GFW across all lambing opportunities (1–8 mating seasons). Total number of lambs weaned over *n* lambing opportunities (TLWn) was computed by adding the number of lambs weaned each ewe had over her lifetime. The weaning live weight for all lambs was adjusted to 120 days of age. Total lamb live weight at weaning over *n* lambing opportunities (TLWWn) was calculated by adding the live weight at weaning (adjusted to 120 days of age) of all lambs each ewe had across her lifetime. In all cases, ewe ages ranged between 2 and 10 years.

Estimated gross income per ewe lifetime

It has been established that the first four lambing opportunities can be utilized as indicative of lifetime reproductive performance in Merino sheep (Snyman, et al., 1997; Duguma et al., 2002). In this study, TWool and TLWW per ewe over four lambing opportunities were calculated and then utilized as indicative of lifetime wool and reproduction performance, respectively. From these data, the impact of reducing FD on gross income per ewe lifetime in the nucleus flock was calculated. Both TWool and TLWW were assumed constant across years. For simplification, it was assumed that all lambs were sold at weaning. The annual average FD of the nucleus flock was calculated and then utilized in this analysis. Average wool and meat prices were calculated for the period 2013–2019

(DIEA, 2022; Cámara Mercantil de productos del País, 2020) and utilized for the entire period (1999–2018).

The same analysis was performed for 40 Merino sheep farmers who, since 2001, had utilized either rams or frozen semen from the nucleus flock. In this case, the impact of reducing FD on gross income per ewe lifetime was calculated for two years only (1999 and 2018). The average FD utilized for commercial flocks was 21 and 18.5 µm for ewes born in 1999 and 2018, respectively. This assumption was based on previously reported FD in adult animals of the same commercial flocks (Montossi et al., 2005; Pérez et al., 2017). In all flocks, FD was measured as described for the nucleus flock (Chapter III; Ramos et al., 2019; Pérez et al., 2017). It was assumed that TWool and TLWW were the same as the nucleus flock. Average wool and meat prices were calculated for the period 2013–2019 (DIEA, 2022; Cámara Mercantil de productos del País, 2020) and utilized for both 1999 and 2018 calculations.

Statistical analysis

Wool and growth traits

Statistical analyses were undertaken utilizing the SAS program (version 9.4, SAS Institute Inc., Cary, NC, USA). Outliers were examined and removed utilizing a robust regression model (PROC ROBUSTREG). A general linear model (PROC GLM) was applied for the wool and growth traits analysis. The model for mixed-age ewe wool traits included “age” (3 levels: 2-year-old; 3–6 years old; ≥ 7 years old), “period” (2 levels: FMP, 2001–2010, and CRILU, 2011–2020), “calendar year” (20 levels: from 2001 to 2020) nested within the period as fixed effects, and “days of wool growth” (number of days between shearing, 268–399 days) as a covariate. Pregnancy-rank and interactions between fixed effects were either non-significant or had little effect and were therefore not included in the model.

The model for LW at mating was as described for wool traits but in this case, “days of wool growth” corresponded to the number of days between shearing and the day the weight was measured

(148–274 days). Ewe LW pre-lambing and weaning were analysed as described for LW at mating but with “pregnancy-rank” added (3 levels: non-pregnant; single fetus; 2 fetuses) as a fixed effect. The model for BCS across all stages of the annual cycle (at mating, pre-lambing, and weaning) was as described for LW but without “days of wool growth” and, in this case, a GENMOD procedure using a Poisson distribution was applied. For LW and BCS at weaning, the lamb rearing type was also tested as a fixed effect.

To examine FD, GFW, and LW at mating trends, a second-degree orthogonal polynomial regressions model (PROC ORTHOREG) was utilized. The regression model for these traits included the same fixed effects described above. The second order was applied in “calendar year” whereas all other effects were treated as first-degree terms. The polynomial regression model for BCS included “age” (3 levels: 2-year-old; 3–6 years old; 7 years old), “period” (2 levels: FMP, 2002–2010, and CRILU, 2011–2020), and “calendar year” (19 levels: from 2002 to 2020) nested within the period as fixed effects. For this trait, a third-degree polynomial was applied in “calendar year”. The wool and growth traits trends were performed for each age group separately (2-year-old; 3–6 years old; ≥ 7 years old), including a 95% confidence interval (CI).

Total wool and reproduction performance per lambing opportunity

Total wool and reproductive data were analysed utilizing a general linear model (PROC GLM). The model for reproductive traits (TLW and TLWW) considered “year of birth” (20 levels: from 1999 to 2018), “number of lambing opportunities” (8 levels: 1–8 mating seasons), and “mating method” (4 levels according to the mating method utilized in the first estrus cycle: 100% IUAI (1), between 40 and 88% of the services covered by IUAI (2), between 17 and 43% of the services covered by IUAI (3), and 100% of the services covered by either CAI or NM (4), as fixed effects. The total wool production across all lambing opportunities was analysed as described for reproductive traits but without “mating method”. To evaluate the trend in TLWW and TWool across all lambing opportunities (1–8 mating seasons), a second-degree orthogonal polynomial regression model (PROC

ORTHOREG) including the same fixed effects described above was utilized. The second order was applied in the "year of birth" whereas all other effects were treated as first-degree terms.

Results

The descriptive statistics for wool, growth, and reproductive traits are shown in Table 4.1. Over the study period (1999–2020), mixed-age ewe FD, GFW, and LW at mating fluctuated between 15.0 and 19.1 µm, 3.1 and 4.1 kg, and 43.1 and 52.3 kg, respectively (Table 4.2).

Table 4.1 Descriptive statistics for mixed-age ewe wool, growth, and reproductive traits over the entire study period (1999–2020).

Traits	Mean	Min[1]	Max[2]	SD[3]	CV	Animals	N
Fibre diameter (FD, µm)	16.6	12.1	22.1	1.7	0.10	2,063	6,988
Greasy fleece weight (GFW, kg)	3.51	1.8	5.9	0.6	0.17	2,052	7,007
Coef. of variation of FD (CVfd, %)	16.3	10.5	25.4	2.0	0.12	1,952	6,693
Staple length (SL, cm)	8.7	4.5	13.5	1.3	0.15	1,766	6,507
Scoured yield (SY, %)	80.0	55.5	90.4	3.9	0.05	1,744	6,477
Live weight at mating (LWM, kg)	47.4	30.0	68.0	6.1	0.13	1,850	6,763
Live weight pre-lambing (LWL, kg)	49.0	28.0	74.5	7.1	0.14	1,801	6,466
Live weight at weaning (LWW, kg)	48.5	28.0	74.0	6.4	0.13	1,306	4,775
Body condition score at mating (BCSM)	3.2	1.5	5.0	0.66	0.21	1,839	6,778
Body condition score pre-lambing (BCSL)	3.1	1.5	5.0	0.61	0.20	1,802	6,490
Body condition score at weaning (BCSW)	2.8	1.5	4.7	0.59	0.21	1,292	4,693
Total number of lambs weaned/ewe[4]	2.4	0	12	1.9	0.79	1,954	1,954
Total lamb live weight at weaning/ewe[5]	58	0	287	48	0.83	1,954	1,954

[1,2,3] Min, Max, SD and CV correspond to the minimum, maximum, standard deviation and coefficient of variation values for each trait. N: number of records. [4,5] correspond to the total number of lambs and total live weight of lambs weaned per ewe across all lambing opportunities (1–8 mating seasons).

Table 4.2 Ewe annual mean, standard deviation (SD), and number of records (N) of the fibre diameter (FD, μm), greasy fleece weight at shearing (GFW, kg), and live weight at mating (LWM, kg) (1999–2020).

Period[1]	**Year**	**Fibre diameter (μm)**			**Greasy fleece weight (kg)**			**Live weight at mating (kg)**		
		Mean	**SD**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**
FMP	2001	19.1	1.3	125	3.4	0.4	124	-	-	-
	2002	19.0	1.2	208	3.4	0.6	210	43.1	4.4	77
	2003	19.0	1.2	257	3.3	0.6	264	44.5	4.3	265
	2004	18.3	1.3	323	3.4	0.6	325	43.8	5.2	323
	2005	18.5	1.3	400	3.5	0.5	404	47.2	5.1	399
	2006	18.0	1.3	371	3.5	0.5	376	45.7	5.4	379
	2007	17.5	1.4	388	3.1	0.5	387	44.9	5.3	373
	2008	17.1	1.3	370	3.5	0.7	364	47.4	6.3	355
	2009	16.7	1.3	418	3.8	0.6	405	49.0	6.2	403
	2010	16.2	1.3	471	3.5	0.7	471	46.3	6.2	475
CRILU	2011	16.7	1.2	400	4.1	0.6	397	50.6	5.2	400
	2012	16.0	1.1	386	3.5	0.6	403	49.7	5.1	391
	2013	15.6	1.1	385	3.6	0.5	388	46.6	5.5	377
	2014	15.2	1.1	325	3.0	0.4	328	44.9	5.2	354
	2015	15.0	1.1	343	3.2	0.5	343	45.6	6.1	350
	2016	15.2	1.0	339	3.4	0.6	340	46.3	6.3	342
	2017	15.6	1.1	314	3.5	0.6	311	48.5	5.8	324
	2018	15.7	1.1	364	3.7	0.7	361	49.5	5.6	369
	2019	15.7	1.1	384	3.7	0.7	385	52.3	5.6	386
	2020	15.5	1.1	417	3.6	0.8	421	49.4	6.0	421

[1] Period: FMP = Fine Merino Project (1999–2010) and CRILU = Regional Consortium for Innovation in Ultrafine Wool (2011–2020).

Wool traits

FD, GFW, CVfd, SL, and SY were all affected by the period ($p < 0.05$, Table 4.3). During the FMP phase, ewes had coarser and longer fibres than those produced in the CRILU period. During the FMP, ewes had lighter fleeces, higher CVfd, and greater SY compared with the CRILU phase.

Table 4.3 Least square means and standard errors of the mean of the fibre diameter (FD, µm), greasy fleece weight (GFW, kg), coefficient of variation of the fibre diameter (CVfd, %), staple length (SL, cm), and scoured yield (SY, %) by period and ewe age (1999–2020).

Traits	**Period[1]**		**SEM**	**Age (years)**			**SEM**
	FMP	**CRILU**		**2**	**2 to 6**	**≥ 7**	
Fibre diameter (FD, µm)	18.1^{a}	15.6^{b}	0.03	16.2^{c}	17.0^{b}	17.4^{a}	0.05
Greasy fleece weight (GFW, kg)	3.4^{b}	3.5^{a}	0.01	3.5^{a}	3.5^{a}	3.1^{b}	0.02
Coef. of variation of FD (CVfd, %)	16.6^{a}	16.1^{b}	0.04	16.3^{b}	16.2^{b}	16.7^{a}	0.07
Staple length (SL, cm)	8.5^{a}	8.3^{b}	0.03	9.1^{a}	8.7^{b}	7.8^{c}	0.04
Scoured yield (SY, %)	79.4^{a}	79.1^{b}	0.08	80.3^{a}	80.0^{a}	77.1^{b}	0.15

[1] Period: FMP = Fine Merino Project (1999–2010) and CRILU = Regional Consortium for Innovation in Ultrafine Wool (2011–2020). Different letters within a row (a,b,c) within a category indicate statistical significance ($p < 0.05$).

All wool traits were affected by ewe age ($p < 0.05$, Table 4.3). Ewe FD increased as animals aged. Two-year-old ewes had the longest fibres and ewes aged seven or older had the shortest fibres. Ewes aged seven or older had the lightest fleeces, the highest CVfd, and the lowest SY, with no differences between the other two age groups for these traits.

Growth traits

Ewe LW across all stages of the annual cycle (at mating, pre-lambing, and weaning) was affected by period, pregnancy-rank (pre-lambing and weaning), and age group ($p < 0.05$, Table 4.4). Ewe LW at mating, pre-lambing, and weaning was higher (2–5%) in the CRILU period compared to the FMP phase. Among pregnancy-ranks, non-pregnant ewes had the lightest LW pre-lambing and multiple-bearing ewes had the heaviest LW pre-lambing. Ewes carrying single or multiple fetuses were lighter (9–11%) at weaning than non-pregnant ewes. Among pregnant ewes, multiple-bearing ewes were lighter at weaning than those bearing singles. Ewe LW across all stages of the annual cycle increased as animals aged.

Table 4.4 Least square means and standard errors of the mean (SEM) of live weight at mating (LWM, kg), pre-lambing (LWL, kg), at weaning (LWW, kg), and body condition score at mating (BSCM), pre-lambing (BCSL), and at weaning (BCSW) by period, pregnancy-rank and age group (1999 - 2020).

Time-point	**Period**[1]		**SEM**	**Pregnancy-rank**[2]			**SEM**	**Age (years)**			**SEM**
	FMP	**CRILU**		**0**	**1**	**≥2**		**2**	**3 to 6**	**≥ 7**	
Live weight											
At mating (LWM, kg)	46.5^{b}	48.6^{a}	0.11	-[3]	-	-	-	44.4^{c}	47.7^{b}	50.6^{a}	0.22
Pre-lambing (LWL, kg)	47.9^{b}	50.5^{a}	0.11	46.2^{c}	49.0^{b}	52.5^{a}	0.14	45.1^{c}	50.3^{b}	52.2^{a}	0.14
At weaning (LWW, kg)	48.7^{b}	49.9^{a}	0.17	52.5^{a}	48.0^{b}	47.4^{c}	0.22	46.4^{c}	50.3^{b}	51.2^{a}	0.21
Body condition score											
At mating (BCSM)	3.6^{a}	3.0^{b}	0.01	-[3]	-	-	-	3.4^{a}	3.3^{b}	3.1^{c}	0.01
Pre-lambing (BCSL)	3.4^{a}	2.9^{b}	0.01	3.1	3.1	3.1	0.01	3.1	3.1	3.1	0.01
At weaning (BCSW)	3.2^{a}	2.8^{b}	0.02	3.4^{a}	2.8^{b}	2.6^{c}	0.02	3.0^{a}	3.0^{a}	2.8^{b}	0.02

[1] Period: FMP = Fine Merino Project (1999–2010) and CRILU = Regional Consortium for Innovation in Ultrafine Wool (2011–2020). [2] 0, 1, and ≥ 2 correspond to non-pregnant ewes, ewes bearing one fetus and ewe bearing two or more fetuses, respectively. Different letters within a row (a,b,c) within a category indicate statistical significance ($p < 0.05$). [3] Data are not available due to the pregnancy-rank not being included in the model for LWM and BCSM.

Ewe BCS at mating, pre-lambing, and weaning was lower (between 0.4 and 0.6 units less) in the CRILU period compared to the FMP phase ($p < 0.05$, Table 4.4). Ewe BCS pre-lambing was unaffected by pregnancy-rank ($p > 0.05$, Table 4.4). At weaning, non-pregnant ewes had the highest ($p < 0.05$) and multiple-bearing ewes the lowest BCS ($p < 0.05$). Within pregnant ewes, multiple-bearing ewes had lower ($p < 0.05$) BCS at weaning than their single-bearing counterparts. Among age groups, BCS at mating decreased ($p < 0.05$) as animals aged, whereas BCS pre-lambing was unaffected ($p > 0.05$) by animal age. Ewes aged seven or older had lower BCS at weaning than the other two age groups ($p < 0.05$, Table 4.4).

The model for LW and BCS at weaning also tested lamb rearing type as a fixed effect. Both LW and BCS at weaning were affected by lamb rearing type ($p < 0.05$, data not shown). Non-pregnant ewes were the heaviest and ewes rearing multiple lambs were the lightest at weaning (51.8 ± 0.33 *vs.*

46.1 ± 0.25 kg). The same trend was observed for BCS (3.5 ± 0.03 and 2.5 ± 0.02, for non-pregnant and ewes rearing multiples, respectively). Ewes rearing multiple lambs were lighter (46.1 ± 0.25 *vs*. 47.3 ± 0.14 kg) and had lower BCS (2.5 ± 0.02 *vs*. 2.8 ± 0.01) at weaning than those rearing single lambs.

Wool traits trends

Throughout the study period (1999–2020), the second-degree polynomial regression model (second order for the "calendar year") explained 61%, 51%, and 45% of the FD changes in 2-year-old, 3–6, and ewes aged seven or older, respectively (Figure 4.1). During the entire study period and across age groups, ewe FD decreased by approximately 3 µm. Two-year-old ewes had the finest ($p < 0.05$) and those aged seven or older the coarsest ($p < 0.05$) fibres, with ewes aged 3–6 being intermediate.

Regardless of ewe age, GFW increased over time (Figure 4.2). Two-year-old ewes had the highest R^2 value (0.22) whereas, the R^2 for 3–6 years old ewes and those aged seven or older were 0.08 and 0.04, respectively. Ewes aged seven or older had the lightest ($p < 0.05$) GFW, with no differences ($p > 0.05$) between the other two age groups.

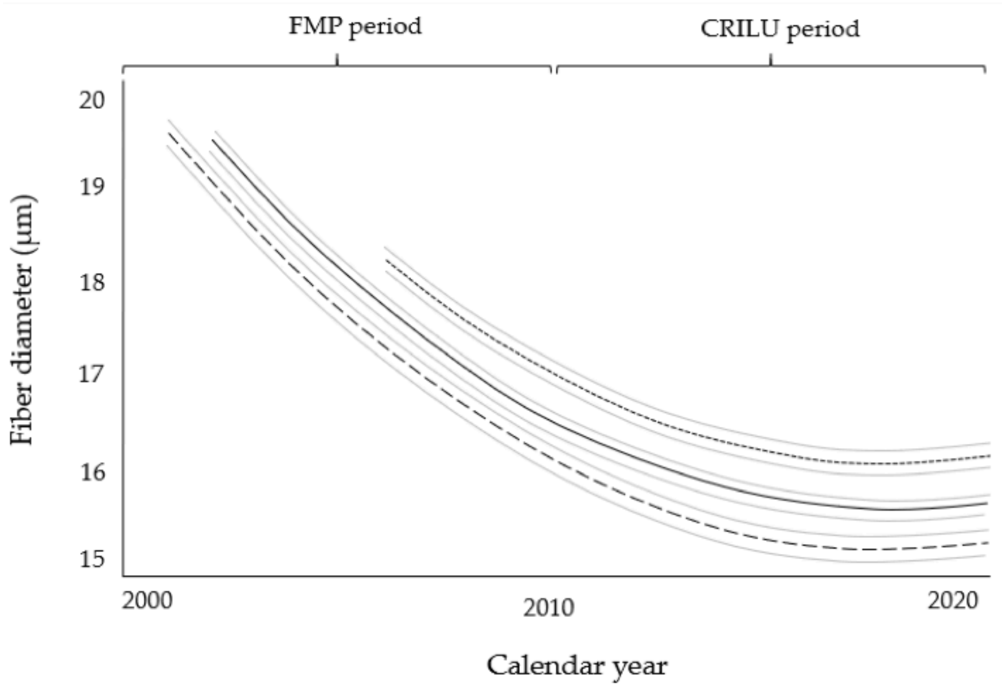

Figure 4.1 Two-year-old ewes (dashed line), 3- to 6-year-old ewes (solid line), and ewes aged seven years or older (dotted line) phenotype trends using a second-degree polynomial regression model for the average fibre diameter across calendar years (2001 - 2020). The light gray lines indicate the 95% confidence interval. R^2 for 2-year-old, 3-to 6-year-old, and ewes aged 7 or older were 0.61, 0.51 and 0.45, respectively. FMP period = Fine Merino project (1999 - 2010), CRILU period = Regional Consortium for Innovation in Ultrafine Wool (2011 - 2020).

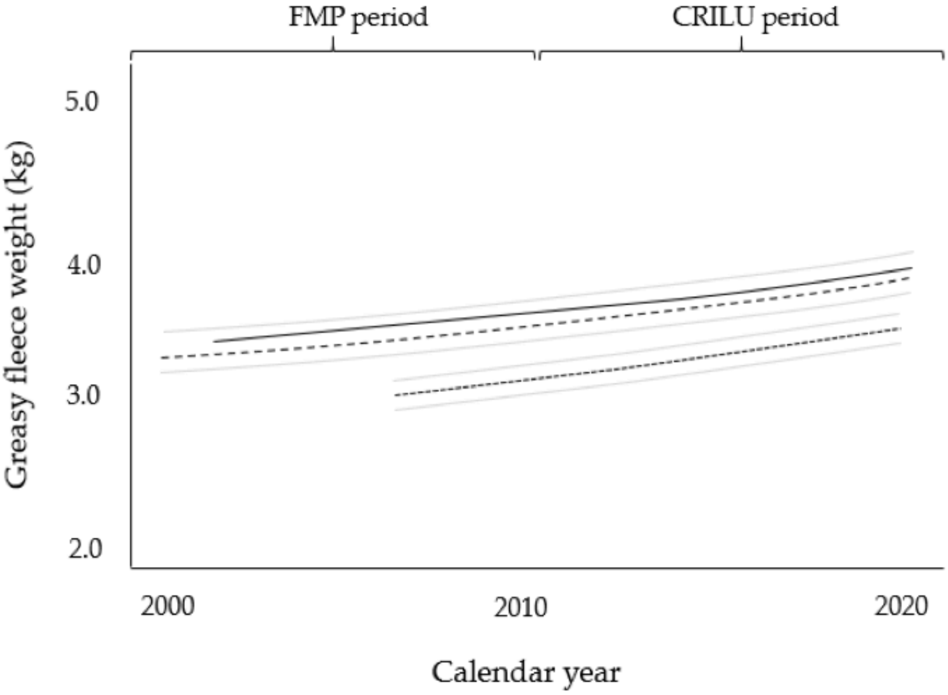

Figure 4.2 Two-year-old ewes (dashed line), 3- to 6-year-old ewes (solid line), and ewes aged seven years or older (dotted line) phenotype trends using a second-degree polynomial regression model for the average greasy fleece weight across calendar years (2001 - 2020). The light gray lines denote the 95% confidence limits. R^2 for 2-year-old, 3- to 6-year-old and ewes aged seven years or older were 0.22, 0.08 and 0.04, respectively. FMP period = Fine Merino project (1999 - 2010), CRILU period = Regional Consortium for Innovation in Ultrafine Wool (2011 - 2020).

Growth traits trends

The second-degree polynomial regression model for LWM is displayed in Figure 4.3. The R^2 of LWM for each age group ranged between 0.06 to 0.10. Ewes aged seven years or older were the heaviest ($p<0.05$), and 2-year-old ewes the lightest ($p<0.05$) at mating. Across all age groups, ewe LWM increased over time (Figure 4.3). Regardless of ewe age, BCSM decreased over time, with scores lower than 3.0 towards the end of the study period. The R^2 value for this trait was higher (0.63) in 2-year-old ewes compared to the other age groups (0.44, 0.43, Figure 4.4).

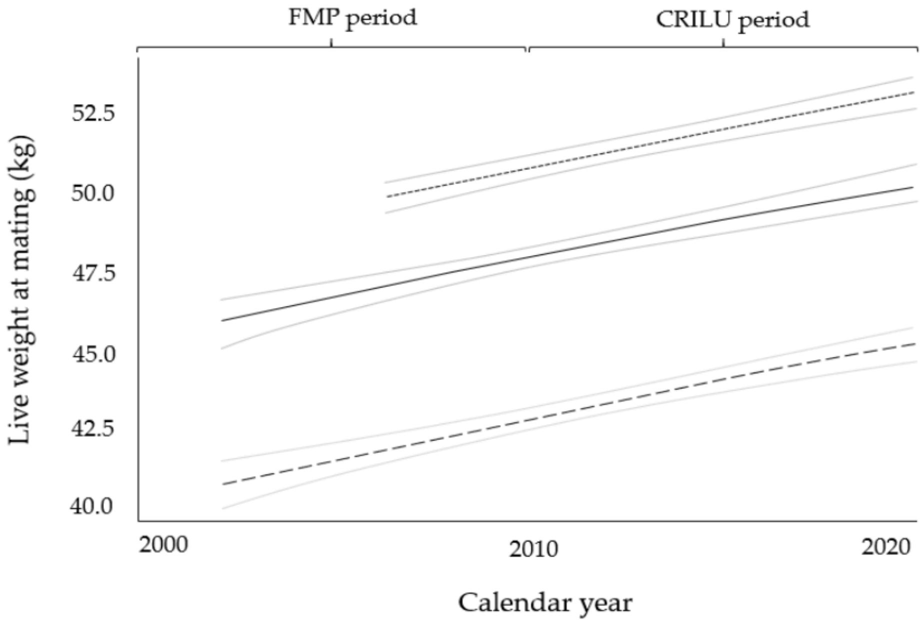

Figure 4.3 Two-year-old ewes (dashed line), 3- to 6-year-old ewes (solid line) and ewes aged 7 or older (dotted line) phenotype trends using a second-degree polynomial regression model for the average live weight at mating across calendar years (2001 - 2020). The light gray lines indicate the 95% confidence limits. R^2 for 2-year-old, 3-to 6-year-old and ewes aged 7 years or older were 0.06, 0.07 and 0.10, respectively. FMP period = Fine Merino project (1999 - 2010), CRILU period = Regional Consortium for Innovation in Ultrafine Wool (2011 - 2020).

Total wool and reproductive traits

The means and standard errors of accumulative TWool, TLW, and TLWW across all lambing opportunities (1–8 mating seasons) are presented in Table 4.5. For a given lambing opportunity, wool production, the number of lambs weaned, and the live weight of lamb weaned per ewe fluctuated between 3.1 and 3.6 kg, 0.7 and 0.8 lambs, and 15.7 and 19.3 kg, respectively. Both TLW and TLWW were affected by the mating method ($p < 0.05$).

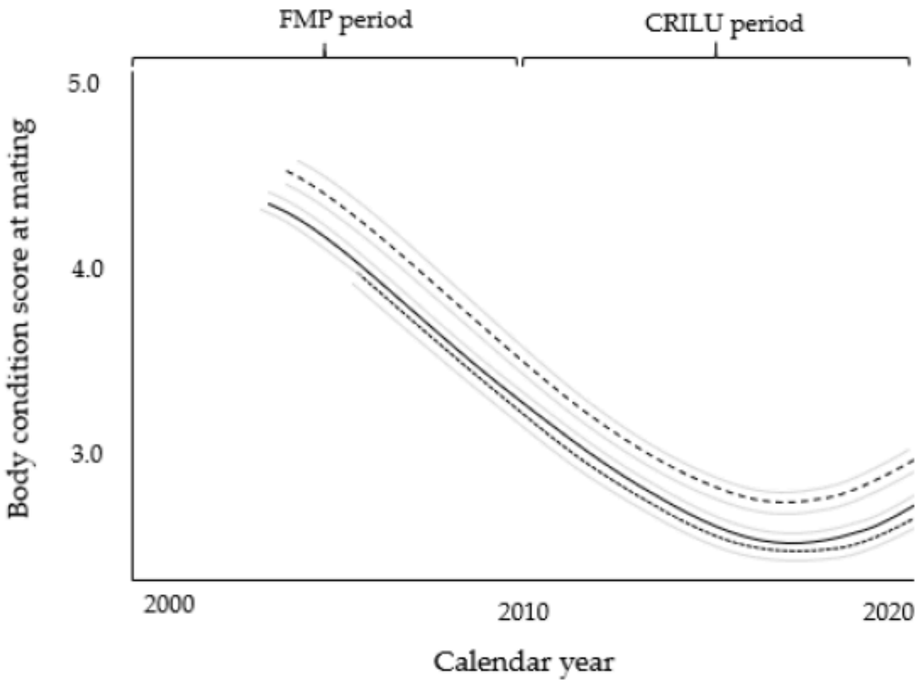

Figure 4.4 Two-year-old ewes (dashed line), 3- to 6-year-old ewes (solid line) and ewes aged seven or older (dotted line) phenotype trends using a third-degree polynomial regression model for the average BCS at mating across calendar years (2002 - 2020). The light gray lines represent the 95% confidence interval. R^2 for 2-year-old, 3- to 6-year-old and ewes aged seven years or older were 0.63, 0.44 and 0.43, respectively. FMP period = Fine Merino project (1999 - 2010), CRILU period = Regional Consortium for Innovation in Ultrafine Wool (2011 - 2020).

Table 4.5 Least square means and standard errors of the mean of accumulative total wool production (TWool, kg), total number of lambs weaned (TLW, n), and total lamb live weight at weaning (TLWW, kg) by lambing opportunity (1999–2020).

Lambing opportunities[1]	Wool and reproductive traits		
	TWool[2] (kg)	**TLW[3] (n)**	**TLWW[4] (kg)**
1	3.1 (0.10)	0.7 (0.11)	15.7 (2.68)
2	6.8 (0.10)	1.3 (0.11)	31.2 (2.68)
3	10.5 (0.10)	2.1 (0.10)	51.4 (2.43)
4	14.5 (0.11)	2.8 (0.10)	68.2 (2.45)
5	18.0 (0.13)	3.9 (0.11)	93.8 (2.6)
6	21.7 (0.14)	4.4 (0.11)	108.9 (2.6)
7	24.0 (0.21)	5.5 (0.15)	134.8 (3.73)
8	27.0 (0.28)	6.1 (0.20)	153.0 (4.95)

[1] correspond to the number of mating seasons each ewe had over her lifetime. [2,3,4] correspond to accumulative total wool production, total number of lambs weaned, and total lamb live weight at weaning, respectively. Standard errors are shown in brackets.

The phenotypic trend for TLWW and TWool for the combined lambing opportunities (1–8 mating seasons) by year of birth is displayed in Figures 4.5 and 4.6, respectively. TLWW was affected by year of birth ($p < 0.05$, $R^2 = 0.56$), whereas this effect was not significant ($p > 0.05$) for TWool. Both traits showed little change across time.

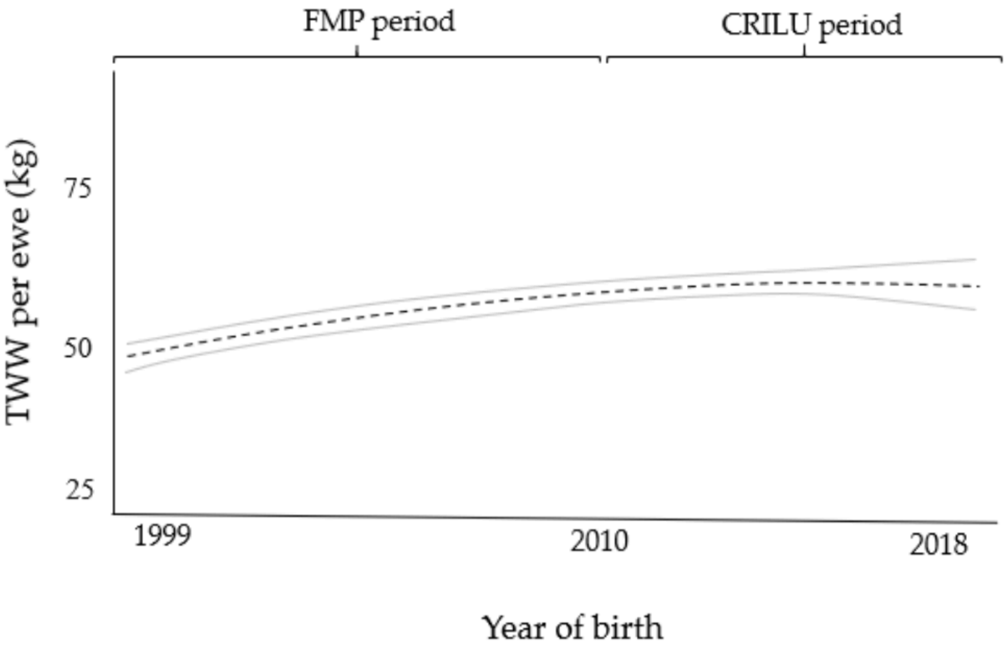

Figure 4.5 Mixed-age ewe phenotype trend for accumulative total lamb live weight at weaning across all lambing opportunities (1 to 8) per year of birth (1999 to 2018) using a second-degree polynomial regression. Lambing opportunities correspond to the number of mating seasons each ewe had over her lifetime. The light gray line indicates the 95% confidence interval. $R^2 = 0.56$. FMP period = Fine Merino project (1999 - 2010), CRILU period = Regional Consortium for Innovation in Ultrafine Wool (2011 - 2020).

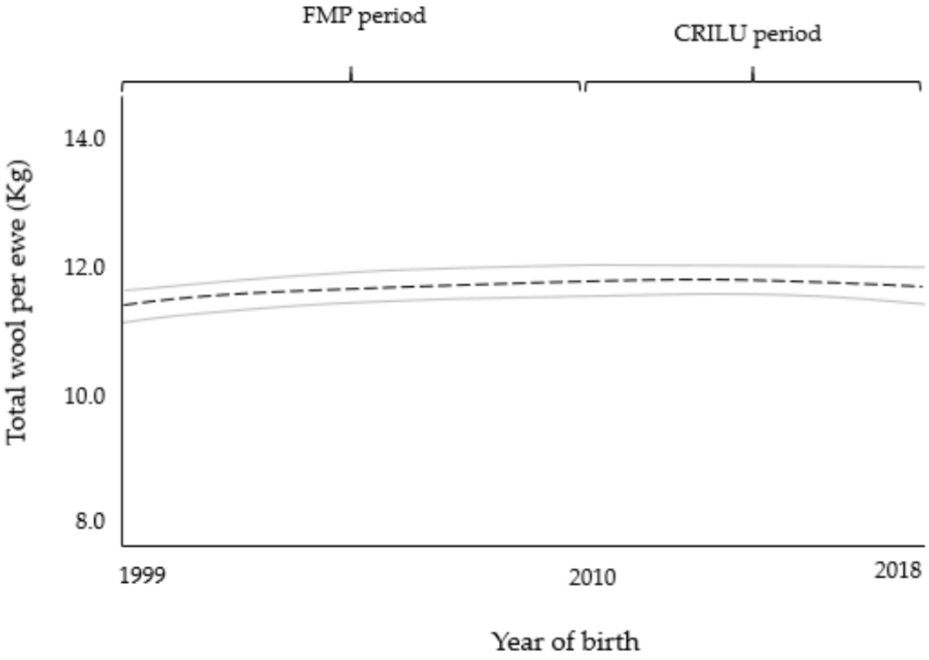

Figure 4.6 Mixed-age ewe phenotype trend for accumulative total wool production across all lambing opportunities (1 to 8) per year of birth (1999 to 2018) using a second-degree polynomial regression. Lambing opportunities correspond to the number of mating seasons each ewe had over her lifetime. The light gray line indicates the 95% confidence interval. R^2= 0.93. FMP period = Fine Merino project (1999 - 2010), CRILU period = Regional Consortium for Innovation in Ultrafine Wool (2011 - 2020).

Estimated gross revenue per ewe lifetime

Gross income per ewe lifetime (across four lambing opportunities) (Snyman et al., 1997; Duguma et al., 2002) over the entire study period is displayed in Figure 4.7. During the FMP (1999–2010), gross income increased by approximately 26%, with little change towards the end of the study period. Overall, during the study period (1999–2018), gross income per ewe lifetime increased by 32% and 21% in the nucleus and in commercial flocks, respectively (Figure 4.8).

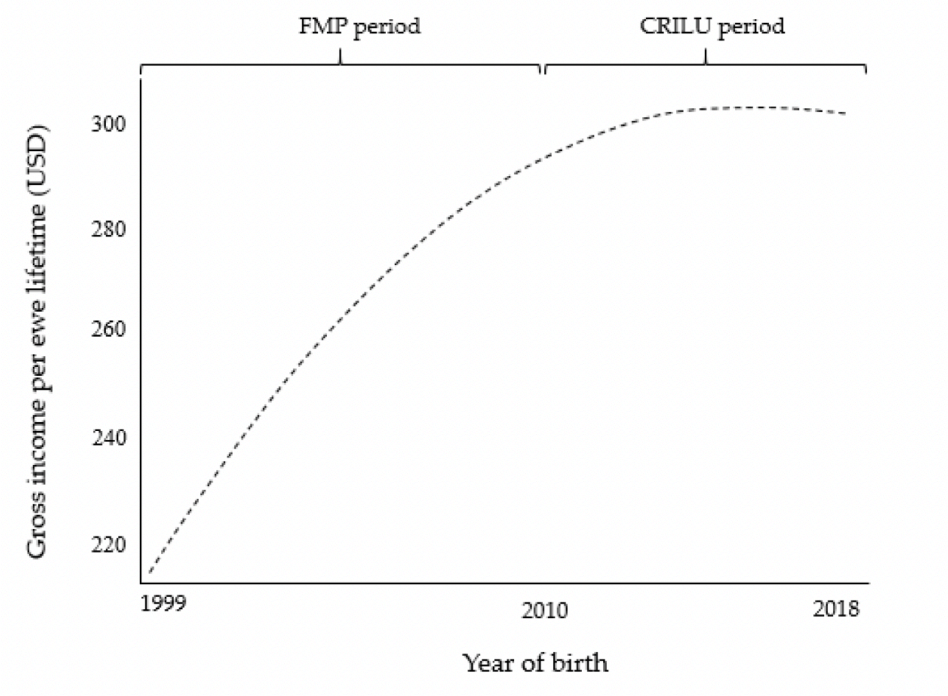

Figure 4.7 Gross income per ewe lifetime (across four lambing opportunities) per year of birth (1999 - 2018) in the nucleus flock. Total wool production and total lamb live weight at weaning across four lambing opportunities were assumed constant across years. It was assumed that all lambs were sold at weaning. Average wool and meat prices were calculated for the period 2013 to 2019 (DIEA, 2022; Cámara Mercantil de productos del País, 2020) and utilized for the entire analysis period (1999 - 2018). FMP period = Fine Merino project (1999 - 2010), CRILU period = Regional Consortium for Innovation in Ultrafine Wool (2011 - 2020).

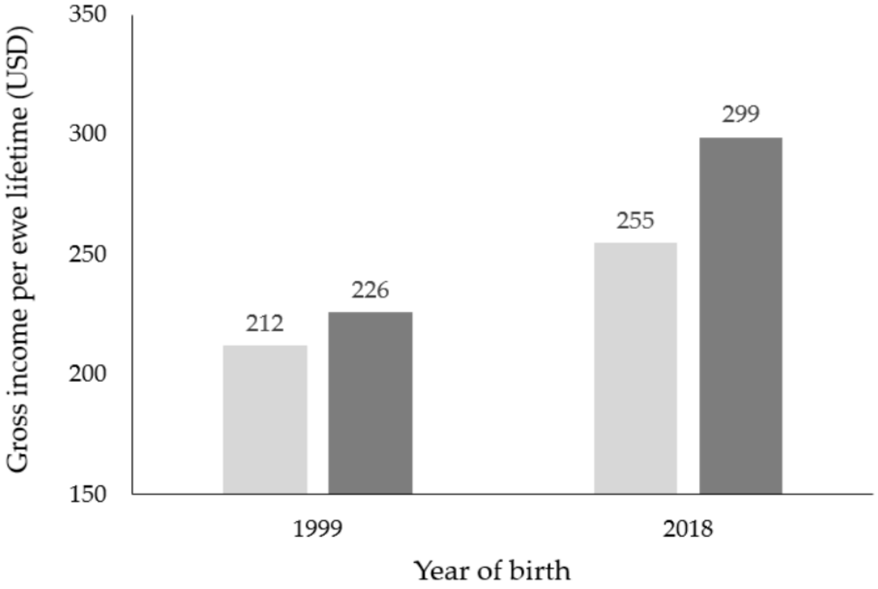

Figure 4.8 Estimated gross income per ewe lifetime (across four lambing opportunities) in commercial flocks (light gray bars) and in the nucleus (dark gray bars) at the beginning and end of the study period. These commercial farmers have utilized either rams or frozen semen from the nucleus flock.

Discussion

This study analysed data from two joint projects (FMP and CRILU), over the period 1999–2020 in a single flock. The FMP (1999–2010) focused on FD reduction based on selection at 12 months of age, whereas in the CRILU project period (2011–2020), the selection objective was to reduce FD while increasing both CFW and LW. This chapter reports the phenotypic trends observed in mixed-age ewes across a twenty-year period.

Adult ewe wool traits are key determinants of Merino flock income (Swan and Brown, 2013; Brown et al., 2013). Wool micron accounts for 80% of the fleece value, with finer wool obtaining the highest prices (McGregor and Butler 2016; Shahinfar and Kahn, 2018; Nolan, 2014). During the FMP period (1999–2010), ewe FD decreased by approximately 3 μm, from 19 to 16 μm, which is comparable with previously reported reductions in FD in yearling lambs of the same flock (Chapter III). This similar trend between one-year-old lambs and adult animals for FD is not unexpected given the high repeatability of this trait (0.76, 0.74, and 0.67) (Manson et al., 1999; Murray et al., 2001; Hatcher et al., 2005, respectively) and the ewe replacement strategy based on including in the adult flock only the genetically finest ewe hoggets. In the present study, fleeces became coarser as ewes aged, which is consistent with that previously reported (Hatcher et al., 2005; Cloete et al., 2003). Despite this, wool micron remained within the highest price category (≤ 18 μm) (Pattinson et al., 2015).

Over the study period, decreases in ewe FD were accompanied by increases in GFW. This result is supported by other studies (Chapter III; Taylor et al., 2007b) that have reported that reductions in FD while increasing GFW can be made by selecting for these traits simultaneously with appropriate weightings. Reducing FD without reducing CFW requires changes in other components of the fleece weight such as, surface area, fibre length, and follicle density (Adams and Cronjé, 2003; Zhang et al., 2017). In this study, ewes with finer wools were heavier (more surface area) likely due to selection on LW and had shorter fibres, which is consistent with positive genetic and phenotypic correlations between FD and SL in adult ewes (Walkom and Brown, 2017; Safari et al., 2005; Huisman and Brown, 2009b). In addition, fine wool and high CFW are associated with increased follicle density (Adams and Cronjé, 2003) but this trait was not examined in this flock.

Throughout the study period, ewe LW increased by approximately 3 kg, which is consistent with increases in LW in yearling lambs of the same flock (Chapter III). This finding is supported by other authors (Manson et al., 1999; Huisman and Brown, 2008) who reported that selection for increased LW at a given age will increase LW at all ages. Previous studies have shown that ewe LW increases with age up to 5 years old and can then either plateau (Semakula et al., 2020) or decrease (Wuliji and Dodds, 2011). In this study, ewe LW increased across all age groups.

Ewe LW is a combination of frame size and BCS (Kenyon et al., 2014). Over the study period, increases in LW at mating were accompanied by decreases in BCS, indicating that ewes became heavier but leaner over time. This loss in BCS is consistent with positive phenotypic and genetic correlations between BCS at mating and FD (Walkom and Brown, 2017; Tait et al., 2018; Tait, 2020). The increased GFW in our study likely contributed to reduced BCS, given the negative phenotypic association between CFW and fat depth (Refshauge et al., 2010). Furthermore, it has been reported that fine wool and high fleece weight together are associated with reduced subcutaneous fat levels (Adams and Cronjé, 2003).

In addition to genetic factors, phenotypic changes in LW and BCS are influenced by reproductive performance and the production environment (Walkom et al., 2014). In this study, at pre-lambing, both single- and multiple-bearing ewes were heavier than their non-pregnant counterpart, but this relationship was reversed by weaning. This finding is not surprising given the influence of conceptus weight and milk production demands during late pregnancy and lactation, respectively (Lee and Atkins, 1995; Geenty, 2010). In the current study, lower BCS at weaning in ewes rearing twins than those rearing single lambs is consistent with a higher milk production demand in multiple-rearing ewes (Walkom et al., 2014; Tait, 2020; Hatfield et al., 1995). This result can also be associated with higher internal parasite load in ewes that suckled twins than those that suckled only one lamb (Notter et al., 2014). Overall, the average ewe BCS reported exceeded the recommended minimum threshold at mating (BCS 3), during gestation (BCS > 2.5), and at weaning (BCS > 2) (Kenyon et al., 2014; Hocking Edwards et al., 2011).

It has been well established that ewe BCS influences her reproductive performance (Kenyon et al., 2014). Ewe BCS at mating between 3 and 3.5 units are positively associated with conception rate and fecundity (Tait, 2020). Over the study period, ewe BCS at mating decreased by approximately 1 unit, although there was a small increase at the end of the study period. This small improvement in ewe BCS is likely associated with improved feeding of the native pasture plus supplement during the summers of 2018 and 2019. During the CRILU period, an average BCS of 3 at mating indicates that 50% of the flock is in a BCS below the optimum (Kenyon et al., 2014). The reduced BCS did not affect TLWW (data not shown), which is consistent with earlier findings (Tait, 2020). The absence of an effect of BCS at mating on TLWW is not unexpected given that there are several environmental and management factors occurring between mating and weaning that influence lamb live weight at weaning (Tait, 2020). In this study, better nutritional status in pregnant and lactating ewes likely attenuated the impact of low BCS on lamb live weight at weaning (Ramos and Montossi, 2014; Thompson et al., 2011b). In addition, it has been reported that ewes inseminated with fresh semen have higher reproductive performance than those covered by frozen semen (Hill et al., 1998; Langford et al., 1979). In this study, the use of different mating methods towards the end of the study period (increased use of fresh semen at the expense of frozen semen) may have confounded the results.

Both fine wool and high CFW are associated with lower reproductive performance (Adams and Cronjé, 2003). In this study, selection for reduced FD and increased CFW were accompanied by a small positive change in ewe lifetime reproduction. This result is consistent with negligible phenotypic correlations (0.03 and 0.01) between these two wool traits (FD and CFW) and the total number of lambs weaned per ewe (Dominik and Swan, 2018). However, a high negative genetic correlation between CFW and the number of lambs weaned per ewe joined has been reported in superfine Merino sheep (Dominik and Swan, 2018). As this study suggested, this inconsistency may be associated with the type of trait analysed (total number of lambs weaned as a single trait across all lambing opportunities vs. number of lambs weaned as repeated records). Furthermore, it has been reported that the negative effects of increased CFW on reproductive performance occur in ewes reared under poor nutrition (Masters and Ferguson, 2019). In this study, ewes were fed according to their nutrient requirement, which likely attenuated the potential negative effect of selection for increased CFW on reproductive performance. In addition, increased ewe LW in this study likely contributed to increased reproductive performance (Safari et al., 2005). Collectively, these results suggest that phenotypic reductions in FD and increases in both GFW and LW can be obtained without compromising phenotypic ewe lifetime reproduction.

In the Uruguayan wool industry, the highest economic reward from Merino sheep is driven by wool income (Chalkling et al., 2019). During the FMP period (1999–2010), estimated gross income per ewe lifetime (across four lambing opportunities) increased by approximately 26%, with little apparent change towards the end of the study period. This result is not unexpected given that over the last decade, the greatest price differentials (+50%) have been observed between the 19- and 17-micron categories (Cámara Mercantil de productos del País, 2020), although 16-micron wool has the highest value with a maximum of 15 USD/kg greasy (Diario el Telégrafo, 2018). During the CRILU period, there was only a small effect of finer wool on gross income due to this trait changing little over time. However, gross income would have increased if one-year-old lambs were included in the analysis given that the finest wool (14.6–15.6 μm) was produced by yearling lambs (Chapter III). In addition, a small positive change in net reproduction performance by the end of the study period would also positively impact on gross income but, this scenario was not evaluated in this chapter. Overall, this study indicates that reducing FD from 19 to 16 μm would increase the gross income per ewe by approximately 32%.

Since 1999, more than 18,500 frozen semen doses and 900 rams of the nucleus flock have been disseminated to commercial farmers throughout Uruguay (De Barbieri et al., 2015). At the same time, adult animal FD of commercial farmers who have utilized rams or semen from the nucleus flock, decreased from 21 to 18.5 µm (Montossi et al., 2005; Pérez et al., 2017). This reduction in FD represented an increase of at least 20% in estimated gross income per ewe lifetime. In commercial flocks, estimated gross income per ewe lifetime could increase 18% (from 255 to 299 USD) if ewe FD was reduced from 18.5 to 16 microns.

Conclusions

This study demonstrated that selection programs (FMP and CRILU) applied between 1999 and 2020 in Uruguay resulted in improvements in economically relevant wool traits in mixed-age ewes. Ewe FD decreased from 19 to 16 µm and GFW increased by approximately 0.2 kg. These favorable phenotypic trends in wool traits were accompanied by an increase of approximately 3 kg in LW at mating but a decrease in BCS at mating, with a small positive change in net reproduction performance. Increased estimated farmer gross income due to finer wool was obtained without compromising lifetime reproduction. However, farmers may wish to consider the potential impacts of increased body size and reduced fatness in adult ewes, especially if the ewes are raised under extensive conditions, facing continuous internal parasite challenges and periods of nutritional deficit. Further research, to evaluate genetic trends in the nucleus flock and genomic associations between wool, body, and reproductive traits is warranted to assist with the optimization of future selection programs in Uruguay.

Chapter V

Genetic and phenotypic relationships between ewe reproductive performance and wool and growth traits in Uruguayan Ultrafine Merino sheep

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Abstract

This study reports genetic parameters for yearling and adult wool and growth traits, and ewe reproductive performance. Data were sourced from an Uruguayan Merino flock involved in a long-term selection program focused on reduced fibre diameter (FD), and increased clean fleece weight (CFW) and live weight (LW). Pedigree and performance data from approximately 5,700 mixed-sex yearling lambs and 2,000 mixed-age ewes born between 1999 and 2019 were analysed. The number of records ranged from 1,267 to 5,738 for yearling traits, and from 1,931 to 7,079 for ewe productive and reproductive performance. Data on yearling and adult wool traits, LW and body condition score (BCS), yearling eye muscle area (Y_EMA), and fat thickness (Y_FAT), and several reproduction traits were analysed. The genetic relationships between FD and reproduction traits were not different from zero. Moderate unfavorable genetic correlations were found between adult CFW and ewe lifetime reproduction traits (−0.34 ± 0.08 and −0.33 ± 0.09 for the total number of lambs weaned and total lamb LW at weaning, respectively). There were moderate to strong positive genetic correlations between yearling LW and all reproduction traits other than ewe-rearing ability (−0.08 ± 0.11) and pregnancy rate (0.18 ± 0.08). The genetic correlations between Y_EMA and reproduction traits were positive and ranged from 0.15 to 0.49. Moderate unfavorable genetic correlations were observed between yearling FD and Y_FAT and between adult FD and BCS at mating (0.31 ± 0.12 and 0.23 ± 0.07, respectively). The genetic correlations between adult fleece weight and ewe BCS at different stages of the cycle were negative, but generally not different from zero. This study shows that selection for reduced FD is unlikely to have any effect on reproduction traits. Selection for increased yearling LW and Y_EMA will improve ewe reproductive performance. On the other hand, selection for increased adult CFW will reduce ewe reproductive performance, whereas selection for reduced FD will negatively impact body fat levels. Although unfavorable genetic relationships between wool traits and both FAT and ewe reproductive performance existed, simultaneous improvements in the traits would occur using appropriately designed indices.

Keywords: body condition score, correlations, heritability, Merino, reproduction, wool

Introduction

In the Australian and New Zealand fine-wool Merino sheep industries, breeding objectives typically include fibre diameter (FD), clean fleece weight (CFW), live weight (LW), and reproduction traits (Fogarty et al., 2006; Sheep Genetics, 2019). Knowledge of the genetic and phenotypic relationships among these traits is crucial to being able to objectively compare breeding strategies (Safari et al., 2007b). Numerous studies have reported genetic and phenotypic relationships among wool, growth, and reproduction traits within Merino sheep populations (e.g., Safari et al., 2007b; Huisman and Brown, 2008, 2009a, 2009b; Dominik and Swan, 2018; Bunter and Swan, 2021; Chapman et al., 2021). These genetic parameters have been utilized by Sheep Genetics through MERINOSELECT to calculate the selection indices.

In Uruguay, genetic improvement of Merino sheep has focused on selection at 12 months of age for an index that rewards reduced FD and increased CFW and LW (Ciappesoni et al., 2014). This index has been developed based on parameter estimates from Uruguayan Merino sheep (Ciappesoni et al., 2006, 2011). Chapter IV showed that simultaneous genetic improvements in FD, CFW, and LW resulted in phenotypically heavier ewes, that produced slightly more weight of lamb weaned over their lifetime. This result agrees with positive genetic correlations between LW and number of lambs weaned per ewe joined (NLWEJ) reported by Safari et al. (2007b) and Chapman et al. (2021). Accordingly, previous Merino studies suggested that selection for reduced FD is unlikely to have any effect on NLWEJ (Safari et al., 2007b; Dominik and Swan, 2018), although Chapman et al. (2021) reported an unfavorable genetic correlation between adult FD and NLWEJ. It also has been found that predictions of genetic gain for an index that rewards reduced FD and increased CFW in Australian Merino sheep resulted in unchanged NLWEJ (Brown and Swan, 2016). In addition, Piper et al. (2007) showed that a multi-trait breeding objective did increase CFW without compromising NLWEJ. However, moderate to high unfavorable genetic correlations between CFW and NLWEJ have been reported in Merino sheep (Piper et al., 2007; Safari et al., 2007b; Dominik and Swan, 2018). This suggests that genetically heavier fleeces are associated with reduced ewe reproductive performance. Although phenotypic responses to the current Uruguayan breeding program have been established (Chapter IV), there is a lack of information on genetic parameters involving reproduction and other production traits in Uruguayan Merino sheep.

The benefit of including non-wool traits in Merino breeding programs has been evaluated in countries like Australia and New Zealand (Walkom and Brown, 2014; Young and Thomson, 2014; Brown and Swan, 2016; Chapman et al., 2021). Predictions of selection response for standard MERINOSELECT indices indicate that measuring fat and eye muscle depth had minimal impact on NLWEJ, whereas measuring reproduction traits directly resulted in 17%, 27%, and 45% additional economic gain for indices focussed on improving wool quality, wool production, and wool and meat production, respectively (Brown and Swan, 2016). Australia now provides breeding values not only for NLWEJ, but also for conception, litter size, and rearing ability (Bunter et al., 2021). Walkom and Brown (2014) showed that including reproduction traits together with ultrasound carcass traits, worm egg count, fly strike, body condition score (BCS), and weight changes within the standard MERINOSELECT indices resulted in greater genetic improvements in profit. With the exception of fly strike, the above-mentioned traits are relevant in Uruguayan Merino sheep (Chapter IV; Sánchez et al., 2021). However, there is no information on the genetic parameters involving ultrasound carcass traits and BCS with other production and reproduction traits in Merino sheep of Uruguay.

This work aimed to report estimates of heritability and genetic and phenotypic relationships among and between yearling wool and growth traits, including ultrasound measures of yearling fat thickness (Y_FAT), adult ewe LW and BCS, and ewe reproductive performance. This study will update the current genetic parameters for production traits used in the Uruguayan genetic evaluation. More importantly, this work will provide for the first time, genetic parameters for ultrasound scan traits, BCS, and reproduction traits in Merino sheep of Uruguay. This information would allow construction of selection indices that incorporate other important traits in breeding objectives for Uruguayan Merino sheep and identification of appropriate selection strategies.

Materials and Methods

Location and period

Pedigree and performance data collected from 1999 to 2020 by the Glencoe Experimental Unit of the National Institute of Agricultural Research of Uruguay (INIA, 32◦00′21” S and 57◦08′06” W) were analysed. This region has a temperate climate, with highly variable annual rainfall. Over the study period, total annual rainfall ranged from 830 to 2,800 mm (Banco de datos agroclimático, INIA Uruguay). This study was conducted with the approval of the INIA Animal Ethics Committee (INIA_2018.2).

Animals and traits

Data from approximately 5,700 mixed-sex yearling progeny and 2,000 mixed-age ewes born in a single Merino flock between 1999 and 2019 were analysed. The establishment, genetic selection objectives, nutritional conditions, and management of this flock have previously been reported in Chapters III and IV. Briefly, the Merino flock was established in 1999, from 475 ewes provided by Uruguayan Merino stud breeders or commercial farmers. Each year, ewes were managed as a single flock and inseminated with either imported semen (from Australia) or flock-born rams. The selection of replacements was based on phenotypic and genetic criteria. All lambs were visually evaluated by the Uruguayan Wool Secretariat staff. Visually acceptable animals were then selected based on the highest selection index values (Chapter III). During the first 10 years, the selection objective of this flock was to reduce FD (to produce 19.0 µm or finer wool) while allowing for a slight loss in CFW, whereas from 2011 to 2020, the breeding objective was focused on maintaining FD (less than 15.5 µm), while increasing both CFW and LW.

Production traits

Wool and growth traits were measured at different stages throughout the animals' life utilizing the procedures described in Chapter III and IV. Briefly, traits recorded at yearling age (298 to 432 d) included fibre diameter (Y_FD), greasy fleece weight (Y_GFW), clean fleece weight (Y_CFW), staple length (Y_SL), and live weight immediately post-shearing (Y_LW). Adult wool traits at mid to late-pregnancy shearing (July and August) were the same as those described at yearling age, but the abbreviations are prefixed "A" rather than "Y" as follows: A_FD, A_GFW, A_ CFW, and A_SL for FD, greasy fleece weight, CFW, and staple length, respectively. Adult growth traits comprised LW and BCS at mating (LWM and BCSM, respectively), pre-lambing (LWPL and BCSPL, respectively), and at weaning (LWW and BCSW, respectively). Yearling eye muscle area (Y_EMA) and Y_FAT were recorded over 9 years (2010, 2011, and from 2013 to 2019) after shearing. Lambs were body condition scored (Y_BCS; five-point scale, from 1 skinny to 5 fat; Jefferies, 1961) after shearing from 2016 to 2020 according to a five-point scale (Jefferies, 1961), whereas all other production traits were generally measured over the whole study period (from 2001 to 2020, ewe LWM information was missing in 2001).

Reproduction traits

Adult ewe reproduction traits analysed included pregnancy rate (PR) and lambing potential (LP) which were defined as ewe pregnancy status (pregnant or non-pregnant) and the number of ultrasound-scanned fetuses per ewe joined (0, 1, or ≥2), respectively. Ewe rearing ability (ERA) was calculated as the number of lambs weaned per number of fetuses scanned (0, 0.5, or 1). As the proportion of triplets was low (1.3%), twins and triplets were merged into one category. The number of lambs weaned (NLWEJ) was calculated as the number of lambs weaned per individual ewe joined. The total number of lambs weaned (TLW) per ewe lifetime was defined as the sum of the number of lambs weaned per ewe across all her lambing opportunities in her lifetime (1 up to 8 mating seasons).

Total lamb LW at weaning per ewe lifetime (TLWW) was calculated by adding the LW at weaning (adjusted to 120 d of age) of all lambs each ewe had throughout her life (Chapter IV). The number of lambing opportunities was calculated as the number of mating seasons each ewe had until she died or was culled.

Statistical analysis

Descriptive statistical analyses were undertaken utilizing the SAS program (version 9.4, SAS Institute Inc., Cary, NC, USA). To identify and exclude outliers, a robust regression model (PROC ROBUSTREG) was applied to each trait separately. Fixed effects were initially tested for significance utilizing the general linear model procedure in SAS version 9.4 (SAS Institute Inc., Cary, NC, USA). The models included only fixed effects that had previously been shown to be significant. Tables 5.1–5.3 present the significant fixed effects for yearling and adult wool and growth, and reproduction traits, respectively. The full model for yearling traits included the interaction of year of birth by sex (42 levels: 1999 to 2019, male and female), birth-rearing rank (3 levels: single-single, multiple (≥2) single, and multiple-multiple), and dam age (3 levels: 2-yr-old, 3 to 6 years old, and 7 years or older) as fixed effects. For all yearling traits, age at the time of measurement was fitted as a covariate in the model.

Table 5.1 Significant fixed effects model for yearling traits.

Trait	**Fixed effect**		
	Year*sex interaction	**Birth-rearing rank**	**Dam age**
Y_FD	√	√	√
Y_CFW	√	√	√
Y_GFW	√	√	√
Y_SL	√	-	-
Y_LW	√	√	√
Y_FAT	√	-	-
Y_EMA	√	√	-

Y_FD, Y_CFW, Y_GFW, Y_SL, Y_LW, Y_EMA, and Y_FAT correspond to yearling fibre diameter, clean fleece weight, greasy fleece weight, staple length, live weight at shearing, eye muscle area, and fat thickness, respectively.

Table 5.2 Significant fixed effects model for adult wool and growth traits.

Trait	**Fixed effect**				
	Record year	**Type of birth**	**Age**	**Lambing potential**	**Lamb rearing type**
A_FD	√	√	√	√	-
A_CFW	√	√	√	√	-
A_GFW	√	√	√	√	-
A_SL	√	√	√	-	-
LWM	√	√	√	-	-
LWPL	√	√	√	√	-
LWW	√	√	√	-	√
BCSM	√	-	√	-	-
BCSPL	√	-	√	√	-
BCSW	√	√	√	-	√

A_FD, A_CFW, A_GFW, and A_SL refer to adult fibre diameter, clean fleece weight, greasy fleece weight, and staple length, respectively. LWM, LWPL, and LWW correspond to ewe live weight at mating, pre-lambing, and at weaning, respectively. BCSM, BCSPL, and BCSW correspond to ewe body condition score at mating, pre-lambing, and at weaning, respectively. Type of birth: 2 levels (single-born or multiple-born).

Table 5.3 Significant fixed effects model for reproduction traits.

Trait	**Fixed effect**						
	Record year	**Type of birth**	**Age**	**Mating method**	**Lambing potential**	**Lambing opportunities**	**Birth year**
PR	√	√	√	√	-	-	-
LP	√	√	√	√	-	-	-
ERA	√	√	√	√	√	-	-
NLWEJ	√	√	√	√	-	-	-
TLW	-	-	-	√	-	√	√
TLWW	-	-	-	√	-	√	√

PR, LP, ERA, and NLWEJ correspond to pregnancy rate, lambing potential, ewe rearing ability, and number of lambs weaned per ewe joined, respectively. Type of birth: 2 levels (single-born or multiple-born).

For adult wool and growth traits, fixed effects included record year (20 levels: 2001 to 2020), type of birth (2 levels: single or multiple), age (6 levels: 2 to ≥ 7 years old), current lambing potential (3 levels: non-pregnant, single fetus, and ≥ 2 fetuses), and lamb rearing type (5 levels: non-lambed, lambed and subsequently lost their lambs, lambed single and weaned one lamb, lambed multiple and weaned one lamb, lambed multiple and weaned multiple lambs). For wool traits, days of wool growth (number of days between shearings) were fitted as a covariate in the model.

With the exception of TLW and TLWW, reproduction traits were analysed as categorical variables. The full model for reproduction traits included record year, birth year, type of birth, age, mating method (three levels according to the mating method utilized in the first estrus cycle: intrauterine artificial insemination, cervical artificial insemination, and natural mating), and the number of lambing opportunities (8 levels: 1 to 8 mating seasons) as fixed effects.

All genetic parameters were estimated utilizing the Julia for Whole-Genome Analyses Software (JWAS) software (Cheng et al., 2018). Estimates of (co) variance components were obtained utilizing a Bayesian method based on Markov chain Monte Carlo (MCMC) sampling (Blasco, 2017). For each parameter, the Gelman–Rubin test was run to test the convergence of the chains (Fernández-i- Marín, 2016). All parameters had R values (potential scale reduction factors) close to 1.0, which suggested MCMC chains converged to the target posterior distributions (Crook et al., 2019). Based on these diagnostics, a chain of 70,000 iterations was run, after a burn-in of 5,000 rounds, and the output was thinned to every 10th iteration.

Definition of genetic groups

It is expected that the locally sourced animals would have had different genetic means to imported sires, and to animals born in the flock. To account for potential genetic differences existing between source flocks, founder animals (and non-founder animals with one or more unknown parents) were accounted for in the model by assigning these animals to distinct unknown parent groups (UPG) (Quaas, 1988; Mrode, 2005; Wolak and Reid, 2017) based on the flock of origin.

Linear models

A univariate model was applied to estimate the heritability for each trait. Bivariate analyses were utilized to estimate genetic and phenotypic correlations among production and reproduction traits. All adult production traits, PR, LP, ERA, and NLWEJ were treated as repeated records across years. The linear mixed model can be written as:

$$y = X\beta + Qg + Za + Wpe + e$$

where y is the vector of observations on one trait, β is the vector of unknown fixed effects, g is the vector of the unknown fixed effects for UPG, a is the vector of random animal effects, pe is a vector of random permanent environmental effects to account for the covariance between observations from the same individual, e is the vector of random residual effect, and X, Q, Z, and W are incidence matrices relating records to fixed, UPG, animal effects, and permanent environmental effects, respectively.

The animal permanent environmental effect was only fitted to the adult traits where records were repeated. A maternal effect on yearling wool traits and LW was tested but were not significant.

Results

A summary of the data is shown in Table 5.4. Yearling expressions include both female and male lambs. The number of records ranged from 1,267 to 5,738 for yearling traits, and from 1,931 to 7,079 for multiple ewe ages (2 to 10 years old). The unadjusted mean FD was 15.8 μm for yearlings and 16.6 μm for adults. Mixed-age ewe LW and BCS at mating were 47.4 kg and 3.2, respectively. Over the study period, the average NLWEJ was 0.71.

To describe the results, mean heritability, and correlations between traits were classified as high ($|r| \geq 0.45$), moderate ($0.2 \geq |r| < 0.45$), or low ($0.2 > |r|$) (Wuliji et al., 2001). The lower and upper bound of the highest posterior density interval at 95% are presented in Appendix I (Tables 2 to 8).

Table 5.4 Descriptive statistics for wool, body growth, and reproduction traits in yearling and adult animals over the entire study period (1999–2020).

Age	Trait	Mean	SD[1]	Min	Max	N
Yearling	Fibre diameter (Y_FD, µm)	15.8	1.61	12.4	22.7	5,704
	Clean fleece weight (Y_CFW, kg)	2.38	0.68	0.78	4.52	5,646
	Greasy fleece weight (Y_GFW, kg)	3.16	0.91	1.15	6.16	5,653
	Staple length (Y_SL, cm)	8.5	1.96	3.5	15.0	5,738
	Live weight (Y_LW, kg)	45.2	10.6	18.5	76.5	5,674
	Eye muscle area (Y_EMA, cm^2)	9.8	2.58	3.7	17.8	2,291
	Fat thickness (Y_FAT, mm)	2.6	0.93	0.6	5.8	2,291
	Body condition score (Y_BCS)	3.5	0.47	2.0	4.5	1,267
Mixed-age ewes	Fibre diameter (A_FD, µm)	16.6	1.75	11.7	24.5	7,079
	Clean fleece weight (A_CFW, kg)	2.80	0.51	1.40	4.50	6,288
	Greasy fleece weight (A_GFW, kg)	3.50	0.63	1.90	5.80	6,812
	Staple length (A_SL, cm)	8.7	1.29	4.5	13.0	6,403
	Live weight at mating (LWM, kg)	47.4	5.97	30.0	70.0	6,589
	Live weight pre-lambing (LWPL, kg)	48.9	7.10	28.0	76.0	6,332
	Live weight at weaning (LWW, kg)	48.4	6.39	29.0	71.5	4,379
	Body condition score at mating (BCSM)[2]	3.2	0.65	1.75	5.0	6,442
	Body condition score pre-lambing (BCSPL)[2]	3.1	0.60	1.5	5.0	6,274
	Body condition score at weaning (BCSW)[2]	2.9	0.60	1.5	5.0	4,064
	Pregnancy rate (PR)	0.73	0.44	0	1	6,376
	Lambing potential (LP)	0.91	0.66	0	3	6,376
	Number of lambs weaned per ewe joined (NLWEJ)	0.71	0.64	0	3	6,376
	Ewe rearing ability (ERA)[3]	0.80	0.38	0	1	4,606
	Total number of lambs weaned (TLW)[4]	2.4	1.95	0	12	1,931
	Total lamb live weight at weaning (TLWW)[5]	58.4	48.17	0	286.5	1,931

[1] SD: standard deviation. N: number of records. [2] Body condition score: scale 1-5. [3] Ewe rearing ability (ERA) was calculated as the number of lambs weaned per number of fetuses scanned.[4,5] TLW and TLWW correspond to the lifetime reproductive performance of each individual ewe (one record per ewe). TLW was computed as the sum of the number of lambs weaned per ewe over her lifetime. TLWW was calculated by adding the LW at weaning (adjusted to 120 days of age) of all lambs each ewe had in her life.

Heritability for production and reproduction traits

Posterior mean and standard deviation of heritability for production traits at yearling and adult ages are shown in Tables 5.5 and 5.6, respectively. The heritabilities for yearling wool traits were moderate to high, and ranged from 0.38 to 0.73. Y_LW and Y_EMA were highly heritable, whereas Y_FAT and Y_BCS showed a moderate level of heritability (0.27 and 0.28, respectively). Heritability values for adult wool traits were generally similar to those described at yearling age, and ranged from 0.30 to 0.71. Ewe LW across all stages of the annual reproductive cycle (at mating, pre-lambing, and at weaning) were highly heritable (0.52 to 0.57), whereas the heritabilities for ewe BCS were low to moderate (0.15 to 0.23). The reproduction traits were lowly heritable (0.14 ± 0.03, 0.11 ± 0.02, 0.04 ± 0.01, and 0.08 ± 0.02 for PR, LP, ERA, and NLWEJ, respectively).

Correlations among and between wool and growth traits

Genetic and phenotypic correlations for wool and growth traits at yearling age are presented in Table 5.5. The genetic correlations between Y_FD and both Y_CFW and Y_LW were low (0.09 and −0.08, respectively). A moderate positive genetic correlation was found between Y_FD and Y_SL (0.23), whereas the genetic correlations between Y_SL and fleece weight were high (0.58 and 0.70 for GFW and CFW, respectively). There was a high positive genetic correlation between Y_CFW and Y_GFW (0.87), and both were moderately positively genetically correlated with Y_LW (0.42 and 0.43, respectively). The genetic correlation between Y_FD and Y_FAT was positive and moderate (0.31), and between Y_FAT and fleece weight was close to zero (around 0.05). For all these traits, the phenotypic correlations were generally in the same direction as the genetic ones.

Table 5.6 summarizes the correlations between wool and growth traits in mixed-age ewes (2 to 10 years old). The genetic and phenotypic correlations between A_FD and both A_CFW and A_GFW were positive and moderate, with estimates of about 0.30. The genetic correlations between adult LW at different stages (at mating, pre-lambing, at weaning) were high, estimates greater than 0.93. Adult BCS across stages was highly positively genetically correlated (estimates of about 0.77). The genetic correlations between adult LW and A_FD were low and not different from zero. There was a moderate positive genetic correlation between A_FD and BCSM (0.23 ± 0.07). The genetic correlations between fleece weight (A_CFW and A_GFW) and ewe BCS at different stages of the cycle were negative, and ranged from −0.05 to −0.23, whereas the phenotypic correlations were generally positive and low.

Table 5.5 Estimates of heritability (posterior mean, bold on diagonal), and genetic (below diagonal), and phenotypic (above diagonal) correlations among wool and growth traits at yearling age. Posterior standard deviations are in parentheses.

Trait	Y_FD	Y_CFW	Y_GFW	Y_SL	Y_LW	Y_BCS	Y_EMA	Y_FAT
Y_FD	**0.73 (0.03)**	0.13 (0.03)	0.15 (0.03)	0.18 (0.03)	0.01 (0.03)	0.22 (0.06)	0.10 (0.05)	0.19 (0.04)
Y_CFW	0.09 (0.07)	**0.38 (0.03)**	0.91 (0.01)	0.45 (0.02)	0.40 (0.02)	0.11 (0.04)	0.15 (0.03)	0.08 (0.03)
Y_GFW	0.11 (0.07)	0.87 (0.01)	**0.38 (0.03)**	0.37 (0.02)	0.40 (0.02)	0.09 (0.03)	0.12 (0.03)	0.06 (0.02)
Y_SL	0.23 (0.07)	0.70 (0.04)	0.58 (0.05)	**0.51 (0.03)**	0.24 (0.02)	0.19 (0.03)	0.16 (0.03)	0.12 (0.03)
Y_LW	-0.08 (0.06)	0.42 (0.05)	0.43 (0.05)	0.27 (0.05)	**0.63 (0.03)**	0.43 (0.03)	0.55 (0.02)	0.36 (0.03)
Y_BCS	0.29 (0.19)	0.07 (0.18)	0.04 (0.17)	0.17 (0.15)	0.60 (0.09)	**0.28 (0.07)**	0.42 (0.03)	0.30 (0.03)
Y_EMA	0.01 (0.11)	0.16 (0.09)	0.12 (0.09)	0.19 (0.09)	0.69 (0.04)	0.68 (0.08)	**0.45 (0.06)**	0.34 (0.02)
Y_FAT	0.31 (0.12)	0.07 (0.12)	0.03 (0.11)	0.22 (0.10)	0.60 (0.07)	0.51 (0.14)	0.56 (0.09)	**0.27 (0.05)**

Y_FD, Y_CFW, Y_GFW, Y_SL, Y_LW, Y_BCS, Y_EMA, and Y_FAT correspond to yearling fibre diameter, clean fleece weight, greasy fleece weight, staple length, live weight at shearing, body condition score, eye muscle area, and fat thickness, respectively.

Table 5.6 Estimates of heritability (posterior mean, bold on diagonal), and genetic (below diagonal), and phenotypic (above diagonal) correlations among wool and growth traits in mixed-age ewes. Posterior standard deviations are in parentheses.

Trait	A_FD	A_CFW	A_GFW	A_SL	LWM	LWPL	LWW	BCSM	BCSPL	BCSW
A_FD	**0.71 (0.02)**	0.33 (0.03)	0.30 (0.03)	0.09 (0.03)	0.12 (0.03)	0.09 (0.03)	0.03 (0.04)	0.18 (0.02)	0.11 (0.03)	0.04 (0.03)
A_CFW	0.32 (0.06)	**0.48 (0.03)**	0.94 (0.01)	0.39 (0.03)	0.25 (0.04)	0.16 (0.04)	0.09 (0.04)	0.18 (0.02)	0.07 (0.03)	-0.02 (0.03)
A_GFW	0.27 (0.06)	0.93 (0.01)	**0.49 (0.02)**	0.32 (0.03)	0.27 (0.03)	0.18 (0.04)	0.12 (0.04)	0.17 (0.03)	0.07 (0.03)	-0.02 (0.03)
A_SL	0.08 (0.06)	0.45 (0.07)	0.34 (0.07)	**0.30 (0.02)**	0.14 (0.03)	0.10 (0.03)	0.08 (0.03)	0.11 (0.02)	0.10 (0.02)	0.05 (0.02)
LWM	0.02 (0.05)	0.07 (0.07)	0.11 (0.07)	0.12 (0.07)	**0.56 (0.02)**	0.75 (0.01)	0.63 (0.02)	0.46 (0.02)	0.36 (0.02)	0.17 (0.03)
LWPL	0.04 (0.05)	0.08 (0.07)	0.11 (0.07)	0.13 (0.07)	0.96 (0.01)	**0.57 (0.02)**	0.63 (0.02)	0.31 (0.02)	0.38 (0.02)	0.20 (0.03)
LWW	0.02 (0.06)	0.11 (0.08)	0.17 (0.08)	0.13 (0.08)	0.96 (0.01)	0.94 (0.01)	**0.52 (0.03)**	0.15 (0.02)	0.21 (0.03)	0.47 (0.02)
BCSM	0.23 (0.07)	-0.05 (0.08)	-0.14 (0.09)	0.20 (0.08)	0.47 (0.06)	0.45 (0.06)	0.48 (0.06)	**0.16 (0.02)**	0.40 (0.02)	0.15 (0.02)
BCSPL	0.13 (0.06)	-0.20 (0.08)	-0.23 (0.08)	0.26 (0.07)	0.46 (0.06)	0.50 (0.06)	0.45 (0.06)	0.80 (0.04)	**0.23 (0.02)**	0.23 (0.02)
BCSW	0.09 (0.08)	-0.13 (0.10)	-0.15 (0.10)	0.13 (0.09)	0.53 (0.07)	0.52 (0.07)	0.57 (0.06)	0.77 (0.04)	0.75 (0.05)	**0.15 (0.02)**

A_FD, A_CFW, A_GFW, and A_SL refer to adult fibre diameter, clean fleece weight, greasy fleece weight, and staple length, respectively. LWM, LWPL, and LWW correspond to ewe live weight at mating, pre-lambing, and at weaning, respectively. BCSM, BCSPL, and BCSW correspond to ewe body condition score at mating, pre-lambing, and at weaning, respectively.

Correlations between yearling and adult traits

Genetic and phenotypic correlations between yearling and adult traits are presented in Table 5.7. The genetic correlations between Y_FD and A_FD, and between Y_CFW and A_CFW were positive and high (0.91 and 0.81, respectively). For these traits, the positive phenotypic correlations were lower than the corresponding genetic correlations (0.55 and 0.77, respectively). Low to moderate negative correlations were found between Y_FAT and A_CFW, with the genetic being −0.26 and phenotypic −0.10. The genetic and phenotypic correlations between Y_FD and ewe BCSM were positive and low (0.16 and 0.06, respectively). High positive genetic (0.95) and phenotypic (0.69) correlations were found between Y_LW and ewe LWM. The same trend was observed between Y_EMA and ewe LWM, but in this case, the genetic and phenotypic correlations were 0.66 and 0.36, respectively. There was a high positive genetic correlation between Y_FAT and BCSM (0.61), although the phenotypic correlation was low (0.18).

Correlations between production and reproduction traits

The phenotypic and genetic correlations between ewe production and reproduction traits are shown in Table 5.8. The genetic relationships between reproduction traits and A_FD were not different from zero (see Appendix I, Table 5 for details). Low to moderate negative genetic correlations were found between reproduction traits and A_CFW, with the highest values being for lifetime reproduction traits (−0.34 and −0.33 for TLW and TLWW, respectively). The phenotypic correlations between reproduction traits and A_CFW were negligible.

Genetic correlations between LWM and reproduction traits were either not different from zero or positive, except for ERA, which was moderately negative. The genetic correlations between BCSM and PR, LP, ERA, NLWEJ were negative, but not different from zero. High negative genetic correlations were found between BCSM and lifetime reproduction traits (−0.54 and −0.44 for TLW and TLWW, respectively). The phenotypic relationships between reproduction traits and both LWM and BCSM were generally positive and low. Moderate to high negative phenotypic correlations were found between BCSW and NLWEJ (−0.32) and ERA (−0.44).

Genetic and phenotypic correlations between yearling production and adult reproduction traits are presented in Table 5.9. Genetic correlations between yearling wool traits and ewe reproductive performance were generally not different from zero. There were positive genetic correlations between ewe reproduction traits and Y_LW, except for ERA which was negative but not different from zero. The genetic correlations between Y_EMA and reproduction traits were positive and ranged from 0.15 to 0.49. The phenotypic relationships between yearling traits and ewe reproductive performance were generally low or close to zero.

Table 5.7 Genetic and phenotypic correlations (posterior mean) among production traits at yearling age and adult ewes. Posterior standard deviations are in parentheses.

Trait	**Y_FD**	**Y_CFW**	**Y_GFW**	**Y_SL**	**Y_LW**	**Y_BCS**	**Y_EMA**	**Y_FAT**
				Genetic correlations				
A_FD	0.91 (0.01)	0.34 (0.06)	0.27 (0.06)	0.32 (0.05)	0.04 (0.05)	0.17 (0.17)	-0.04 (0.09)	0.19 (0.14)
A_CFW	0.27 (0.06)	0.81 (0.03)	0.79 (0.03)	0.31 (0.05)	0.25 (0.05)	0.20 (0.22)	-0.16 (0.08)	-0.26 (0.11)
A_GFW	0.25 (0.05)	0.71 (0.03)	0.84 (0.02)	0.22 (0.05)	0.28 (0.05)	0.08 (0.22)	-0.18 (0.09)	-0.26 (0.10)
LWM	0.09 (0.06)	0.46 (0.05)	0.50 (0.05)	0.15 (0.05)	0.95 (0.01)	0.72 (0.09)	0.66 (0.05)	0.47 (0.09)
BCSM	0.16 (0.08)	0.08 (0.08)	0.06 (0.08)	0.19 (0.07)	0.48 (0.06)	0.51 (0.14)	0.61 (0.08)	0.61 (0.08)
				Phenotypic correlations				
A_FD	0.77 (0.01)	0.20 (0.03)	0.16 (0.03)	0.22 (0.03)	0.08 (0.03)	0.18 (0.07)	0.09 (0.06)	0.14 (0.06)
A_CFW	0.23 (0.04)	0.55 (0.02)	0.54 (0.02)	0.19 (0.03)	0.23 (0.03)	0.08 (0.07)	-0.01 (0.05)	-0.10 (0.06)
A_GFW	0.21 (0.03)	0.50 (0.02)	0.61 (0.02)	0.16 (0.03)	0.26 (0.03)	0.01 (0.07)	-0.03 (0.06)	-0.10 (0.05)
LWM	0.06 (0.04)	0.19 (0.03)	0.21 (0.03)	0.07 (0.03)	0.69 (0.01)	0.37 (0.05)	0.36 (0.04)	0.17 (0.04)
BCSM	0.06 (0.03)	0.01 (0.02)	-0.01 (0.02)	0.05 (0.02)	0.15 (0.02)	0.21 (0.05)	0.23 (0.04)	0.18 (0.04)

Y_FD, Y_CFW, Y_GFW, Y_SL, Y_LW, Y_BCS, Y_EMA, and Y_FAT correspond to yearling fibre diameter, clean fleece weight, greasy fleece weight, staple length, live weight at shearing, body condition score, eye muscle area, and fat thickness, respectively. A_FD, A_CFW, A_GFW, and A_SL correspond to adult fibre diameter, clean fleece weight, greasy fleece weight, and staple length, respectively. LWM and BCSM refer to ewe live weight and body condition score at mating, respectively.

Table 5.8 Genetic and phenotypic correlations (posterior mean) between reproductive performance and production traits in adult ewes. Posterior standard deviations are in parentheses.

Trait	**PR**	**LP**	**ERA**	**NLWEJ**	**TLW**	**TLWW**
			Genetic correlations			
A_FD	-0.01 (0.09)	-0.08 (0.09)	-0.01 (0.12)	-0.04 (0.10)	-0.09 (0.09)	-0.03 (0.09)
A_CFW	-0.21 (0.09)	-0.21 (0.10)	-0.14 (0.13)	-0.22 (0.10)	-0.34 (0.08)	-0.33 (0.09)
A_GFW	-0.17 (0.09)	-0.17 (0.10)	-0.14 (0.13)	-0.18 (0.11)	-0.30 (0.09)	-0.30 (0.08)
A_SL	-0.07 (0.09)	0.02 (0.10)	-0.16 (0.12)	-0.05 (0.11)	-0.05 (0.10)	-0.01 (0.10)
LWM	0.07 (0.08)	0.21 (0.10)	-0.23 (0.11)	0.06 (0.11)	-0.03 (0.08)	0.21 (0.09)
LWPL	0.16 (0.08)	0.31 (0.09)	-0.14 (0.11)	0.18 (0.11)	0.15 (0.09)	0.36 (0.08)
LWW	0.15 (0.08)	0.45 (0.09)	-0.21 (0.13)	0.23 (0.12)	0.27 (0.09)	0.38 (0.09)
BCSM	-0.12 (0.09)	-0.09 (0.11)	-0.16 (0.13)	-0.17 (0.12)	-0.54 (0.06)	-0.44 (0.08)
BCSPL	-0.03 (0.09)	0.00 (0.11)	-0.02 (0.13)	0.00 (0.12)	-0.31 (0.09)	-0.17 (0.10)
BCSW	0.04 (0.09)	0.23 (0.12)	-0.12 (0.14)	0.03 (0.14)	0.06 (0.13)	0.10 (0.12)
			Phenotypic correlations			
A_FD	-0.06 (0.07)	-0.09 (0.07)	0.01 (0.02)	0.01 (0.03)	0.03 (0.03)	0.04 (0.03)
A_CFW	-0.04 (0.10)	0.06 (0.09)	0.03 (0.02)	0.04 (0.03)	-0.02 (0.03)	-0.01 (0.03)
A_GFW	-0.04 (0.09)	0.00 (0.08)	0.03 (0.02)	0.04 (0.03)	0.01 (0.03)	-0.01 (0.03)
A_SL	-0.04 (0.03)	-0.02 (0.02)	0.01 (0.02)	-0.01 (0.02)	0.01 (0.03)	0.01 (0.03)
LWM	0.12 (0.03)	0.16 (0.02)	0.05 (0.02)	0.14 (0.02)	0.19 (0.03)	0.26 (0.03)
LWPL	0.08 (0.07)	0.09 (0.07)	0.07 (0.02)	0.16 (0.03)	0.11 (0.03)	0.17 (0.03)
LWW	-0.03 (0.06)	-0.02 (0.04)	-0.49 (0.06)	-0.19 (0.05)	0.11 (0.03)	0.15 (0.03)
BCSM	0.07 (0.02)	0.08 (0.02)	0.04 (0.02)	0.09 (0.02)	0.04 (0.03)	0.10 (0.03)
BCSPL	0.04 (0.09)	0.01 (0.10)	0.05 (0.02)	0.09 (0.03)	0.04 (0.03)	0.08 (0.03)
BCSW	-0.13 (0.06)	-0.04 (0.04)	-0.44 (0.08)	-0.32 (0.06)	0.02 (0.03)	0.03 (0.03)

A_FD, A_CFW, A_GFW, and A_SL correspond to adult fibre diameter, clean fleece weight, greasy fleece weight, and staple length, respectively. LWM, LWPL, and LWW correspond to live weight at mating, pre-lambing, and at weaning, respectively. BCSM, BCSPL, and BCSW refer to body condition score at mating, pre-lambing, and at weaning, respectively. PR, LP, ERA, and NLWEJ correspond to pregnancy rate, lambing potential, ewe rearing ability, and number of lambs weaned per ewe joined, respectively. All these production and reproduction traits were repeat measures across years. TLW and TLWW correspond to lifetime reproductive performance of each individual ewe (one record per ewe). TLW represents the total number of lambs weaned, which was computed as the sum of the number of lambs weaned per ewe over her lifetime. TLWW correspond to the total lamb live weight at weaning, which was calculated by adding the LW at weaning (adjusted to 120 days of age) of all lambs each ewe had in her life.

Table 5.9 Genetic and phenotypic correlations (posterior mean) between reproductive performance and production traits at yearling age. Posterior standard deviations are in parentheses.

Trait	PR	LP	ERA	NLWEJ	TLW	TLWW
			Genetic correlations			
Y_FD	0.05 (0.08)	0.05 (0.09)	-0.03 (0.12)	0.05 (0.10)	0.03 (0.15)	0.13 (0.14)
Y_CFW	0.11 (0.08)	0.12 (0.09)	0.02 (0.12)	0.16 (0.10)	0.09 (0.14)	0.24 (0.14)
Y_GFW	0.10 (0.09)	0.13 (0.10)	-0.03 (0.13)	0.05 (0.11)	0.15 (0.13)	0.26 (0.13)
Y_SL	0.02 (0.08)	0.02 (0.09)	0.08 (0.12)	0.10 (0.10)	0.00 (0.14)	0.12 (0.13)
Y_LW	0.18 (0.08)	0.31 (0.08)	-0.08 (0.11)	0.26 (0.09)	0.26 (0.12)	0.50 (0.11)
Y_BCS	0.09 (0.13)	0.08 (0.19)	0.07 (0.16)	0.03 (0.14)	0.16 (0.24)	0.21 (0.19)
Y_EMA	0.19 (0.10)	0.30 (0.11)	0.15 (0.16)	0.39 (0.12)	0.33 (0.17)	0.49 (0.14)
Y_FAT	0.06 (0.12)	0.00 (0.16)	0.17 (0.16)	0.21 (0.17)	0.06 (0.22)	0.18 (0.20)
			Phenotypic correlations			
Y_FD	0.05 (0.04)	0.03 (0.03)	0.05 (0.03)	0.05 (0.03)	0.03 (0.03)	0.05 (0.03)
Y_CFW	0.02 (0.03)	0.04 (0.03)	0.07 (0.02)	0.07 (0.03)	0.07 (0.03)	0.06 (0.02)
Y_GFW	0.01 (0.03)	0.03 (0.03)	0.06 (0.03)	0.07 (0.03)	0.06 (0.02)	0.05 (0.02)
Y_SL	0.10 (0.03)	0.08 (0.03)	0.06 (0.02)	0.09 (0.03)	0.06 (0.02)	0.08 (0.03)
Y_BCS	0.19 (0.07)	0.12 (0.06)	0.05 (0.06)	0.07 (0.09)	0.10 (0.06)	0.16 (0.06)
Y_LW	0.08 (0.03)	0.09 (0.02)	0.03 (0.03)	0.09 (0.03)	0.09 (0.02)	0.14 (0.03)
Y_EMA	0.21 (0.05)	0.15 (0.04)	0.03 (0.04)	0.17 (0.04)	0.17 (0.04)	0.21 (0.04)
Y_FAT	0.05 (0.05)	0.01 (0.04)	0.05 (0.04)	0.04 (0.04)	0.07 (0.04)	0.10 (0.04)

Y_FD, Y_CFW, Y_GFW, Y_SL, Y_LW, Y_BCS, Y_EMA, and Y_FAT correspond to yearling fibre diameter, clean fleece weight, greasy fleece weight, staple length, live weight at shearing, body condition score, eye muscle area, and fat thickness, respectively. PR, LP, ERA, and NLWEJ correspond to pregnancy rate, lambing potential, ewe rearing ability, and number of lambs weaned per ewe joined. These traits were repeat measures across years. TLW and TLWW correspond to lifetime reproductive performance of each ewe (one record per ewe). TLW represents the total number of lambs weaned, which was computed as the sum of the number of lambs weaned per ewe in her lifetime. TLWW correspond to the total lamb live weight at weaning, which was calculated by adding the LW at weaning (adjusted to 120 days of age) of all lambs each ewe had in her life.

Discussion

The present study reported heritability estimates for yearling and adult expressions of economically relevant traits in Uruguayan Merino sheep. In the current work, adult expression of major wool traits (FD and CFW) and LW were highly heritable, which is consistent with other Merino studies (Huisman et al., 2008; Dominik and Swan, 2018; Chapman et al., 2021). Low heritabilities for reproduction traits found in the current study agreed well with literature estimates (Safari et al., 2007a; Dominik and Swan, 2018; Bunter et al., 2021; Chapman et al., 2021).

The high heritability for Y_FD found in the present study was consistent with that previously reported in Merino sheep (Ciappesoni et al., 2010; Fozi et al., 2012; Swan et al., 2016; Mortimer et al., 2017; Dominik and Swan, 2018). The heritability estimate for Y_CFW was similar to the reports of Swan et al. (2016; 0.38 ± 0.06) and Huisman et al. (2008; 0.36 ± 0.02), while slightly lower than Dominik and Swan (2018, 0.43 ± 0.03), Safari et al. (2007a; 0.42 ± 0.01), and Ciappesoni et al. (2010; 0.46 ± 0.03). The heritability estimate for Y_LW (0.63) agreed with the estimate of 0.59 presented by Dominik and Swan (2018) in fine-wool Merino sheep but lower values have been reported by Swan et al. (2008; 0.54 ± 0.04), Huisman et al. (2008; 0.43 ± 0.02), Lee et al. (2002; 0.38 ± 0.08), Safari et al. (2007a; 0.36 ± 0.02), and Ciappesoni et al. (2010; 0.49 ± 0.03).

Uruguayan studies have reported that selection at 12 months of age for an index that focused on reduced FD and increased CFW and LW, resulted in phenotypically heavier animals that produced finer and heavier fleeces at yearling and adult ages (Chapters III and IV). These results are consistent with the high genetic correlations between yearling and adult expressions of FD (0.91), CFW (0.81), and LW (0.95) reported in the present study. This is also in agreement with Huisman and Brown (2008, 2009b) who suggested that genetic merit for FD, CFW, and LW in yearlings can be used as an indicator of genetic merit for these traits later in life. Taken together, these results show that yearling assessments of major wool traits (FD and CFW) and LW are effective tools for improving later life trait expressions.

It has been established that selecting for reduced FD as a component of a multi-trait breeding program resulted in a small positive change in net reproduction performance (Chapter IV). In the present study, genetic relationships between Y_FD and reproduction traits were not different from zero, indicating that selection for reduced FD will not necessarily affect ewe reproductive performance. This result agreed with estimates by Safari et al. (2007b) in Merino sheep. Dominik and Swan (2018) also reported no relationships between FD and NLWEJ, although, in their study, they found a favorable genetic correlation between FD and lamb survival. On the other hand, an unfavorable genetic correlation between adult FD and NLWEJ (0.33 ± 0.16) has been observed by Chapman et al. (2021). At a phenotypic level, no relationships between Y_FD and reproduction traits were found in the present study, which is consistent with reports from Dominik and Swan (2018).

There are conflicting reports on the impacts of selecting for increased fleece weight on ewe reproductive performance. Some studies indicate either no effects (Piper et al., 2011, 2013; Chapman et al., 2021) or negative effects (Safari et al., 2007b; Dominik and Swan, 2018) of selection for fleece weight on NLWEJ in Merino sheep. Piper et al. (2007) showed that a multi-trait breeding objective did increase CFW without altering NLWEJ, although, in their study, they found a negative genetic correlation between these traits (−0.42). These inconsistencies in research findings have been related to different nutritional conditions and the ratio CFW/LW (Masters and Ferguson, 2019) and differences in the Merino types used, amount and structure of the data, and models fitted to the data. In the current work, estimated genetic correlations between A_CFW and PR, LP, NLWEJ, TLW, and TLWW, were negative. This indicates that genetically heavier fleeces are associated with reduced ewe reproductive performance. Dominik and Swan (2018) also reported negative genetic relationships between adult fleece weight and NLWEJ and LP in fine-wool Merino sheep, although they found no genetic relationships between adult CFW and TLW. Phenotypically, the relationships between fleece weight and ewe reproductive performance were negligible, which agrees with reports from Dominik and Swan (2018) and Chapman et al. (2021) for Australian Merino sheep.

Moderate to strong positive genetic correlations between Y_EMA and several reproduction traits were observed. These findings are similar to those reported by Huisman and Brown (2009a), Brown and Swan (2016), and Chapman et al. (2021), and indicate that selection for higher muscularity at 1-year of age will improve ewe reproductive performance. In this study, Y_LW and all reproduction traits other than ERA, were positively correlated, indicating that genetically heavier yearling ewes will have better reproductive performance, which agrees with Safari et al. (2007b). These results are supported by Dominik and Swan (2018) who reported positive genetic relationships between Y_LW and lifetime reproduction traits. Huisman and Brown (2008) found that the genetic correlation between Y_LW and NLWEJ was positive but not different from zero. Combined, these findings indicate that indirect selection for reproduction traits is possible through Y_LW, but increased Y_LW will lead to increased ewe mature weight and, consequently higher ewe maintenance costs (Swan et al., 2007). Therefore, care should be taken in breeding programs that increase Y_LW to avoid large increases in mature ewe weight that require changes in stocking rates.

It has been reported that Y_FAT is positively associated with ewe reproductive performance, although this relationship is variable across years (Ferguson et al., 2010). Positive genetic correlations between Y_FD and Y_FAT found in this study indicate that genetically finer fleeces are associated with leaner animals. This unfavorable genetic correlation was similar to that reported by Brown and Swan (2016; 0.25 ± 0.03), while higher than Greeff et al. (2008; 0.07 ± 0.06) and Huisman and Brown (2009a; 0.14 ± 0.04), and lower than the estimate of 0.38 ± 0.07 observed by Mortimer et al. (2017). On the other hand, low to moderate negative genetic correlations between fleece weight and FAT have been reported in Merino sheep (Huisman and Brown, 2009a; Greeff et al., 2008; Brown and Swan, 2016). In this study, genetic correlations between yearling fleece weight and Y_FAT were not different from zero. Thus, although unfavorable genetic correlations between major wool traits (FD and CFW) and ewe fatness levels existed, simultaneous improvements in the traits should occur using appropriately designed indices.

Predictions of selection response for standard MERINOSELECT indices indicate that measuring fat and eye muscle depth had minimal impact on NLWEJ (Brown and Swan, 2016). A number of Merino studies have suggested that to achieve farm-relevant genetic gains in reproduction, NLWEJ should be included in the breeding objective and also measured as a selection criterion (Swan et al., 2007; Brown and Swan, 2016; Chapman et al., 2021). Additionally, Chapman et al. (2021) suggested that, when NLWEJ is already included as a selection criterion, the addition of ultrasound carcass traits will increase genetic gain for NLWEJ. Based on these predictions, reproduction should be strongly considered as a selection criterion in the current Uruguayan Merino breeding program.

Body condition score is an indicator of the available body reserves that can be utilized by animals when feed demand is high or in periods of suboptimal nutrition (Kenyon et al., 2014). Therefore, having suitable fat reserves plays an important role in extensive sheep systems, especially under restricted feeding conditions (Ferguson et al., 2007; Van Burgel et al., 2011). In this study, heritabilities for Y_BCS, and ewe BCS ranged from 0.15 to 0.28, which is comparable to previously published estimates for Merino sheep (Walkom et al., 2014), although Tait (2020) reported moderate to high heritability for Merino ewe BCS (0.32 to 0.66). Strong positive genetic correlations between ewe BCS across the production cycle (at mating, pre-lambing, at weaning) were found in the current study. These results support earlier findings that suggest a single measurement of BCS will capture the genetic variation of this trait (Walkom et al., 2014; Tait, 2020). High positive genetic correlations between Y_FAT and BCS observed in this study suggest that Y_FAT could be an indicator trait for body condition.

Sheep genetic evaluations were initiated by INIA and SUL in Uruguay in 1995 (Ciappesoni et al., 2013). Initial genetic parameters used were based on published values from Australia and unpublished reports from Uruguay. The first genetic parameter estimates were published in 2006 (Ciappesoni et al., 2006). In 2011, genetic parameters were updated to include estimates from data sourced from the INIA nucleus flock, including data from adult animals (Ciappesoni et al., 2011). The current study reports genetic parameters for an extensive range of traits which are normally not measured in the Uruguayan

Merino industry (e.g., ultrasound carcass traits at yearling age, ewe LW and BCS, and reproduction traits), and will be used to update the Uruguayan sheep genetic evaluation system. While the data used for genetic parameter estimation did not include Merinos from commercial Uruguayan flocks, the parameters are likely appropriate as approximately 12% of the rams utilized in the Uruguayan Merino industry were born in the nucleus flock. Additionally, the nucleus flock represents between 7% and 10% of the total Merino flocks evaluated in the last 10 years. Nevertheless, it would be useful to have genetic parameters based on a wider representation of the Uruguayan sheep industry and further studies are recommended.

Conclusion

This study has extended the genetic parameter estimates to include not just reproduction but correlation estimates between yearling and adult expressions of wool production and LW traits in Uruguayan Merino sheep. The results indicate that selecting for reduced FD will not adversely affect ewe reproduction traits. On the other hand, selection for increased adult CFW may reduce ewe reproductive performance, whereas selection for increased yearling LW will positively impact reproduction traits. Strong genetic correlations between yearling and adult expressions of FD, CFW, and LW indicate that one measurement at a young age is an effective tool to identify the genetic merit of an individual for any of these traits. Most genetic parameters reported in this study were supported by literature estimates.

The results of this work will update the current genetic parameters utilized for the Uruguayan Merino Genetics evaluations. The genetic parameters, including those for reproduction and other production traits, will be utilized to calculate selection indices that incorporate reproduction as a selection criterion in the current Uruguayan Merino breeding program. Further studies are required to evaluate the benefit of including other non-wool traits such as ultrasound carcass traits in a multi-trait breeding program for Uruguayan Merinos.

Chapter VI

Genetic trends for wool, growth, and reproduction traits in Ultrafine Merino sheep of Uruguay

Abstract

Genetic trends were estimated for production and reproduction traits in an Uruguayan Merino flock. Two periods with different selection objectives were studied. During the first period (1999 – 2010), the selection objective of this flock focused on reducing fibre diameter (FD), while allowing for a slight loss in clean fleece weight (CFW). From 2011 to 2018, the breeding objective was focused on maintaining FD, while increasing both CFW and live weight (LW). Data from approximately 5,380 yearling lambs and 2,000 ewes born between 1999 and 2018 were analysed. Genetic trends were estimated for yearling and adult FD (Y_FD and A_FD, respectively), yearling and adult CFW (Y_CFW and A_CFW, respectively), yearling LW (Y_LW), 2-year-old ewe mating live weight and mating body condition score (2-yo_LWM and 2-yo_BCSM, respectively), and the number of lambs weaned per ewe joined (NLWEJ). Estimated breeding values were predicted to calculate genetic trends for the two periods of selection. From 1999 to 2010, yearling lambs showed significant reductions in FD (-0.21 μm/year, corresponding to 1.28% of the mean of the trait for that period). Before 2010, yearling lambs showed reductions of -0.01 kg/year (0.62%) in CFW, whereas from 2011 to 2018, this trait increased by 0.05 kg/year (1.81%). The annual genetic gain for Y_LW was greater in the second period than in the first period (0.29 *vs* 0.09 kg/year). Except for 2-yo_BCSM, the genetic trends for all traits were affected by period ($P<0.001$), indicating that the change in the selection index applied in the flock was effective. Over the entire study period (1999 – 2018), the total genetic responses for 2-yo_BCSM and NLWEJ were near zero. These results indicate that the breeding program utilized in the flock improved the traits under selection (FD, CFW, and LW) and had marginal impact on 2-yo_BCSM and NLWEJ. To achieve relevant genetic gains in ewe reproductive performance, in the future reproduction should be incorporated into the selection programme for Uruguayan fine-wool sheep. The results obtained in this study will be used to refine the breeding programmes for Merino sheep in Uruguay.

Introduction

Selection is a powerful tool for the genetic improvement of economically important traits in sheep. Defining clear breeding objectives and developing selection criteria based on them, are key in any sheep breeding program. Numerous studies have reported the success of breeding schemes within Merino sheep populations (Taylor et al., 2007b; Di et al., 2014; Swan et al., 2009; Ciappesoni et al., 2014).

In Uruguay, the current selection indices for Merinos include fibre diameter (FD), clean fleece weight (CFW), and live weight (LW). This approach has been successful in producing animals with high genetic merit for the traits under selection (https://www.geneticaovina.com.uy/evaluaciones.php). More recently, Uruguayan Merino breeders have become interested in producing an easy-care ewe that performs well, not only in wool and growth traits, but also in reproduction and BCS (Ciappesoni 2022, personal communication). Phenotypic responses in mixed-age ewes to a long-term breeding program for Merino sheep have been reported (Chapter IV), although ewe traits are not usually recorded by Uruguayan Merino breeders. It is of interest to know to what extent those phenotypic responses for wool, growth, and reproduction traits can be explained by the selection program.

Data from a long-term selection Merino flock established in Uruguay in 1999 were analysed in the present study. During the first 10 years (1999 – 2010), the selection objective of this flock focused on reducing FD (19 μm or finer), while allowing for a slight loss in CFW (Chapter V). From 2011 to 2018, the breeding objective was focused on maintaining FD (less than 15.5 μm), while increasing both CFW and LW (Chapter V). The purpose of the present study was to estimate the genetic trends for wool and growth traits at yearling and adult age, ewe BCS and reproduction for both the selection strategies used in the period 1999 – 2018.

Material and Methods

Location

This study was conducted at the Glencoe Experimental Unit of the National Institute of Agricultural Research of Uruguay (INIA, 32◦00′21” S and 57◦08′06” 115 W). Information on the region and details of the flock analysed were provided in Chapters III and IV. This study was carried out with the approval of the INIA Animal Ethics Committee (INIA_2018.2).

Data

Data analysed in this study were a subset of the data presented in Chapter V and included 5,381 mixed-sex yearling lambs born between 1999 and 2018 and subsequent records on 2,000 of these animals as ewes. Traits recorded at yearling age included fibre diameter (Y_FD), clean fleece weight (Y_CFW), greasy fleece weight (Y_GFW), staple length (Y_SL), and live weight post-shearing (Y_LW). Adult wool traits at mid- to late-pregnancy shearing were the same as those described at yearling age, but the abbreviations utilized for fibre diameter, clean fleece weight, greasy fleece weight, and staple length, were A_FD, A_CFW, A_GFW, and A_SL, respectively. Ewe LW and BCS at mating measured at 2 years of age (2-yo_LWM and 2-yo_BCSM, respectively) was utilised for this study. The number of lambs weaned per ewe joined (NLWEJ) was measured as an indicator of ewe reproductive performance and had repeated records across years. The measurements of these traits were described in Chapter III and IV.

Statistical analysis

Descriptive statistical analyses, outlier detection, and definition of fixed effects were performed as described in Chapter V. Estimated breeding values (EBVs) for production and reproduction traits were predicted using an animal model implemented in Julia for Whole-Genome Analyses Software (JWAS, Cheng et al., 2018). A multi-trait model was applied to EBVs for FD, CFW, GFW, SL, and LW. Single-trait models were utilized to estimate breeding values for 2-yo_LWM, 2-yo_BCSM and NLWEJ. Adult wool traits and NLWEJ were treated as repeated records across years. The model for each trait was defined in Chapter V.

The model equation was:

$$y = X\beta + Qg + Za + Wpe + e$$

where y is the vector of observations on one trait, β is the vector of unknown fixed effects, g is the vector of the unknown fixed effects for unknown parent groups (UPG), a is the vector of random animal effects, pe is a vector of random permanent environmental effects to account for the covariance between observations from the same individual, e is the vector of random residual effect, and X, Q, Z, and W are incidence matrices relating records to fixed, UPG, animal effects, and permanent environmental effects, respectively. The animal permanent environmental effect was only fitted to adult wool traits and NLWEJ as these traits had repeated observations on the same individuals.

The total EBVs which account for selection on unknown parents were predicted by adding the product of the UPG covariates times the group solutions to the within-group EBV (estimate of a in the model equation). Genetic trends were obtained by averaging the total EBVs of each trait within years of birth (from 1999 to 2018). Annual genetic gains were calculated via the regression of the EBVs for each trait on the birth year utilizing the regression procedure of the SAS software package (version 9.4, SAS Institute Inc., Cary, NC, USA). The slopes of the regression of the EBVs on year of birth as well as the period were tested for significance. Based on the presentation of genetic trends for the Uruguayan Merino sheep evaluation (https://www.geneticaovina.com.uy/tendencias.php) the genetic base for all traits was defined as the average total EBVs of all animals born in 2002.

Results and discussion

Summary statistics for yearling and adult traits are shown in Table 6.1. The dataset contained 5,381 records for each yearling trait, which includes both female and male lambs. The number of records ranged from 1,776 to 1,821 for 2-year-old ewe traits, and from 6,288 to 7,079 for mixed-age ewes (2 to 10 years old).

The standardised selection differentials (SSD) averaged over the two sexes by year over the study period are presented in Table 6.2. The SSD reflects the superiority of the selected animals over the average of the group from which they were selected by truncation, expressed in standard deviation units (Blair and Garrick, 2007) and reflects the proportion selected. In the current study, the SSD by year ranged from 1.2 to 1.5. This result is comparable with previously reported SSD in the New Zealand sheep industry, which ranged from 1.3 to 1.7 (Blair and Garrick, 2007). Potential SSD have been calculated for the Uruguayan Merino sheep industry as shown in Appendix III, Table 1.

Table 6.1 Descriptive statistics for wool, body growth, and reproduction traits in yearling and adult animals over the entire study period (1999 - 2020).

Trait	**Mean**	**SD[1]**	**Min**	**Max**	**N**
Y_FD (µm)	15.8	1.61	12.4	22.7	5,381
A_FD (µm)	16.6	1.75	11.7	24.5	7,079
Y_CFW (kg)	2.35	0.68	0.78	4.86	5,381
A_CFW (kg)	2.80	0.51	1.40	4.50	6,288
Y_GFW (kg)	3.16	0.91	1.15	6.16	5,381
A_GFW (kg)	3.50	0.63	1.90	5.80	6,812
Y_SL (cm)	8.4	1.84	3.5	14.0	5,381
A_SL (cm)	8.7	1.29	4.5	13.0	6,403
Y_LW (kg)	45.2	10.6	18.5	76.5	5,674
2-yo_LWM (kg)	43.3	4.50	30.0	58.5	1,821
2-yo_BCSM (kg)	3.4	0.62	2.0	4.75	1,776
Number of lambs weaned per ewe joined (NLWEJ)	0.71	0.64	0	3	6,376

[1] SD: standard deviation. N: number of records. Y_FD, Y_CFW, Y_GFW, Y_SL, and Y_LW correspond to yearling fibre diameter, clean fleece weight, greasy fleece weight, staple length, and live weight post-shearing, respectively. A_FD, A_CFW, A_GFW and A_SL correspond to adult fibre diameter, clean fleece weight, greasy fleece weight, and staple length, respectively. 2_yo_LWM and 2-yo_BCSM refer to 2-year-old ewe mating live weight and mating body condition score (scale 1-5), respectively. NLWEJ = number of lambs weaned per ewe joined.

Table 6.2 Total annual number of ewes and rams, number of animals selected, and overall standardised selection differential (SSD) over the study period.

Year	**Total lambs**		**Selected lambs**[1]		**Overall SSD ($\bar{I}$ overall)**[2]
	Females	**Males**	**Females**	**Males**	
1999	189	142	130	2	1.5
2000	119	124	83	3	1.4
2001	116	101	85	2	1.4
2002	94	96	82	2	1.3
2003	161	171	124	3	1.4
2004	132	149	126	3	1.2
2005	166	180	133	3	1.4
2006	159	146	124	4	1.3
2007	128	125	117	2	1.3
2008	157	153	129	2	1.4
2009	141	126	88	3	1.5
2010	132	174	114	2	1.4
2011	179	181	125	3	1.5
2012	130	134	97	4	1.3
2013	146	136	90	4	1.4
2014	82	65	59	1	1.4
2015	96	99	64	4	1.3
2016	132	110	117	4	1.2
2017	101	125	92	4	1.2
2018	141	144	120	4	1.3

[1]Selected lambs: number of offspring who became parents. [2]Overall SSD ($\bar{I}$ overall) = ($\bar{I}$ male + $\bar{I}$ female)/2

Genetic trends for wool traits and live weight

Long-term responses in individual traits will vary depending on the selection program applied in the flock. During the first period, from 1999 to 2010, the selection objective of this flock was to reduce FD, while allowing for a slight loss in CFW. From 2011 to 2018, the breeding objective was focused on maintaining FD, while increasing both CFW and LW (Chapter V). The regression coefficients of mean annual EBV on birth year for each trait over both the selection strategies are given in Table 6.3. The genetic trends are shown graphically in Figures 6.1 to 6.5.

From 1999 to 2010, yearling lambs showed significant reductions in FD (Table 6.3 and Figure 6.1). This is consistent with the negative selection pressure applied by the selection index, which was focused on FD reduction, and the high heritability of this trait (Ciappesoni et al., 2010; Fozi et al., 2012; Swan et al., 2016; Dominik and Swan, 2018; Mortimer et al., 2017; Chapter V). The annual genetic progress for Y_FD during the first study period was approximately two times greater than those obtained in the Uruguayan Merino sheep industry between 2001 to 2011 (1.28 *vs* 0.64%; Ciappesoni et al., 2014). Favourable genetic progress for reduced FD has also been reported in the Australian, South African, and Chinese Merino sheep populations, although the magnitude of the changes varied across studies (Cloete et al. 2007; Taylor et al., 2007b; Di et al., 2014). In the current study, the genetic gain of Y_FD was almost three times greater in the first period than in the second period (-0.21 *vs* -0.08 µm/year, Table 6.3). This result reflected the change in trait emphasis in the selection index utilized in the second period, which focused on maintaining FD, while increasing both CFW and LW. Overall, the genetic progress of Y_FD agreed well with the phenotypic trend of this trait reported in Chapter III.

Over the entire study period (1999 - 2018), the total response indicated a genetic decrease of -2.7 and -1.8 µm for Y_FD and A_FD, respectively. A similar pattern for Y_ FD and A_FD is expected given the high positive genetic correlations between yearling and adult expressions of FD (0.75, 0.83, 0.91, Fozi et al., 2012; Huisman and Brown, 2009b; Chapter V, respectively). This pattern was also observed in the genetic trends for the MERINOSELECT analysis (Sheep Genetics, 2023, personal communication).

The genetic trends for Y_CFW and A_CFW are given in Table 6.3. Before 2010, yearling lambs showed reductions of -0.013 kg/year (0.62%) in CFW. The negative genetic gain for CFW observed in this study, is likely a correlated response of selection for reduced FD, due to the positive genetic correlation between the two traits (Safari et al., 2007; Ciappesoni et al., 2006 and 2013). From 2011 to 2018, the genetic trend of Y_CFW showed a steady increase (0.05 kg/year, corresponding to 1.81% of the mean of the trait for that period). This result seems to be reasonable given the positive selection pressure placed on CFW post-2011. It could also be due to selection pressure being placed on LW, which is positively genetically correlated with CFW (0.54, 0.27, 0.23; Mortimer et al., 2017; Safari et al., 2007b; Ciappesoni et al., 2013).

During the entire study period (1999 to 2018), the total genetic progress for Y_CFW and A_CFW was 0.355 and 0.198 kg, respectively. A similar rate of genetic gain between Y_CFW and A_CFW was expected considering the high positive genetic correlations between the two traits (0.57, 0.81; Huisman and Brown, 2009; Chapter V). Favourable genetic progress for increased Y_CFW and A_CFW were reported by the Australian Merino evaluation (Sheep Genetics, 2023, personal communication).

Table 6.3 Genetic trend estimates (b) with respective standard errors (SE) and percent change for yearling and adult traits by period.

Trait	First period (1999 - 2010)[1]		Second period (2011 - 2018)[2]		Interaction b*period
	b ± SE	Percent (%)[3]	b ± SE	Percent (%)[3]	
Y_FD (µm)	-0.21 ± 0.004*	-1.28	-0.08 ± 0.006*	-0.53	*
A_FD (µm)	-0.28 ± 0.07*	-1.63	0.11 ± 0.01*	0.71	*
Y_CFW (kg)	-0.01 ± 0.0008*	-0.62	0.05 ± 0.002*	1.81	*
A_CFW (kg)	-0.01 ± 0.002*	-0.39	0.02 ± 0.003*	0.71	*
Y_LW (kg)	0.09 ± 0.012*	0.20	0.29 ± 0.02*	0.62	*
2-yo_LWM (kg)	0.02 ± 0.03NS	0.05	0.31 ± 0.05*	0.71	*
2-yo_BCSM	0.002 ± 0.0015NS	0.06	0.007 ± 0.0016*	0.23	NS
NLWEJ	-0.01 ± 0.0006*	-1.47	0.01 ± 0.001*	1.30	*

Y_FD, Y_CFW, and Y_LW correspond to yearling fibre diameter, clean fleece weight, and live weight post-shearing, respectively. A_FD and A_CFW correspond to adult fibre diameter and clean fleece weight, respectively. 2-yo_LWM and 2-yo_BCSM refer to 2-year-old ewe mating live weight and mating body condition score, respectively. NLWEJ = number of lambs weaned per ewe joined. *Significant effect at $P < 0.001$; NS: non-significant.[1]First period (1999 - 2010): the selection objective focused on reducing FD (19 µm or finer), while allowing for a slight loss in CFW. [2]Second period (2011 - 2018): the breeding objective was focused on maintaining FD (less than 15.5 µm), while increasing both CFW and LW.[3]Percent (%): corresponds to the annual genetic change as a percentage of the mean of the trait of each period.

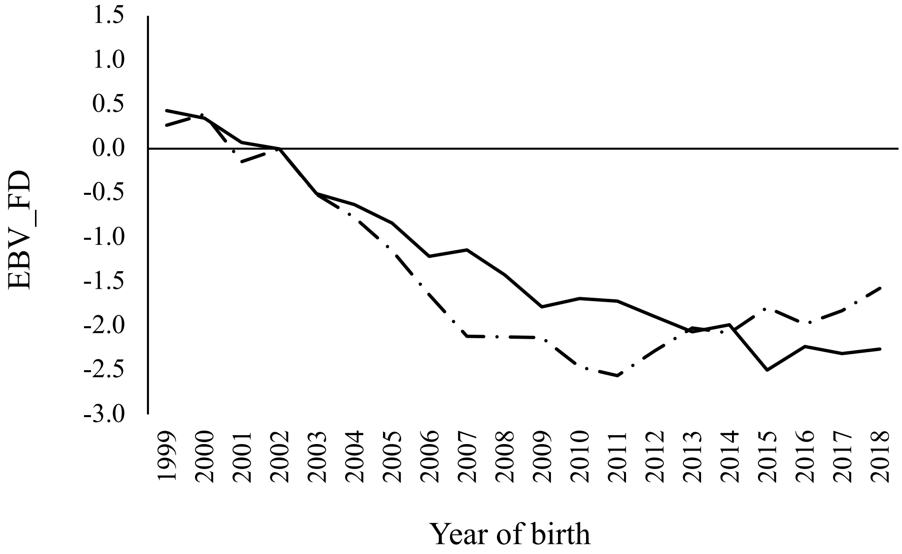

Figure 6.1 Annual means of estimates of breeding value (EBV) for yearling (solid line) and adult (non-solid line) fibre diameter by year of birth.

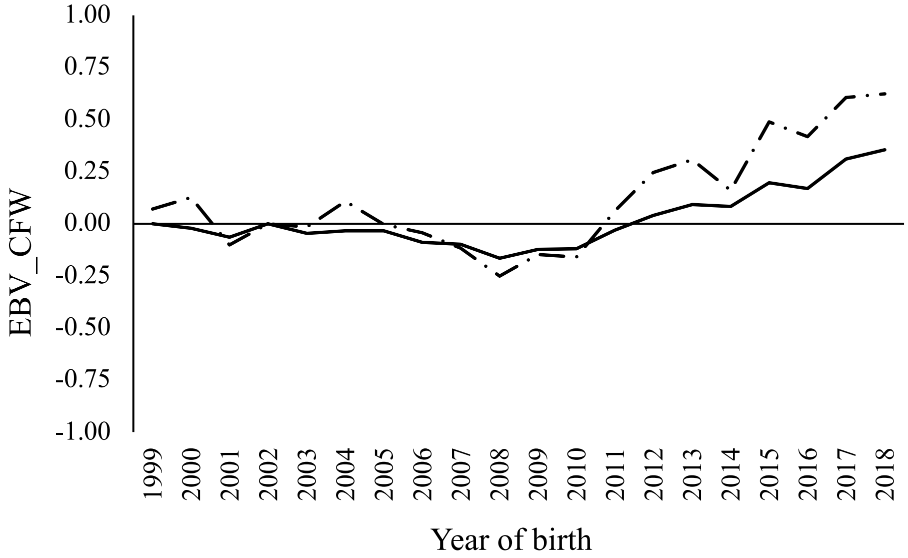

Figure 6.2 Annual means of estimates of breeding value (EBV) for yearling (solid line) and adult (non-solid line) clean fleece weight by year of birth.

Regression of mean annual EBVs on birth year for Y_LW and 2-yo_LWM are shown in Table 6.3. The annual genetic gain for Y_LW was greater in the second period than in the first period (0.29 *vs* 0.09 kg/year). This result is consistent with the selection index applied post-2011, which applied increased selection pressure on LW. Substantial increases in Y_LW observed in 2017 could, in part, be due to the influence of new groups of animals imported from Australia and introduced into the flock in 2015 (EBVs for LW of those animals are currently within the top 1% of the Uruguayan Merino population). Increases in Y_LW have been accompanied by increases in 2-yo_LWM (Figure 6.3). This result is consistent with the high positive genetic correlation between yearling and 2-year-old ewe expressions of LW (0.90; Huisman and Brown, 2008).

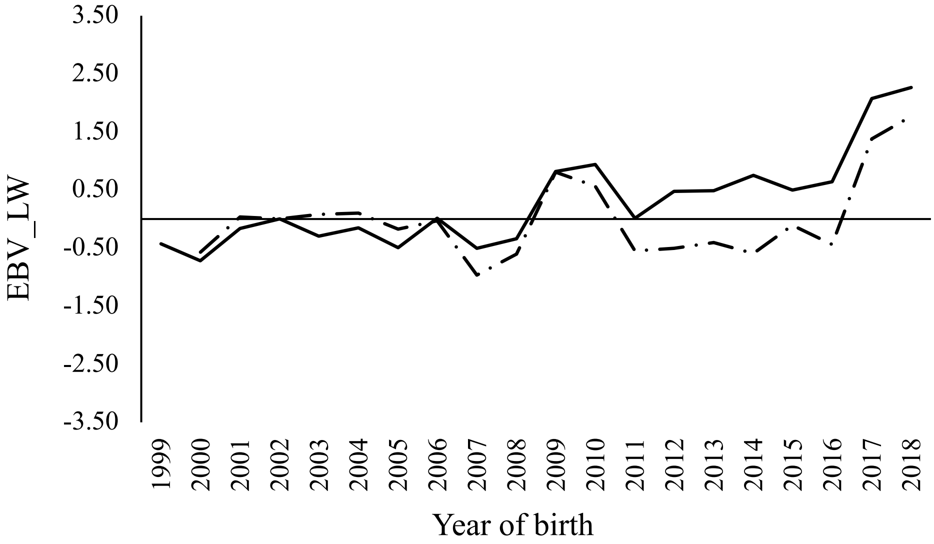

Figure 6.3 Annual means of estimates of breeding value (EBV) for yearling live weight (solid line) and 2-year-old ewe live weight at mating (non-solid line) by year of birth.

Genetic progress is a profit driver for the Merino sheep industry. In the present study, total genetic responses for FD, CFW and LW were in desirable direction. Based on the average of all animals recorded in 2000 and 2020, selection indices available for Uruguayan Merino sheep increased by approximately

30% (Gimeno and Ciappesoni, 2022). Combined, these findings indicate that breeding programmes applied during the study period resulted in increased productivity, therefore it is highly likely that income has also increased as shown in Chapter IV.

Genetic trends for body condition score at mating and reproduction traits

As shown in Table 6.3, a non-significant genetic trend for 2-yo_BCSM was observed in the first period. Post-2011, this trait had a small increase of 0.007 points/year, corresponding to 0.23% of the average of 2-yo_BCSM of that period. The positive genetic trend for 2-yo_BCSM observed in the second period, could be due to selection pressure being placed on Y_LW, which is positively genetically correlated with ewe BCSM (Chapter V). The genetic responses for 2-yo_BCSM were of a very low magnitude and would have minimal impact on phenotype.

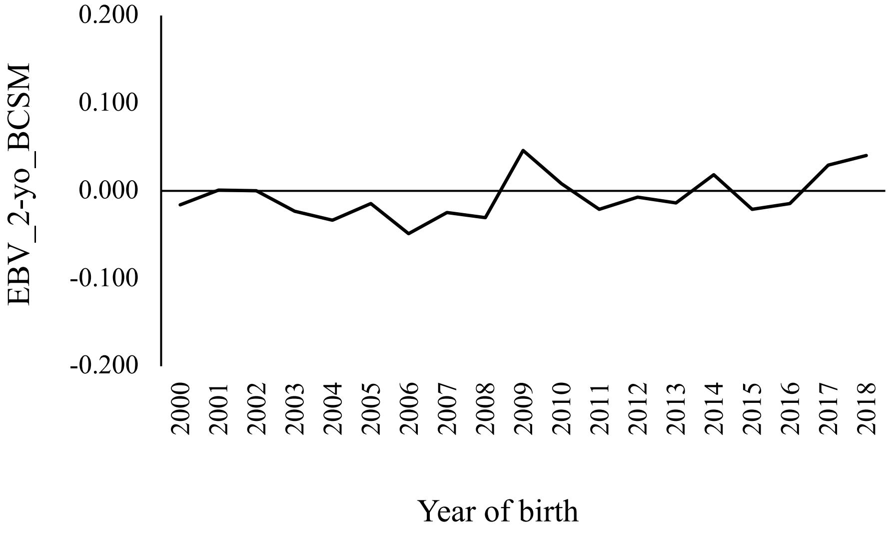

Figure 6.4 Annual means of estimates of breeding value (EBV) for 2-year-old ewe body condition score by year of birth.

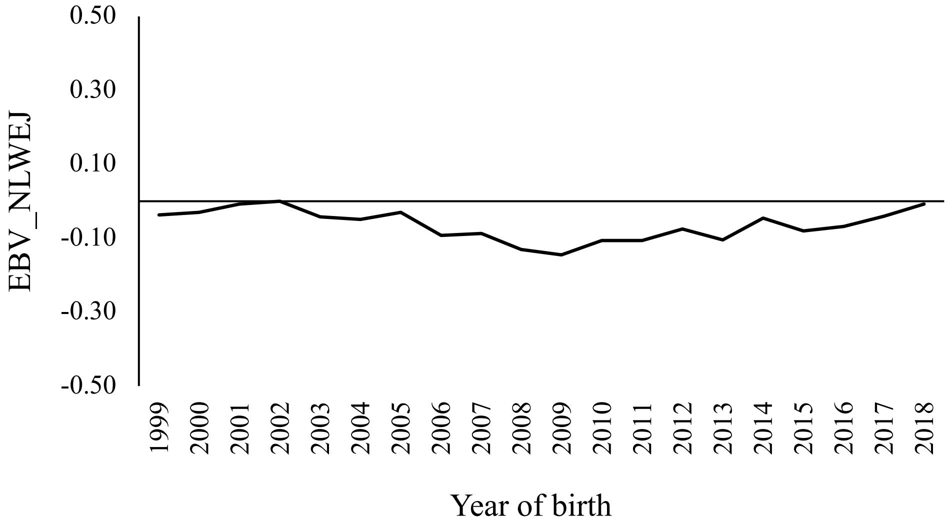

Figure 6.5 Annual means of estimates of breeding value (EBV) for the number of lambs weaned per ewe joined by year of birth.

From 1999 to 2010, the regression coefficient for NLWEJ was negative (Table 6.3). This result is consistent with a positive genetic correlation between adult FD and NLWEJ (0.33, Chapman et al., 2021), although no genetic relationships between the two traits were found by Safari et al. (2007b), Dominik and Swan (2018) and, Chapter V. Post-2011, the annual genetic gain for NLWEJ was positive (0.01 lambs/ewe per year). This could be due to selection pressure being placed on Y_LW, which is positively genetically correlated with NLWEJ (0.26; Chapter V). Over the entire study period (1999 - 2018), the total response indicated no genetic change for NLWEJ.

To achieve relevant genetic gains in ewe reproductive performance, reproduction should be included in the Merino breeding objective (Swan et al., 2007; Brown and Swan, 2016; Chapman et al., 2021). In Australia, the Genetic Evaluation system MERINOSELECT provides selection indices with varying emphases on wool traits, LW at yearling and adult age, worm egg count and NLWEJ (Sheep Genetic, 2019). Over the last 20 years, genetic trends in MERINOSELECT have shown an improvement in most economically relevant traits (Van Der Werf et al., 2022). In the last 10 years, there has been a growing interest in including other traits such as ultrasound carcass measures and ewe body condition score into MERINOSELECT indices (Walkom et al., 2014; Brown and Swan, 2016). Based on these findings, and the results obtained in the present study, the current breeding objectives and selection indices for Uruguayan Merino sheep should be refined to improve farm profitability.

Conclusion

This study estimated the genetic trends for production and reproduction traits in an Uruguayan Merino flock which had undergone 20 years of selection representing two distinct periods with different selection emphases. The results indicate that substantial genetic gains have been achieved in Y_FD, Y_CFW, and Y_LW. Therefore, the breeding program applied during the study period was effective in achieving its aims and efficacious in improving genetic gain in the traits under selection. Furthermore, the results demonstrate that selection at yearling age is effective in improving FD, CFW, and LW at later ages. The selection programs applied in the flock resulted in only marginal net genetic changes in 2-yo_BCSM and NLWEJ, which were unlikely to have any major impact on flock performance for these traits. However, to achieve relevant genetic gains in reproduction, NLWEJ should be incorporated into breeding objectives of Uruguayan fine-wool sheep. The results obtained in this study will be used to refine the breeding programmes for Merino sheep in Uruguay. This refinement would benefit from further research using a wider representation of the Uruguayan Merino sheep industry.

Chapter VII

Genomic regions associated with wool, growth and reproduction traits in Uruguayan Merino sheep

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Abstract

The aim of this study was to identify genomic regions and genes associated with the fibre diameter (FD), clean fleece weight (CFW), live weight (LW), body condition score (BCS), pregnancy rate (PR) and lambing potential (LP) of Uruguayan Merino sheep. Phenotypic records of approximately 2000 mixed-age ewes were obtained from a Merino nucleus flock. Genome-wide association studies were performed utilizing single-step Bayesian analysis. For wool traits, a total of 35 genomic windows surpassed the significance threshold (PVE ≥ 0.25%). The proportion of the total additive genetic variance explained by those windows was 4.85 and 9.06% for FD and CFW, respectively. There were 42 windows significantly associated with LWM, which collectively explained 43.2% of the additive genetic variance. For BCS, 22 relevant windows accounted for more than 40% of the additive genetic variance, whereas for the reproduction traits, 53 genomic windows (24 and 29 for PR and LP, respectively) reached the suggestive threshold of 0.25% of the PVE. Within the top 10 windows for each trait, we identified several genes showing potential associations with the wool (e.g., IGF-1, TGFB2R, PRKCA), live weight (e.g., CAST, LAP3, MED28, HERC6), body condition score (e.g., CDH10, TMC2, SIRPA, CPXM1) or reproduction traits (e.g., ADCY1, LEPR, GHR, LPAR2) of the mixed-age ewes.

Keywords: GWAS; gene; sheep; fibre diameter; body condition score; reproduction

Introduction

The genetic improvement of livestock has traditionally been based on phenotypic and pedigree information. Advances in molecular DNA technologies offer the opportunity to increase the rate of genetic gain using genetic markers (e.g., single-nucleotide polymorphisms, SNPs) (Van Eenennaam et al., 2011; Bouquet and Juga 2013). For several species, including sheep, panels of more than 50,000 SNPs are currently available (Meuwissen et al., 2013). This technology enables the identification of genes or chromosomal segments that are associated with the traits of interest (Genome-Wide Association Studies, GWAS) (Fernando et al., 2017). A number of statistical methods, including the single-step Bayesian regression approach, which combines all available pedigrees and phenotypic and genomic data, have been employed to conduct GWAS (Fernando et al., 2017; Fernando and Garrick, 2013; Fernando et al., 2014; Cheng et al., 2018) and have been used for a number of livestock species.

In sheep, GWAS analyses have been performed for economically relevant traits such as the fibre diameter (FD), clean fleece weight (CFW), live weight (LW) and reproduction (Wang et al., 2014; Al-Mamun et al., 2015; Abdoli et al., 2019). These traits are influenced by many genes, each with a small effect, and involve various cell types and tissues (Parsons et al., 1994; Kominakis et al., 2017; Zhao et al., 2021a). Nevertheless, candidate genes associated with major wool traits (FD and CFW) have been reported in the Australian and Chinese Merino sheep populations (Wang et al., 2014; Zhao et al., 2021a and 2021b; Bolormaa et al., 2021). Genomic regions related to live weight have also been found in Merino sheep in Australia (Al-Mamun et al., 2015) and New Zealand (Hess et al., 2019). A French study reported candidate genes associated with ewes' body condition score (BCS) (Macé et al., 2022).

In Uruguay, few GWAS of livestock species have been undertaken or published (Carracelas et al., 2022a; Grasso et al., 2014; Jara et al., 2022). There are no published GWAS of the wool, growth, or reproduction traits of Uruguayan sheep. The aim of this study was to detect the genomic regions and genes associated with the FD, CFW, LW, BCS and reproduction traits of Uruguayan ultrafine Merino ewes.

Materials and Methods

Ethical Statement

All animal work was approved by the INIA Animal Ethics Committee (INIA_2018.2).

Phenotypic and pedigree data

The data were derived from a Uruguayan Merino nucleus flock involved in a genetic program, as described in Chapters III and IV. The selection objectives, nutritional conditions and management of this flock were previously reported in Chapters III and IV. Phenotypic records of the following six traits were obtained from approximately 2,000 mixed-age ewes born between 1999 and 2018. The traits evaluated were the adult fibre diameter and clean fleece weight at late-pregnancy shearing (A_FD and A_CFW, respectively); live weight and body condition score at mating (LWM and BCSM, respectively); pregnancy rate (PR: pregnant or non-pregnant); and lambing potential (LP: the number of ultrasound scanned fetuses per ewe joined: 0, 1 or ≥ 2). Details of the trait measurements were described in Chapters III and IV. The complete pedigree included 7,168 animals.

Genotyping and quality control

Blood samples were collected by jugular´s vein puncture using tubes with K2 EDTA anticoagulant (6-mL BD Vacutainer). Genomic DNA extraction from the blood samples was performed as described by Carracelas et al. 2022b. The animals were genotyped using the GeneSeek® Genomic Profiler™ Ovine 50K panel. Quality control was performed to remove SNPs with a minor allele frequency (MAF) lower than 1% and call rate below 85%, as well as animals with a call rate lower than 90%. After applying the quality control measures, 1,133 animals and 40,036 SNPs were retained and utilized in the analyses.

Genome-Wide Association Study

Genome-Wide Association Studies were performed utilizing single-step Bayesian regression analyses implemented in the JWAS package (Cheng et al., 2018). A Bayes C linear mixed model that included the genotyped and non-genotyped ewes was constructed. The model equation for the single-step Bayesian GWAS was as follows for the genotyped animals:

(1) $y = X\beta + Zu + Wpe + M\alpha + e$

where:

y = vector of phenotypes for the genotyped individuals,

β = vector of fixed effects,

u = vector of random animal genetic effects not explained by the markers,

pe = vector of random permanent environmental effects accounting for the covariance between observations of the same individual,

α = vector of marker effects (random regression coefficients),

e = vector of random residual effects,

X, Z and W = incidence matrices relating records to fixed, animal and permanent environmental effects,

M = genotype covariate (each coded as 0, 1 or 2).

The model equation for the non-genotyped individuals can be written as:

(2) $y = X\beta + Zu + Wpe + M\alpha + Zn\epsilon + e$

where:

y = vector of phenotypes for the non-genotyped individuals,

M = genotype covariate matrix for the non-genotyped individuals imputed from the genotyped relatives,

Zn = incidence matrix corresponding to the imputation residual,

ϵ = vector of imputation residuals accounting for errors in the genotype imputation.

All the other terms are as described in Equation (1).

A Markov chain Monte Carlo (MCMC) method was utilized to obtain samples from the posterior distributions of all unknown parameters, including the marker effects. A total of 70,000 iterations were run after a burn-in of 5,000 cycles and a sampling interval each 10 interactions. The probability that the markers would have null effect was set to 99% (parameter $\pi = 0.99$), that is, 1% of the 40,036 SNPs (approximately 400 SNPs) was assumed to contribute to the genetic variance.

Detection of important windows associated with the trait and candidate genes

The genome was partitioned into 2015 non-overlapping windows of 20 consecutive SNPs which, on average, represented 1 Mb. Assuming that all the windows explained the same amount of variation, the expected proportion of genetic variance explained (PVE) by each window was 0.05% ([1/2015] *100). The 1 Mb windows that explained at least 0.25% of the genetic variance, which was 5 times the expected proportion of variance (0.05 x 5 = 0.25%), were considered to be the most important regions associated with the trait (Onteru et al., 2013; Sollero et al., 2017). The top 10 windows for each trait that explained the largest PVE were examined to identify candidate genes. The annotated genes in those regions were extracted from the OAR v3.1 Ovine (Texel) Genome Assembly, available in the Ensembl database (http://www.ensembl.org/Biomart, accessed on 10 August 2022) (Cunningham et al., 2021). The biological functions of the genes were identified using the functional annotation tools in DAVID (https://david.ncifcrf.gov/tools.jsp, accessed on 10 August 2022) (Sherman et al., 2022). Gene ontology (GO) enrichment analysis was conducted using g:Profiler (https://biit.cs.ut.ee/gprofiler/gost, accessed on 1 September 2022) (Raudvere et al., 2019). Pathways with a p-value < 0.05 were considered significantly enriched.

Results

Descriptive statistics

A summary of the phenotypic records of the traits analysed is shown in Table 7.1. The number of records ranged from 6,288 to 7,079.

Table 7.1 Descriptive statistics for the wool, body growth and reproduction traits of mixed-age ewes born between 1999 and 2018.

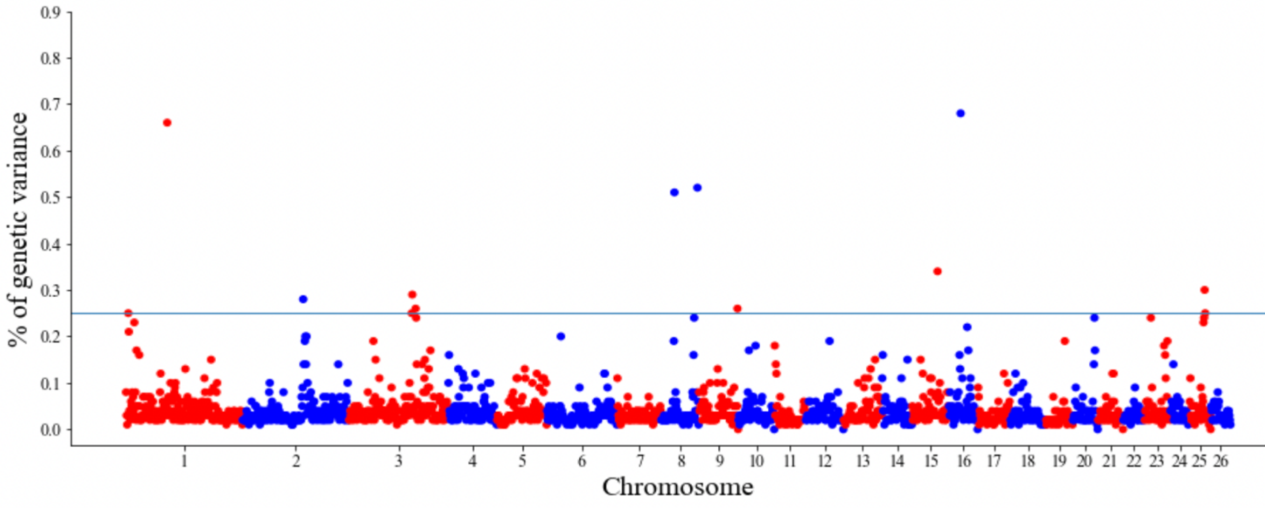
Trait	Mean	SD[1]	N
Fibre diameter (A_FD, µm)	16.6	1.75	7,079
Clean fleece weight (A_CFW, kg)	2.80	0.51	6,288
Live weight at mating (LWM, kg)	47.4	5.97	6,589
Body condition score at mating (BCSM)	3.2	0.65	6,442
Pregnancy rate (PR)	0.73	0.44	6,376
Lambing potential (LP)	0.91	0.66	6,376

[1] SD: standard deviation of the raw phenotypic records. N: number of records.

Genome-Wide Association Study (GWAS)

The GWAS results are presented as the proportion of additive genetic variation explained by the windows of 20 consecutive SNPs, as reported by other authors (Zhao et al., 2021a). Manhattan plots illustrating the proportion of additive genetic variation explained by each window of 20 adjacent SNPs for the wool, body and reproduction traits are presented in Figures 7.1–7.3, respectively. The suggestive threshold of 0.25% of the PVE is indicated by the horizonal blue line.

A - Fibre diameter



B - Clean fleece weight

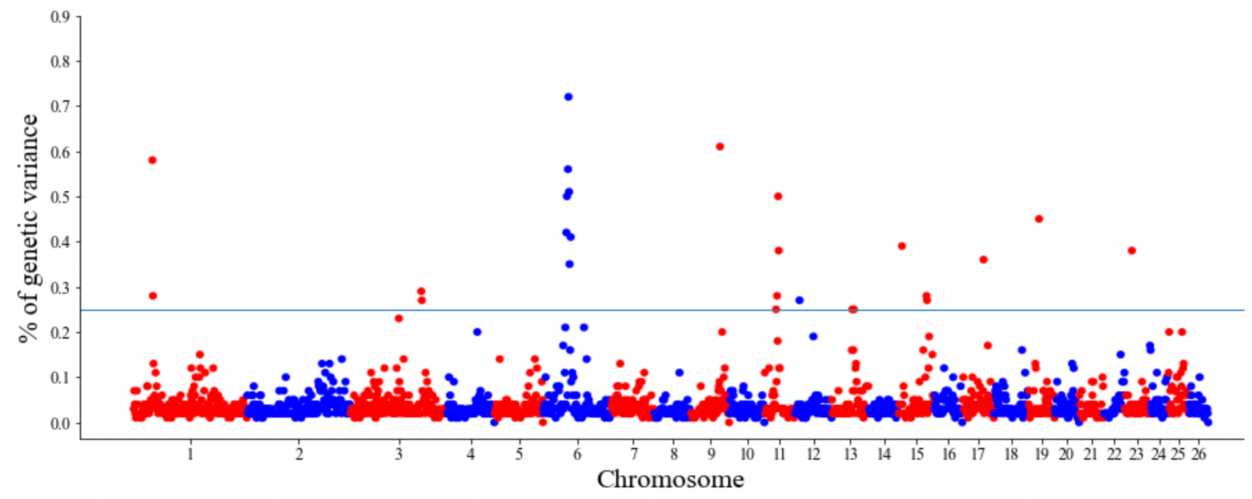
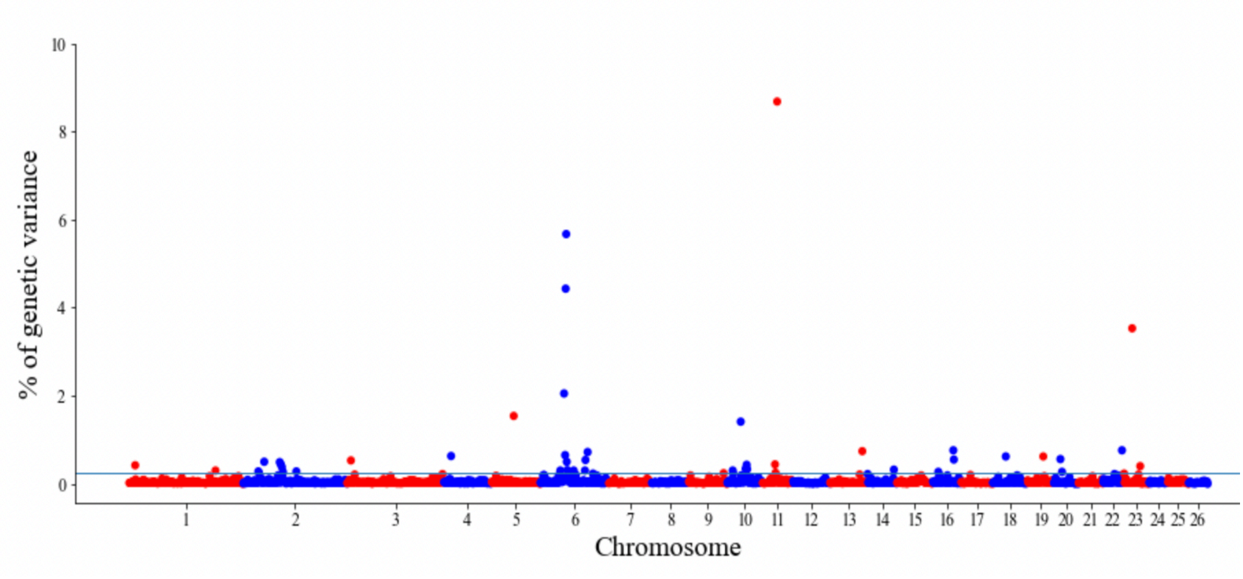


Figure 7.1 Manhattan plots of the genetic variance explained (%) by 20 adjacent SNP windows for the ewe fibre diameter (A) and clean fleece weight (B). Each dot represents a window. The % of additive genetic variance explained by each window and chromosomes 1-26 are shown on the Y-axis and X-axis, respectively. The horizontal line indicates the suggestive threshold of 0.25% of the PVE.

A - Live weight at mating



B - Body condition score at mating

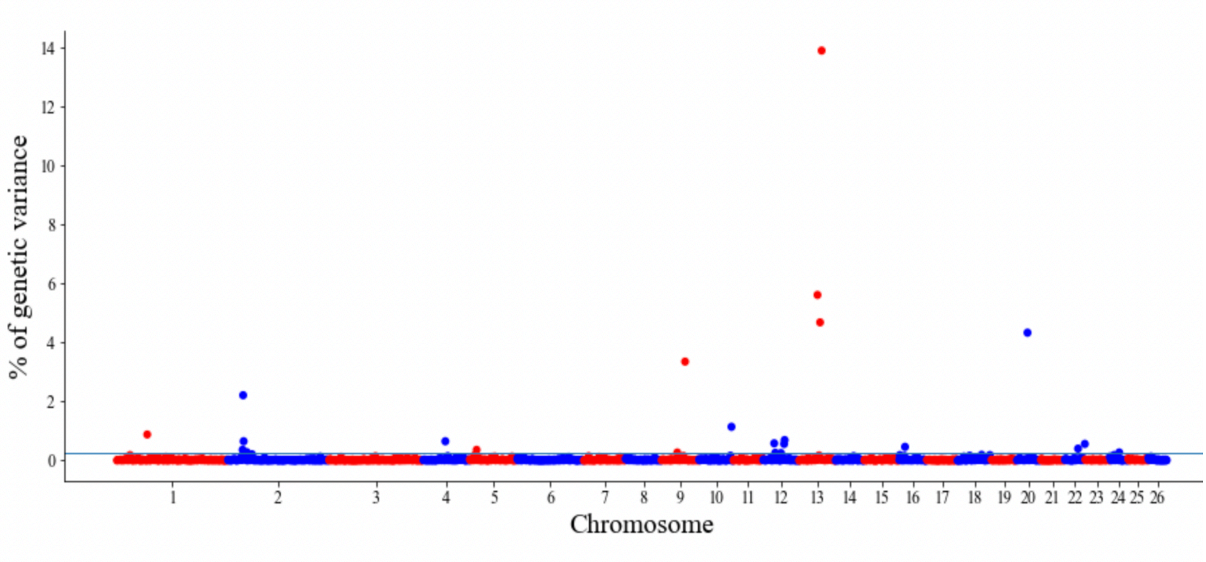
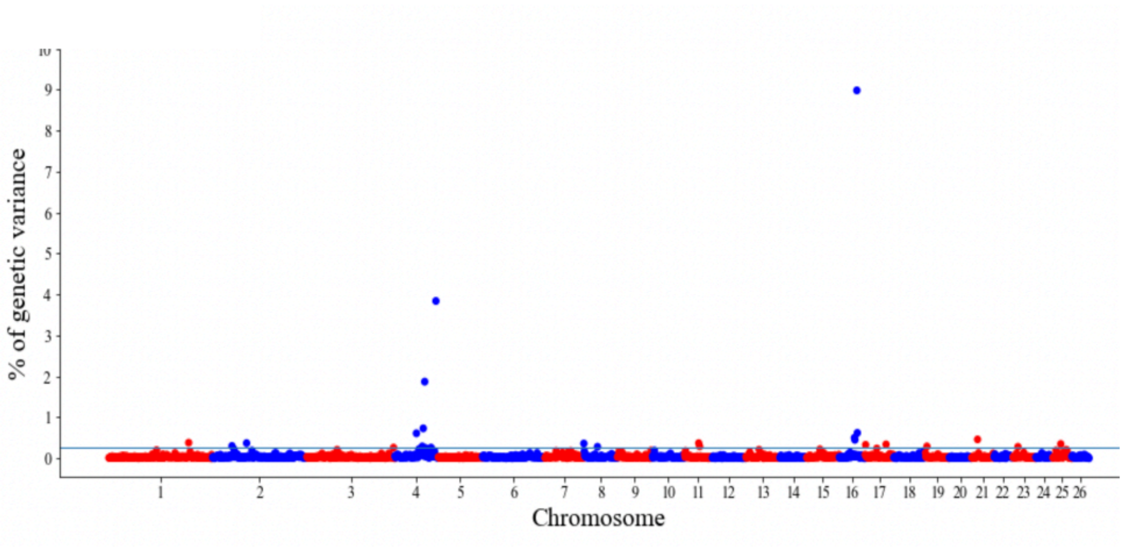


Figure 7.2 Manhattan plots of the genetic variance explained (%) by 20 adjacent SNP windows for the ewe live weight (A) and body condition score at mating (B). Each dot represents a window. The % of additive genetic variance explained by each window and chromosomes 1–26 are shown on the Y-axis and X-axis, respectively. The horizontal line indicates the suggestive threshold of 0.25% of the PVE.

For the wool traits, a total of 35 windows (13 for FD and 22 for CFW) surpassed the significance threshold (PVE ≥ 0.25%, Figure 7.1). The proportion of the total additive genetic variance explained by these windows was 4.85 and 9.06% for FD and CFW, respectively. There were 42 windows significantly associated with LWM, which collectively explained 43.2% of the additive genetic variance. For BCS, 22 relevant windows accounted for more than 40% of the additive genetic variance (Figure 7.2). For the reproduction traits, 53 genomic windows (24 and 29 for PR and LP, respectively) reached the suggestive threshold of 0.25% of the PVE (Figure 7.3).

A - Pregnancy rate



B - Lambing potential

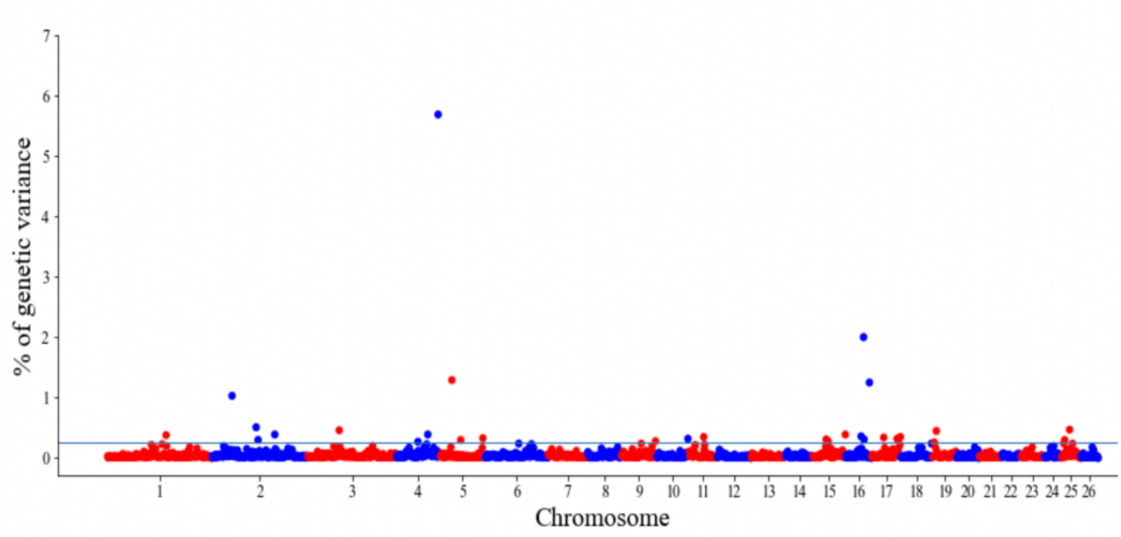


Figure 7.3 Manhattan plots of genetic variance explained (%) by 20 adjacent SNP windows for the pregnancy rate (A) and lambing potential (B). Each dot represents a window. The % of additive genetic variance explained by each window and chromosomes 1–26 are shown on the Y-axis and X-axis, respectively. The horizontal line indicates the suggestive threshold of 0.25% of the PVE.

Top 10 genomic regions and candidate genes

The chromosome, location, PVE and candidate genes within the top 10 windows for each trait are shown in Tables 7.2–7.4. The top 10 windows cumulatively explained 4.1, 5.3, 29.6, 37.4, 18.4 and 13.5% of the additive genetic variance for the A_FD, A_CFW, LWM, BCSM, PR and LP, respectively. Some of these windows were associated with more than one trait. For example, three genomic regions on chromosome 6 were associated with both the CFW and LWM. Similarly, two overlapping regions were associated with the PR and LP. A total of 240 genes were contained within the top 10 genomic regions across the six traits.

Enrichment analysis

A gene ontology (GO) enrichment analysis of the genes within the top 10 windows for each trait was performed. GO terms with a p-value < 0.05 were considered significantly enriched. The enriched terms were associated with molecular functions (MF), biological processes (BP) and/or cellular components (CC). In total, 20 GO terms were enriched (p-value < 0.05). More information from the GO analysis is available in Appendix II.

Table 7.2 Chromosome, location, proportion of additive genetic variance (PVE, %) and candidate genes within the top 10 windows associated with the fibre diameter (A_FD) and clean fleece weight (A_CFW) of Merino ewes.

Trait	Chr	Window Bounds (bp)	PVE (%)	Candidate Genes
A_FD	1	221133506–241462240	0.66	-
	2	132440576–134761891	0.28	HOXD10, OLA1, SP9, CHN1, CHRNA1, MTX2
	3	171178810–174258094	0.29	IGF-1, PAH, STAB2, NT5DC3, GLT8D2, SLC41A2, TDG
	3	191554038–194804430	0.26	PDE3A, C2CD5, ST8SIA1, HPCAL1, KCNJ8, PYROXD1, SLCO1C1
	8	35247461–84539654	0.52	ESR1, PLEKHG1, NT5E, NHSL1, ANKRD6, CGA, PLEKHG1
	8	66612859–69354718	0.51	ADGRG6, PHACTR2, UTRN, VTA1
	9	48994813–16528100	0.26	PRDM14, WWP1, EXT1, MATN2, PTDSS1, ZNF704
	15	47505272–4779161	0.34	DYNC2H1, LOC101106199, LOC101105437
	16	52688043–60285005	0.68	ARHGAP22, CDH18, TSNAX
	25	36631465–40822020	0.30	WAPL, GRID1
A_CFW	1	111294404–122825051	0.58	UHMK1, DDR2, NUF2, ATF6, INPP5B, RGS5
	6	36295216–36872516	0.72	BBS7, HERC6, CCNA2, LOC101120495,
	6	36066911–36286475	0.56	HERC3, HERC5, HERC6, PYURF, PIGY
	6	36905457–37129550	0.51	LAP3, MED28,
	6	35191867–35728962	0.50	GPRIN3, TIGD2
	6	33844752–35184703	0.42	MMRN1, CCSER1,
	6	37767491–38052441	0.41	-
	9	77283695–85378072	0.61	STK3, MTDH, MATN2, OSR2, VPS13B
	11	66432553–10722809	0.50	PRKCA, DHX40, LOC101102402, COIL, INTS2, PPM1E, SRSF1
	19	4811675–54605752	0.45	PBRM1, TGFBR2, BAC5, RBM6, CACNA2D3, DCP1A, MAP4

Chr, chromosome; PVE (%), proportion of additive genetic variance explained by each window; A_FD, adult fibre diameter; A_CFW, adult clean fleece weight, bp: base pairs.

Table 7.3 Chromosome, location, proportion of additive genetic variance (PVE, %) and candidate genes within the top 10 windows associated with the live weight (LWM) and body condition score (BCSM) at mating of Merino ewes.

Trait	Chr	Window Bounds (bp)	PVE (%)	Candidate Genes
LWM	5	93416569–93461942	1.54	CAST
	6	36905457–37129550	5.67	LAP3, MED28
	6	36295216–36872516	4.43	BBS7, HERC6, CCNA2, LOC101120495
	6	35191867–35728962	2.05	GPRIN3, TIGD2
	10	57396545–59143370	1.41	-
	11	13795276–16306848	8.68	LOC101110777, AP2B1, CCT6B, ZNF830
	13	85702745–58406417	0.74	GPR158, MKX, SYNDIG1, PREX1
	16	54796169–58047574	0.76	MYO10, CPEB4
	22	55395817–44154558	0.76	A1CF, CTBP2, GRK5, XPNPEP1, CFAP46, DOCK1, INSYN2A, LIPA, MUOF, PLCE1
	23	36106915–38820448	3.53	MYOM1, DLGAP1, SMCHD1
BCSM	1	173862929–190851636	0.88	ATP6V1A, CD200, ATG3, CFAP44, CCDC191, NECTIN3, NEPRO, PLCXD2, SLC9C1
	2	111201892–114207253	2.21	HPGD, ECPAS, FBXO8, GLRA3
	2	114746188–116378689	0.65	GALNTL6
	9	57388779–56572469	3.35	STMN2, TPD52, ZBTB10
	10	56843164–69129301	1.14	LOC101115632, SPATA13
	12	36958022–40040678	0.69	FMO1, FMO2, FMO4, MTHFR, MFN2, PRRC2C, TNFRF1B
	13	51269879–54158422	13.89	TMC2, SIRPA, CPXM1, KCNQ2, RBBP8NL, DNAAF9
	13	26807364–30712871	5.61	ITGA8, FRMD4A, MINDY3, RSU1, ANKEF1, CUBN, FAM171A1, PTER, PRPF18, TRDMT1
	13	42377205–45741876	4.68	PGF2, LOC106990122, LOC101108592
	20	52019528–6887963	4.33	KHDRBS2, F13A1, GMDS, CDYL, HCRTR2, LRRC1, LOC101114063

Chr, chromosome; PVE (%), proportion of additive genetic variance explained by each window; LWM and BCS, live weight and body condition score at mating, respectively.

Table 7.4 Chromosome, location, proportion of additive genetic variance (PVE, %) and candidate genes within the top 10 windows associated with the pregnancy rate (PR) and lambing potential (LP) of Merino ewes.

Trait	Chr	Window Bounds (bp)	PVE (%)	Candidate Genes
PR	1	40646909–41530079	0.38	LEPR, DNAJC6
	4	107666587–70951540	3.84	ADCY1, PDIA4, LOC101113583, LRRC4, SND1, TAC1
	4	52544546–58541568	1.87	-
	4	42940192–48319572	0.73	NAPEPLD, PTPN12, RELN, FBXL13, GSAP, FAM185A, ORC5
	4	113244910–125545756	0.61	RBM33, XRCC2, CNPY1, LMBR1, PPP1R9A, RNF32
	16	45966691–50076565	8.98	CDH10
	16	50280874–54676335	0.62	CDH12
	16	25883094–30276428	0.50	PARP8
	16	30392117–33873022	0.45	OXCT1, CARD6, GHR, CCL28, RIMOC1, RANBP17, MROH2B, PAIP1
	21	18437167–23229347	0.46	FAT3, LOC101117547, LUZP2
LP	2	138951962–150539090	1.03	LRP2, CERS6, STK39
	2	67932661–69907932	0.51	ABHD17B, GDA, TRPM3
	2	195395266–197769393	0.39	HECW2, DNAH7, SLC39A10
	3	192191853–194520670	0.46	PDE3A, LOC101117577, C2CD5, SLCO1A2, SPX, LOC101115359
	4	107666587–70951540	5.68	ADCY1, PDIA4, LOC101113583, LRRC4, SND1, TAC1
	5	30712220–3475920	1.29	LPAR2, DMXL1, FLT4,
	16	45966691–50076565	2.00	CDH10
	16	1653965–4370649	1.25	DOCK2, MROH2B, BDP1, LOC101122306, ANKRD55, SLIT3, SGTB
	19	60339892–10882333	0.45	LRRFIP2, STAC, TRANK1
	25	38239943–41537781	0.47	CCSER2

Chr, chromosome; PVE (%), expected proportion of additive genetic variance explained by each window; PR, pregnancy rate; LP, lambing potential.

Discussion

The present study reports on chromosome segments associated with economically relevant traits of Uruguayan Merino sheep. The genomic regions of interest on chromosomes 1, 3, 4, 5, 6, 8, 9, 11, 12, 13, 16, 19 and 22 identified in this study contain known candidate genes related to the wool traits, live weight, body condition score and reproduction traits of sheep and other species (see the following paragraphs). The next sections focused on some of the genes located within the top 10 windows for each trait that explained the largest proportion of the additive genetic variance.

Wool follicle regulation involves several genes, including IGF and TGFB (Liu et al., 2014). The candidate genes for the wool traits identified in this study included IGF-1, TGFBR2, PDE3A, STK3, PRKCA, ZNF704 and EXT1. These genes have previously been associated with hair (Lin and Yang, 2013; Kim, 2020; Heilmann-Heimbach et al., 2020), cashmere (Su et al., 2018; Han et al., 2021) and wool (Damak et al., 1996; Darwish et al., 2017; Zhao et al., 2021c). In this study, the functional analysis indicated that the genes WAPL, ESR1 and IGF-1 were significantly enriched in the regulation of fibroblast proliferation (Appendix II), which is crucial for hair follicle formation (Chen et al., 2012). Overall, the proportion of additive genetic variance explained by each window was relatively small (lower than 0.75%), which reflects the polygenic nature of wool traits.

The identification of genes associated with the live weight is of particular interest for sheep breeding programs (Zhao et al., 2021a; Lu et al., 2020). Some of the potential genes for the ewe LWM are known to be involved in the LW of young sheep. For example, CAST has been related to the birth weight and growth rate of lambs (Jawasreh et al., 2017; Armstrong et al., 2018). The genes LAP3, MED28, and HERC6, located on chromosome 6, have previously been identified as candidate genes for the post-weaning LW in Australian Merino sheep (Al-Mamun et al., 2015). The identification of genes commonly affecting the LW at both early and adult ages is unsurprising, given the moderate to high genetic correlations between these traits (Safari et al., 2005; Huisman and Brown, 2008). The genes HERC6 and MED28 have been also associated with gastrointestinal nematode infection, which is one of the most important health problems in grazing sheep (Al Kalaldeh et al., 2019). This is in agreement with earlier studies that suggested that some SNPs associated with gastrointestinal nematode resistance are involved in growth traits (Álvarez et al., 2019). In sheep, the gene GPRIN3 was also reported to be associated with litter size (Tao et al., 2021). Other genes that were found to be associated with the ewe LWM in the present study have been reported as candidate genes for LW-related traits in different species. For example, A1CF, ZNF830, CCT6B and MYO10 were associated with residual feed intake in cattle (Karisa et al., 2013; de Las Heras-Saldana et al., 2019; Dlamini et al., 2022), while the genes CTBP2 and AP2B1 have been linked to meat quality and lipid metabolism in pigs (Ponsuksili et al., 2009; Piórkowska et al., 2018).

In sheep, the body condition score is an indicator of the available body reserves (fat and muscle) (Kenyon et al., 2014). Several genes that are known to be involved in fat storage and metabolism were associated with the ewe BCS in the present study. For example, TMC2, SIRPA and CPXM1 have been reported as candidate genes for tail fat deposition in sheep (Yuan et al., 2017). The gene CPXM1 was also identified as a positive regulator of adipogenesis in mice and humans (Kim et al., 2016). In mice, FMO1, a member of the flavin-containing mono-oxygenase (FMO) gene family, was associated with energy homeostasis and metabolic efficiency (Veeravalli et al., 2014). TPD52 is a regulator of lipid metabolism and is involved in fatty acid storage (Ha et al., 2019). Early studies indicated that the overexpression of ATG3 favors lipid deposition in mice (da Silva Lima et al., 2022). In humans, LRRC1 is involved in adipocytic differentiation (Wang et al., 2022), whereas F13A1 is expressed at high levels in the adipose tissue of obese individuals (Dull et al., 2021).

The present study identified two common regions associated with pregnancy and the lambing potential, suggesting that the same genes may play a role in the regulation of these reproduction traits. These regions are located on chromosomes 4 and 16 and contain genes that have previously been associated with several reproduction traits. For example, ADCY1 has been related to pubertal initiation in sheep (Zhang et al., 2022), fertility in dairy cattle (Höglund et al., 2014) and fecundity in goats (Lai et al., 2016; Islam et al., 2019). The gene CDH10 was associated with several reproduction traits in buffaloes (Li et al., 2018). Furthermore, PDIA4 was found to be involved in the litter size in sheep and pigs (Wang et al., 2020; Liu et al., 2018). In the present work, LEPR was identified as a candidate gene for the pregnancy rate. This gene has already been associated with several reproduction traits, including pregnancy (Moschos et al., 2002; Taheri and Parham, 2016; Juengel et al., 2016; Lakhssassi et al., 2020). The genes GHR and LPAR2 are associated with sheep reproduction (Akhatayeva et al., 2020; Li et al., 2020), while DMXL1 is related to reproduction traits in heifers (Mohammadi et al., 2022). Therefore, there is evidence supporting the concept that the genes located on chromosomes 4 and 16 play an important role in the reproduction traits of Merino sheep.

This work was the first to perform a single-step Genome-Wide Association Study of the production and reproduction traits of mixed-age ewes in Uruguay. As mentioned above, several of the candidate genes detected were also reported in other studies, which provides confidence in our results. A limitation of this study was the small sample size, which affected the power of detection. Future analyses based on larger populations would improve the identification of candidate genes for traits of interest in sheep. These results will contribute to the Uruguayan Merino genetic evaluation, as some of identified genes are good targets for selection. In addition, the genomic regions identified here should be utilized as targets in further studies.

Conclusions

This study performed a single-step GWAS of six traits in a Uruguayan Merino sheep population. A total of 13, 22, 42, 22, 24 and 29 genomic regions were significantly associated with the fibre diameter, clean fleece weight, live weight at mating, body condition score at mating, pregnancy rate and lambing potential, respectively. The study detected several genes, some of which were novel, showing potential associations with the wool (IGF-1, TGFB2R, PRKCA), live weight (CAST, LAP3, MED28, HERC6), body condition score (CDH10, TMC2, SIRPA, CPXM1) or reproduction traits (ADCY1, LEPR, GHR, LPAR2) of mixed-age ewes. These results require validation using a larger dataset before their implementation in genomic selection among Uruguayan Merino sheep. Overall, our findings will be useful for further genomic studies and genetic improvement programs in Uruguay.

Chapter VIII

General discussion and conclusions

The aim of this thesis was to evaluate the impact of the selection program utilized in an Uruguayan Merino flock on ewe productive (wool traits, LW, and BCS) and reproductive performance. Data from a long-term selection Merino flock established in Uruguay in 1999 were analysed. Data included two distinct periods with different selection emphases. During the first 10 years (1999 – 2010), the selection objective of this flock focused on reducing FD (19 µm or finer), while allowing for a slight loss in CFW. From 2011 to 2018, the breeding objective was focused on maintaining FD (less than 15.5 µm), while increasing both CFW and LW. The general discussion and conclusion section summarizes the main findings, limitations, and contributions of this thesis.

Chapter summaries

The data from the Uruguayan long-term Merino selection flock were examined from a phenotypic (Chapters III and IV), genetic (Chapters V and VI), and genomic (Chapter VII) perspective. Chapter III provides information on the establishment, genetic selection objectives, nutritional conditions, and management of the flock. This information was utilized throughout the thesis to explain the performance of lambs and ewes.

Chapter III evaluated the phenotypic trends observed over the period 1999 to 2018 in FD, GFW, and LW at yearling age. The results indicate that by using suitable selection indices, reductions of approximately 3 µm in FD (from 18 to 15 µm) and increases in both GFW (at least 0.5 kg) and LW (approximately 3 kg) can be achieved. Overall, Chapter III demonstrated that the selection strategies applied in the flock resulted in phenotypic improvements in economically relevant traits in yearling lambs.

Adult ewe traits are important determinants of overall Merino flock income, and Chapter IV focused on the phenotypic changes observed over the period 1999 to 2018 for major wool, growth, and reproduction traits in mixed-age ewes. The results show that ewe FD decreased by approximately 3 µm (from 19 to 16 µm), GFW increased by approximately 0.2 kg, whereas LW at mating increased by 3 kg. These phenotypic changes were accompanied by decreases of BCS at mating (approximately by 1 unit), and a small positive change in ewe lifetime reproduction. Gross income estimates indicated that increasing farmer income by selecting for finer wool, heavier fleeces, and heavier animals could be obtained without compromising ewe reproductive performance.

The estimation of genetic parameters is an essential step to develop an effective breeding program. Chapter V aimed to update the current genetic parameters for production traits utilized in the Uruguayan genetic evaluation. More importantly, this Chapter estimated, for the first time, genetic parameters for ultrasound scanning traits, BCS, and reproduction traits in Uruguayan Merino sheep. The main findings of this Chapter indicated that selection for reduced FD will not adversely affect ewe reproductive performance, with selection for increased yearling LW improving reproduction traits. On the other hand, selection for increased adult CFW will reduce ewe reproductive performance, and selection for reduced FD will negatively impact on BCS. While there were some unfavorable genetic correlations between traits, desirable genetic progress can be obtained simultaneously in wool, growth, and reproduction traits by using suitable selection indices. Overall, most genetic parameters reported in this study were reasonably similar to those previously reported in other non-uruguayan Merino studies.

Estimating genetic trends is an important tool to evaluate the success of any breeding program. Chapter VI estimated genetic trends for production and reproduction traits in a Merino flock having undergone 20 years of selection, representing two distinct periods with different selection emphasis. From 1999 to 2010, the selection objective of this flock focused on reducing FD, while allowing for a slight loss in CFW. From 2011 to 2018, the breeding objective was focused on maintaining FD, while increasing both CFW and LW. The genetic trends reported in this Chapter indicated that, from 1999 to 2010, yearling lambs showed significant reductions in FD. Before 2010, yearling lambs displayed reductions in CFW, whereas from 2011 to 2018, weights increased. The annual genetic gain for LW was greater in the second period than in the first period. Over the whole study period, the total response indicated a genetic decrease of -2.7 and -1.8 µm for Y_FD and A_FD, respectively. The total genetic progress for Y_CFW and A_CFW was 0.355 and 0.198 kg, respectively. These genetic responses were accompanied by marginal or no genetic changes in BCS at mating and NLWEJ. Therefore, the breeding strategies applied during the study period were effective in achieving the objectives.

Identification of genomic regions associated with economically relevant traits has the potential to improve the rate of genetic improvement in breeding programs. In Chapter VII, the first genome-wise association study (GWAS) for wool traits, LW, BCS and reproduction traits of Uruguayan Merino sheep was performed. The results indicated that a total of 13, 22, 42, 22, 24, and 29 genomic regions were significantly associated with A_FD, A_CFW, LWM, BCSM, pregnancy rate, and lambing potential, respectively. Within the top 10 windows for each trait, several genes associated with the traits of interest were identified. Some of the candidate genes detected in this Chapter were also reported in other studies. The genomic regions and genes reported here should be utilized as targets in further studies. Overall, the results of this Chapter will assist the Uruguayan Merino genetic evaluation.

Limitations of the study

This study did not include data from Uruguayan Merino breeders. It would be useful to have phenotypic responses from different production environments and genetic parameters based on a wider representation of the Uruguayan Merino sheep industry. Nowadays, the Uruguayan genetic evaluation database for Merinos contains 91,000 animals with phenotypic and pedigree data, with an annual intake of approximately 5,000 animals (Gimeno and Ciappesoni, 2022). Each year, records of production traits come from approximately 20 different Merino flocks. Future studies will estimate genetic parameters based on the national genetic evaluation database.

The small sample size utilized in GWAS affected the statistical power of detection. Although the sample size was good enough to detect genes and genomic regions affecting production and reproduction traits, the general recommendation is to use at least 1,000 genotyped animals in GWAS (Garrick and Fernando, 2013). Nowadays, approximately 3,200 Uruguayan Merino lambs have been genotyped and measured for the traits evaluated in this thesis (wool and growth traits, ultrasound carcass traits, BCS, and reproduction traits). This information will be included in future GWAS studies.

This study did not estimate the economic benefit of including other traits in selection indices for Merinos. The role and economic importance of reproduction, ultrasound carcass traits, and BCS in current selection indices for Uruguayan Merinos require further exploration. A more in-depth financial analysis is needed to encourage government and breeder investment.

Contributions and next steps

In Uruguay, genetic evaluation for Merinos is carried out by the Uruguayan Secretariat of Wool (SUL) and the National Institute of Agricultural Research (INIA). This evaluation uses performance and pedigree data to produce EBVs of individuals for wool production and quality, LW, and faecal worm egg count. To achieve genetic improvement toward a more profitable and sustainable Merino sheep, it is important to broaden the breeding objective to include other traits of economic and environmental relevance. Two challenges that the Uruguayan Merino genetic evaluation will face in the future include developing new selection indices and implementing a successful genomic selection.

Developing new selection indices

In Uruguay, selection indices for Merinos include FD, CFW, and LW. Some Merino studies have suggested that to achieve relevant genetic gains in ewe reproductive performance, reproduction should be included in the breeding objective and measured as a selection criterion. The results of this thesis (Chapters IV, V, and VI) demonstrate that the current Uruguayan breeding program is unlikely to have a major impact on ewe reproduction performance. Therefore, an important next step will be to explore how best to incorporate reproduction into Uruguayan Merino selection indices.

Traits associated with resilience are likely to grow in importance in the future. The role of BCS and ultrasound fatness in Merino breeding programs have been evaluated in countries like Australia and New Zealand. The results of this thesis indicate that there is low to moderate genetic variation with some scope to improve BCS and FAT. Incorporating these traits into the national genetic evaluation database for Uruguayan Merino sheep would enable breeders to place emphasis on these traits. Further studies are required to account for the economic impact of including resilience traits and longevity in Uruguayan Merino breeding programs.

In the context of climate change, methane emissions are a major concern for livestock. Reducing methane emissions by animal selection is possible as this trait is heritable (Wahinya et al., 2022). In Uruguay, methane emissions and feed efficiency are being recorded by research entities to evaluate strategies to incorporate these traits into the breeding programs for Merinos. Nowadays, there are approximately 1,200 Merino lambs with records of these traits. Further research is needed to obtain accurate data related to methane emissions from experimental flocks and other Uruguayan Merino farms.

Genomic prediction

Genomics gives the potential to select for traits that are hard or expensive to measure such as ewe reproductive performance, methane emissions, and feed efficiency. In Uruguay, data from intensive phenotyping and genotyping of a training population of approximately 3,200 Merino lambs are being used to develop a model for predicting genomic estimated breeding values (GEBVs) for several traits. In addition to genomic selection, SNP data will be used to identify genes associated with traits of relevance, including methane emissions, feed intake, and feed efficiency. There is a huge opportunity to improve the current Uruguayan selection program for Merinos. International and regional collaboration between researcher groups, extensionists, consultants, and Merino breeders could assist with the refinement of breeding programs for Merino sheep.

General conclusion

The results of this thesis provided valuable information to improve the current genetic evaluation of Merino sheep in Uruguay. Phenotypic responses for production and reproduction traits at yearling and adult age demonstrate that by using suitable selection indices and recommended nutritional and management practices, it is possible to produce ultrafine wool without compromising ewe reproductive performance. Genetic parameters reported in this thesis indicate that selecting for reduced FD will not adversely affect reproduction traits, and selection for increased yearling LW will improve ewe reproductive performance. Selection for increased adult CFW will reduce ewe reproductive performance, whereas selection for reduced FD will negatively impact on BCS. Although unfavorable genetic relationships between wool traits and both BCS and ewe reproductive performance exist, simultaneous improvements in the traits would happen using appropriately designed indices.

The results of this work will update the current genetic parameters utilized for the Uruguayan Merino genetics evaluation. More importantly, the genetic parameters for a wide range of traits will be utilized to calculate selection indices that incorporate new traits, such as reproduction, in the Uruguayan Merino breeding program. Several genomic regions and candidate genes reported in this thesis will be useful for further genomic studies and genetic improvement programs in Uruguay.

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Appendices

Appendix I

Appendix I. Table 1. Supplementary example pedigrees containing individuals with unknown parents assigned to distinct unknown parent groups (a), and Q matrix for individuals with known pedigree (b).

a) *Pedigree containing individuals with unknown parents assigned to distinct unknown parent groups*

ID[1]	Dam	Sire	Unknown parent groups (UPG)[2]									
			1	2	3	4	5	6	7	8	9	10
A	NA	NA	0	0	1	0	0	0	0	0	0	0
B	NA	NA	0	1	0	0	0	0	0	0	0	0
C	NA	NA	0	0	0	0	0	0	0	0	1	0
D	NA	NA	0	0	0	0	0	0	0	0	0	1

b) *Pedigree containing individuals with known parents and their corresponding Q matrix*

ID[1]	Dam	Sire
E	A	C
F	B	C
G	D	C
H	E	C

$$Q = \begin{array}{cccccccccc} \mathbf{1} & \mathbf{2} & \mathbf{3} & \mathbf{4} & \mathbf{5} & \mathbf{6} & \mathbf{7} & \mathbf{8} & \mathbf{9} & \mathbf{10} \\ \left[\begin{array}{cccccccccc} 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 \\ 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0.5 \\ 0 & 0 & 0.25 & 0 & 0 & 0 & 0 & 0 & 0.75 & 0 \end{array} \right] \end{array}$$

NA = pedigree information not available.

[1] Animal identification. A = original ewe sourced from a commercial farmer; B = original ewe provided by a Merino stud breeder; C = imported sire; D = ewe born in the flock with unknown parents. E, F, G, and H = animals born in the flock with known parents.

Q = matrix generated from the pedigree file (a,b). Rows of Q for individuals with known parents were calculated as: $Q = 0.5\,(Q_{\text{sire}} + Q_{\text{dam}})$. Each row of Q indicates the contributions of each UPG to an individual.

[2] Unknown parent groups (UPG) 1, 2, and 3 account for the flock of origin of base population animals. UPGs 4 to 9 represent the flock of origin of imported sires, whereas UPG 10 was created to allocate all individuals born in the flock but without pedigree.

Appendix I. Table 2. High posterior density range of the genetic and phenotypic correlations among wool and growth traits at yearling age.

Traits	**Genetic correlations**		**Phenotypic correlations**	
	95%HPD$_L$	**HPD$_U$**	**95%HPD$_L$**	**HPD$_U$**
Y_FD – Y_CFW	-0.06	0.23	0.06	0.19
Y_FD – Y_GFW	-0.02	0.26	0.09	0.21
Y_FD – Y_SL	0.10	0.36	0.12	0.24
Y_FD – Y_FAT	0.07	0.53	0.10	0.26
Y_FD – Y_EMA	-0.20	0.23	-0.01	0.19
Y_FD – Y_LW	-0.19	0.03	-0.06	0.07
Y_FD – Y_BCS	-0.11	0.63	0.10	0.35
Y_CFW – Y_GFW	0.84	0.89	0.90	0.92
Y_CFW – Y_SL	0.62	0.76	0.41	0.48
Y_CFW – Y_FAT	-0.15	0.29	0.03	0.13
Y_CFW – Y_EMA	0.00	0.36	0.10	0.20
Y_CFW – Y_LW	0.32	0.51	0.36	0.43
Y_CFW – Y_BCS	-0.30	0.39	0.04	0.18
Y_GFW – Y_SL	0.49	0.67	0.33	0.41
Y_GFW – Y_FAT	-0.19	0.24	0.01	0.11
Y_GFW – Y_EMA	-0.06	0.29	0.08	0.18
Y_GFW – Y_LW	0.33	0.53	0.37	0.44
Y_GFW – Y_BCS	-0.30	0.34	0.03	0.16
Y_SL – Y_FAT	0.03	0.40	0.08	0.18
Y_SL – Y_EMA	0.04	0.37	0.11	0.22
Y_SL – Y_LW	0.17	0.36	0.20	0.29
Y_SL – Y_BCS	-0.12	0.46	0.13	0.25
Y_LW – Y_BCS	0.42	0.77	0.37	0.48
Y_LW – Y_EMA	0.61	0.77	0.50	0.59
Y_LW – Y_FAT	0.46	0.72	0.31	0.41
Y_FAT – Y_BCS	0.23	0.75	0.24	0.35
Y_FAT – Y_EMA	0.40	0.72	0.30	0.39
Y_EMA – Y_BCS	0.52	0.83	0.37	0.47

95%HPDL and HPDU correspond to the lower and upper bound of the highest posterior density interval at 95%, respectively.

Appendix I. Table 3. High posterior density range of the genetic and phenotypic correlations among wool and growth traits in mixed-age ewes.

Traits	**Genetic correlations**		**Phenotypic correlations**	
	95%HPD$_L$	**HPD$_U$**	**95%HPD$_L$**	**HPD$_U$**
A_FD – A_CFW	0.20	0.43	0.26	0.40
A_FD – A_GFW	0.16	0.38	0.24	0.37
A_FD – A_SL	-0.03	0.20	0.04	0.15
A_FD – LWM	-0.09	0.12	0.05	0.19
A_FD – LWP	-0.06	0.15	0.02	0.16
A_FD – LWW	-0.09	0.13	-0.04	0.10
A_FD – BCSM	0.10	0.36	0.13	0.22
A_FD – BCSPL	0.00	0.25	0.06	0.16
A_FD – BCSW	-0.07	0.24	-0.02	0.10
A_CFW – A_GFW	0.92	0.95	0.93	0.95
A_CFW – A_SL	0.33	0.58	0.34	0.44
A_CFW – LWM	-0.07	0.21	0.18	0.32
A_CFW – LWPL	-0.04	0.23	0.09	0.23
A_CFW – LWW	-0.05	0.26	0.00	0.17
A_CFW – BCSM	-0.21	0.11	0.14	0.23
A_CFW – BCSPL	-0.35	-0.04	0.02	0.13
A_CFW – BCSW	-0.32	0.06	-0.07	0.04
A_GFW – A-SL	0.20	0.47	0.26	0.37
A_GFW – LWM	-0.03	0.24	0.21	0.34
A_GFW – LWPL	-0.02	0.25	0.12	0.26
A_GFW – LWW	0.03	0.32	0.04	0.21
A_GFW – BCSM	-0.32	0.03	0.11	0.22
A_GFW – BCSPL	-0.38	-0.08	0.01	0.12
A_GFW – BCSW	-0.34	0.04	-0.07	0.04
A_SL – LWM	-0.02	0.27	0.08	0.20
A_SL – LWPL	0.00	0.27	0.04	0.15
A_SL – LWW	-0.03	0.27	0.02	0.15
A_SL – BCSM	0.04	0.37	0.07	0.15
A_SL – BCSPL	0.10	0.39	0.06	0.14
A_SL – BCSW	-0.06	0.31	0.00	0.10
LWM – LWPL	0.95	0.97	0.73	0.78
LWM – LWW	0.95	0.97	0.59	0.68
LWM – BCSM	0.33	0.58	0.41	0.51
LWM – BCSPL	0.33	0.57	0.32	0.41
LWM – BCSW	0.39	0.67	0.12	0.23
LWPL – LWW	0.92	0.96	0.59	0.68
LWPL – BCSM	0.33	0.57	0.27	0.35
LWPL – BCSPL	0.40	0.61	0.33	0.42
LWPL – BCSW	0.38	0.67	0.14	0.26
BCSM – BCSPL	0.73	0.86	0.37	0.43
BCSM – BCSW	0.61	0.81	0.13	0.22
BCSPL – BCSW	0.65	0.83	0.19	0.28

95%HPDL and HPDU correspond to the lower and upper bound of the highest posterior density interval at 95%, respectively.

Appendix I. Table 4. High posterior density range of the genetic and phenotypic correlations among productive traits at yearling age (Y) and adult (A) ewes.

Traits	**Genetic correlations**		**Phenotypic correlations**	
	95%HPD$_L$	**HPD$_U$**	**95%HPD$_L$**	**HPD$_U$**
A_FD – Y_FD	0.89	0.93	0.75	0.80
A_FD – Y_CFW	0.23	0.45	0.14	0.25
A_FD – Y_GFW	0.16	0.39	0.09	0.22
A_FD – Y_SL	0.22	0.43	0.16	0.28
A_FD – Y_LW	-0.07	0.13	0.02	0.15
A_FD – Y_BCS	-0.16	0.50	0.06	0.32
A_FD – Y_EMA	-0.19	0.14	-0.02	0.20
A_FD – Y_FAT	-0.07	0.46	0.02	0.25
A_CFW – Y_FD	0.15	0.38	0.16	0.30
A_CFW – Y_CFW	0.76	0.86	0.50	0.58
A_CFW – Y_GFW	0.73	0.85	0.49	0.58
A_CFW – Y_SL	0.21	0.42	0.14	0.25
A_CFW – Y_LW	0.15	0.34	0.17	0.29
A_CFW – Y_BCS	-0.21	0.62	-0.06	0.21
A_CFW – Y_EMA	-0.32	-0.01	-0.11	0.10
A_CFW – Y_FAT	-0.46	-0.02	-0.22	-0.01
A_GFW – Y_FD	0.14	0.35	0.15	0.29
A_GFW – Y_CFW	0.66	0.78	0.46	0.54
A_GFW – Y_GFW	0.79	0.88	0.57	0.65
A_GFW – Y_SL	0.11	0.32	0.09	0.22
A_GFW – Y_LW	0.19	0.36	0.20	0.32
A_GFW – Y_BCS	-0.31	0.48	-0.13	0.14
A_GFW – Y_EMA	-0.35	-0.02	-0.14	0.09
A_GFW – Y_FAT	-0.48	-0.09	-0.20	0.01
A_LWM – Y_FD	-0.01	0.22	-0.01	0.13
A_LWM – Y_CFW	0.36	0.56	0.14	0.25
A_LWM – Y_GFW	0.41	0.61	0.16	0.26
A_LWM – Y_SL	0.05	0.25	0.01	0.12
A_LWM – Y_LW	0.93	0.96	0.66	0.71
A_LWM – Y_BCS	0.55	0.87	0.27	0.47
A_LWM – Y_EMA	0.56	0.77	0.28	0.44
A_LWM – Y_FAT	0.27	0.64	0.09	0.26
A_BCSM – Y_FD	0.01	0.32	0.01	0.11
A_BCSM – Y_CFW	-0.07	0.24	-0.03	0.06
A_BCSM – Y_GFW	-0.11	0.21	-0.05	0.03
A_BCSM – Y_SL	0.06	0.32	0.01	0.09
A_BCSM – Y_LW	0.37	0.58	0.11	0.19
A_BCSM – Y_BCS	0.24	0.76	0.10	0.30
A_BCSM – Y_EMA	0.45	0.75	0.16	0.31
A_BCSM – Y_FAT	0.46	0.76	0.10	0.25

95%HPD$_L$ and HPD$_U$ correspond to the lower and upper bound of the highest posterior density interval at 95%, respectively.

Appendix I. Table 5. High posterior density range of the genetic and phenotypic correlations between reproductive performance and productive traits in adult ewes.

Traits	Genetic correlations		Phenotypic correlations	
	95%HPD$_L$	HPD$_U$	95%HPD$_L$	HPD$_U$
PR – A_FD	-0.17	0.16	-0.20	0.08
PR – A_CFW	-0.39	-0.03	-0.24	0.15
PR – A_GFW	-0.34	0.01	-0.22	0.13
PR – A_SL	-0.25	0.13	-0.08	0.01
PR – LWM	-0.09	0.22	0.06	0.17
PR – LWPL	0.01	0.31	-0.05	0.24
PR – LWW	-0.01	0.30	-0.16	0.08
PR – BCSM	-0.29	0.06	0.03	0.12
PR – BCSPL	-0.22	0.14	-0.13	0.20
PR – BCSW	-0.15	0.22	-0.24	-0.01
LP – A_FD	-0.25	0.10	-0.22	0.06
LP – A_CFW	-0.41	-0.03	-0.12	0.22
LP – A_GFW	-0.35	0.02	-0.15	0.16
LP – A_SL	-0.18	0.22	-0.06	0.02
LP – LWM	0.02	0.39	0.11	0.21
LP – LWPL	0.14	0.48	-0.05	0.22
LP – LWW	0.28	0.63	-0.09	0.05
LP – BCSM	-0.31	0.12	0.04	0.12
LP – BCSPL	-0.22	0.22	-0.19	0.20
LP – BCSW	-0.01	0.47	-0.12	0.04
ERA – A_FD	-0.24	0.21	-0.04	0.06
ERA – A_CFW	-0.39	0.11	-0.01	0.08
ERA – A_GFW	-0.39	0.13	-0.01	0.08
ERA – A_SL	-0.40	0.08	-0.03	0.05
ERA – LWM	-0.44	-0.02	0.00	0.09
ERA – LWPL	-0.36	0.09	0.03	0.12
ERA – LWW	-0.45	0.04	-0.60	-0.37
ERA – BCSM	-0.40	0.09	0.00	0.08
ERA – BCSPL	-0.27	0.23	0.02	0.09
ERA – BCSW	-0.41	0.15	-0.58	-0.28
NLWEJ – A_FD	-0.25	0.16	-0.04	0.06
NLWEJ – A_CFW	-0.41	-0.01	-0.02	0.09
NLWEJ – A_GFW	-0.39	0.02	-0.01	0.10
NLWEJ – A_SL	-0.27	0.16	-0.05	0.03
NLWEJ – LWM	-0.15	0.26	0.09	0.19
NLWEJ – LWPL	-0.03	0.38	0.11	0.22
NLWEJ – LWW	0.00	0.48	-0.29	-0.09
NLWEJ – BCSM	-0.40	0.06	0.05	0.13
NLWEJ – BCSPL	-0.22	0.24	0.04	0.14
NLWEJ – BCSW	-0.24	0.31	-0.42	-0.20

95%HPD$_L$ and HPD$_U$ correspond to the lower and upper bound of the highest posterior density interval at 95%, respectively.

Appendix I. Table 6. High posterior density range of the genetic and phenotypic correlations between lifetime reproductive performance and productive traits in adult ewes.

Traits	**Genetic correlations**		**Phenotypic correlations**	
	95%HPD$_L$	**HPD$_U$**	**95%HPD$_L$**	**HPD$_U$**
TLW – A_FD	-0.24	0.12	-0.03	0.08
TLW – A_CFW	-0.50	-0.19	-0.08	0.05
TLW – A_GFW	-0.46	-0.13	-0.06	0.07
TLW – A_SL	-0.25	0.14	-0.04	0.07
TLW – LWM	-0.20	0.13	0.13	0.25
TLW – LWPL	-0.04	0.31	0.05	0.17
TLW – LWW	0.09	0.44	0.06	0.17
TLW – BCSM	-0.66	-0.42	-0.02	0.10
TLW – BCSPL	-0.49	-0.13	-0.01	0.09
TLW – BCSW	-0.20	0.30	-0.03	0.08
TLWW – A_FD	-0.21	0.14	-0.01	0.10
TLWW – A_CFW	-0.50	-0.16	-0.08	0.06
TLWW – A_GFW	-0.46	-0.15	-0.07	0.06
TLWW – A_SL	-0.21	0.20	-0.04	0.07
TLWW – LWM	0.03	0.40	0.20	0.32
TLWW – LWPL	0.20	0.52	0.11	0.22
TLWW – LWW	0.21	0.56	0.09	0.21
TLWW – BCSM	-0.59	-0.28	0.05	0.16
TLWW – BCSPL	-0.34	0.02	0.03	0.13
TLWW – BCSW	-0.12	0.33	-0.03	0.07

95%HPD$_L$ and HPD$_U$ correspond to the lower and upper bound of the highest posterior density interval at 95%, respectively.

Appendix I. Table 7. High posterior density range of the genetic and phenotypic correlations between reproductive performance and productive traits at yearling age.

Traits	Genetic correlations		Phenotypic correlations	
	95%HPDL	HPDU	95%HPDL	HPDU
PR – Y_FD	-0.11	0.21	-0.02	0.12
PR – Y_CFW	-0.06	0.26	-0.04	0.09
PR – Y_GFW	-0.07	0.27	-0.05	0.07
PR – Y_SL	-0.13	0.18	0.03	0.16
PR – Y_LW	0.04	0.33	0.02	0.15
PR – Y_BCS	-0.17	0.35	0.05	0.33
PR – Y_EMA	0.00	0.39	0.11	0.31
PR – Y_FAT	-0.18	0.28	-0.06	0.15
LP – Y_FD	-0.13	0.22	-0.02	0.08
LP – Y_CFW	-0.05	0.30	-0.01	0.09
LP – Y_GFW	-0.05	0.32	-0.02	0.08
LP – Y_SL	-0.16	0.20	0.04	0.14
LP – Y_LW	0.16	0.46	0.04	0.14
LP – Y_BCS	-0.29	0.41	0.01	0.24
LP – Y_EMA	0.07	0.51	0.07	0.23
LP – Y_FAT	-0.29	0.33	-0.07	0.10
ERA – Y_FD	-0.28	0.19	0.00	0.11
ERA – Y_CFW	-0.22	0.25	0.02	0.11
ERA – Y_GFW	-0.28	0.21	0.01	0.11
ERA – Y_SL	-0.15	0.32	0.01	0.11
ERA – Y_LW	-0.30	0.14	-0.02	0.08
ERA – Y_BCS	-0.27	0.37	-0.08	0.17
ERA – Y_EMA	-0.17	0.43	-0.05	0.12
ERA – Y_FAT	-0.15	0.51	-0.03	0.13
NLWEJ – Y_FD	-0.16	0.24	0.00	0.11
NLWEJ – Y_CFW	-0.04	0.35	0.01	0.11
NLWEJ – Y_GFW	-0.18	0.27	0.01	0.13
NLWEJ – Y_SL	-0.09	0.29	0.04	0.14
NLWEJ – Y_LW	0.07	0.43	0.03	0.14
NLWEJ – Y_BCS	-0.26	0.30	-0.09	0.25
NLWEJ – Y_EMA	0.14	0.61	0.10	0.25
NLWEJ – Y_FAT	-0.13	0.51	-0.04	0.12

95%HPD_L and HPD_U correspond to the lower and upper bound of the highest posterior density interval at 95%, respectively.

Appendix I. Table 8. High posterior density range of the genetic and phenotypic correlations between lifetime reproductive performance and productive traits at yearling age.

Traits	**Genetic correlations**		**Phenotypic correlations**	
	95%HPD$_L$	**HPD$_U$**	**95%HPD$_L$**	**HPD$_U$**
TLW – Y_FD	-0.25	0.31	-0.03	0.09
TLW – Y_CFW	-0.16	0.38	0.02	0.12
TLW – Y_GFW	-0.10	0.42	0.02	0.11
TLW – Y_SL	-0.27	0.26	0.01	0.11
TLW – Y_LW	0.02	0.48	0.04	0.13
TLW – Y_BCS	-0.30	0.58	-0.02	0.22
TLW – Y_EMA	-0.02	0.63	0.10	0.25
TLW – Y_FAT	-0.32	0.48	-0.01	0.14
TLWW – Y_FD	-0.16	0.38	0.00	0.11
TLWW – Y_CFW	-0.04	0.50	0.01	0.11
TLWW – Y_GFW	-0.01	0.51	0.01	0.10
TLW W – Y_SL	-0.14	0.36	0.03	0.12
TLWW – Y_LW	0.29	0.69	0.09	0.19
TLWW – Y_BCS	-0.15	0.57	0.05	0.28
TLWW – Y_EMA	0.22	0.72	0.14	0.28
TLWW – Y_FAT	-0.19	0.53	0.03	0.18

95%HPD$_L$ and HPD$_U$ correspond to the lower and upper bound of the highest posterior density interval at 95%, respectively.

Appendix II

Appendix II. Table 1. Significant gene ontology terms associated with biological processes (BP), molecular functions (MF), and cellular components (CC) associated with fibre diameter (A), clean fleece weight (B), body condition score (C), pregnancy rate (D) and lambing potential (E).

A: Fibre diameter

GO category	GO term	adjusted_p_value	Gene names
MF	oxygen carrier activity	3.936×10^{-3}	LOC101106199, LOC101105437
	oxygen binding	2.539×10^{-2}	LOC101106199, LOC101105437
BP	regulation of oocyte development	6.077×10^{-3}	IGF-1, PDE3A
	regulation of oogenesis	6.077×10^{-3}	IGF-1, PDE3A
	positive regulation of fibroblast proliferation	1.372×10^{-2}	WAPL, ESR1, IGF-1
	oxygen transport	4.163×10^{-2}	LOC101106199, LOC101105437
	regulation of fibroblast proliferation	4.883×10^{-2}	WAPL, ESR1, IGF-1
	gas transport	4.994×10^{-2}	LOC101106199, LOC101105437
CC	hemoglobin complex	2.988×10^{-3}	LOC101106199, LOC101105437

B: Clean fleece weight

GO category	GO term	adjusted_p_value	Gene names
MF	protein kinase activity	1.869×10^{-2}	UHMK1,DDR2, STK3, LOC101102402, PRKCA
MF	phosphotransferase activity, alcohol group as acceptor	3.972×10^{-2}	UHMK1, DDR2, STK3, LOC101102402, PRKCA
CC	neuronal ribonucleoprotein granule	2.143×10^{-2}	UHMK1

C: Body condition score

GO category	GO term	adjusted_p_value	Gene names
GO:MF	N,N-dimethylaniline monooxygenase activity	5.740×10^{-4}	FMO1, FMO2, FMO3
	NADP binding	3.879×10^{-3}	GMDS, FMO1, FMO2, FMO3
	oxidoreductase activity, acting on paired donors	3.175×10^{-2}	FMO1, FMO2, FMO3

D: Pregnancy rate

GO category	GO term	adjusted_p_value	Gene names
GO:BP	postsynaptic membrane organization	1.002×10^{-2}	LRRC4,ENSOARG00000017524, Membrane associated guanylate kinase, WW and PDZ domain containing 2, RELN
GO:BP	postsynaptic density protein 95 clustering	2.604×10^{-2}	LRRC4, RELN
GO:CC	integral component of postsynaptic density membrane	2.945×10^{-2}	ADCY1, LRRC4
GO:CC	intrinsic component of postsynaptic density membrane	3.577×10^{-2}	ADCY1, LRRC4

E: Lambing potential

GO category	GO term	adjusted_p_value	Gene names
GO:BP	transmembrane transport	1.749×10^{-2}	LRP2, STK39, TRPM3, SLC39A10, LOC101117577, C2CD5, SLCO1A2

BP: Biological processes; **MF**: Molecular functions; **CC**: Cellular components.

Appendix III

Appendix III. Table 1. Potential standardised selection differential (SSD) for the Uruguayan Merino sheep industry.

Year	Number of animals born*	Selected**		Overall SSD
		Dams	Sires	
1999	3611	307	70	1.8
2000	3632	340	66	1.8
2001	3717	406	67	1.8
2002	5318	557	77	1.8
2003	5836	698	77	1.8
2004	5065	967	81	1.6
2005	4753	852	76	1.6
2006	5006	955	89	1.6
2007	4838	862	75	1.6
2008	6558	1387	114	1.5
2009	5056	1045	112	1.5
2010	5233	1079	110	1.5
2011	6735	1354	113	1.6
2012	6327	1021	125	1.6
2013	5383	955	114	1.6
2014	3993	491	97	1.7
2015	4006	488	89	1.7

*Number of animals born: includes female and males. **Selected: Those animals born in the given year which became parents later. **Potential SSD** was calculated as the number of selected animals divided by the total number of animals born. **Overall SSD**: averaged over both sexes.

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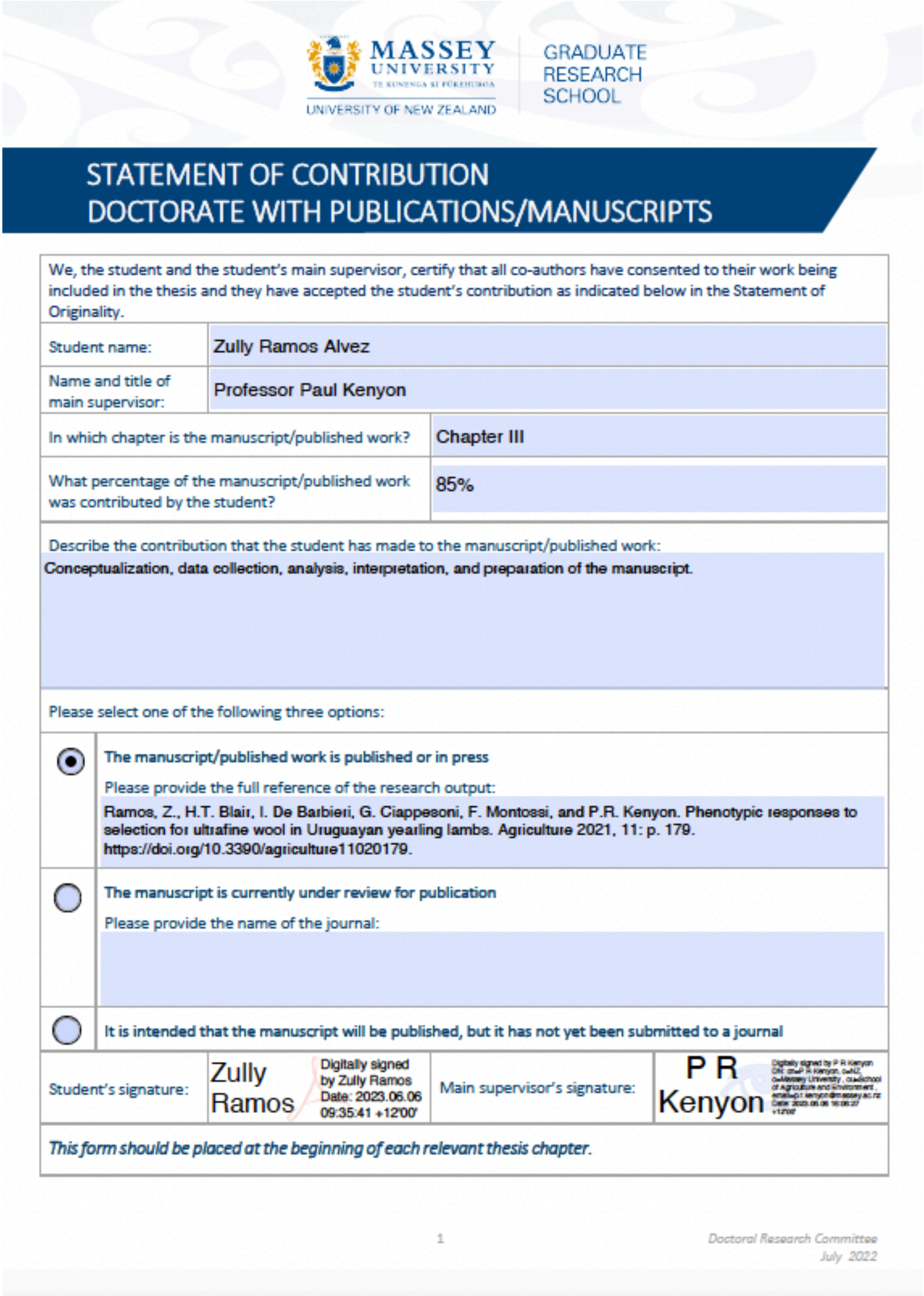

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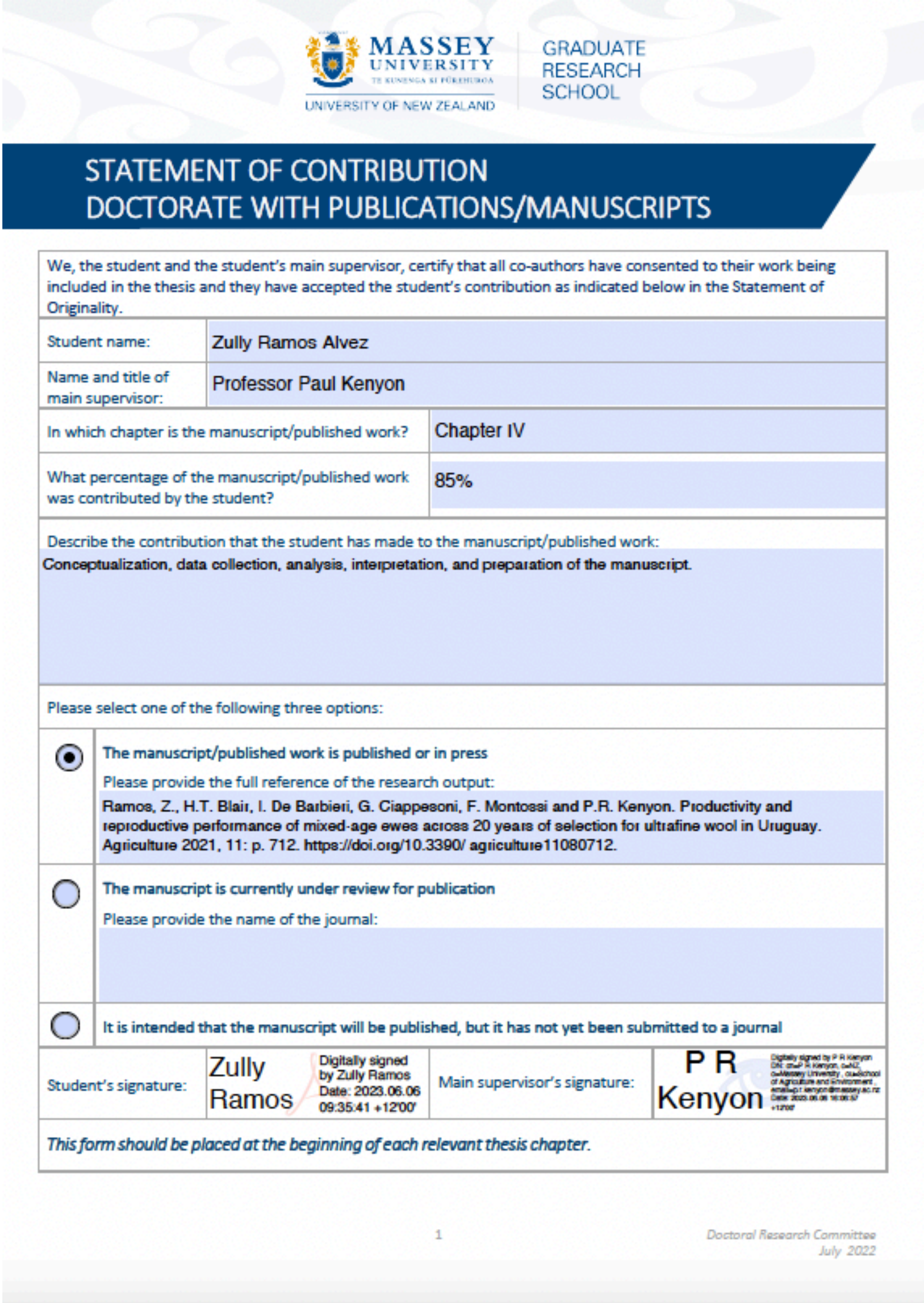

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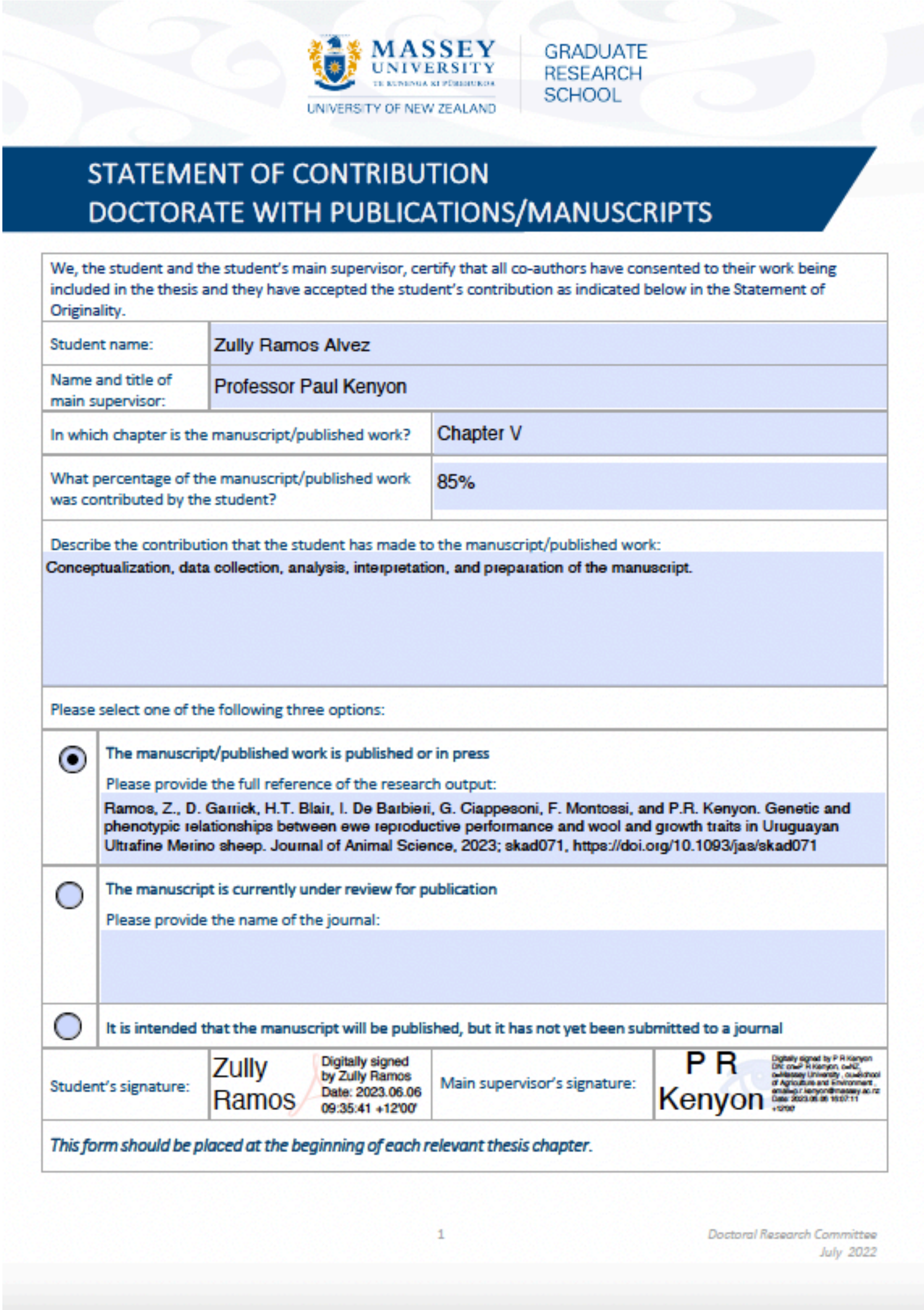

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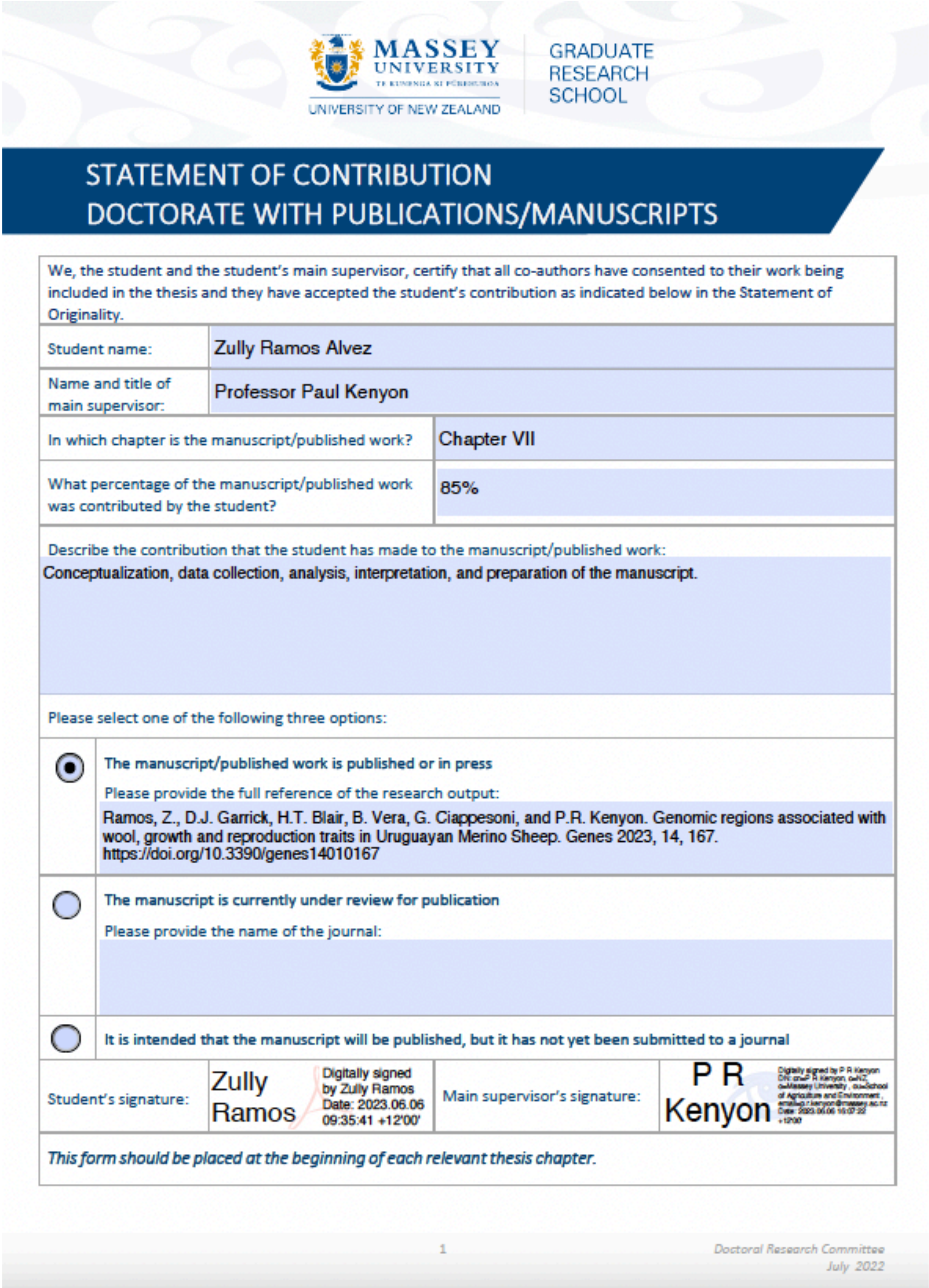

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