OXFORD

AMERICAN SOCIETY OF **ANIMAL SCIENCE**

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 fiber 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 analyzed. 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 analyzed. 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 indexes.

Lay Summary

Fiber diameter (**FD**), clean fleece weight (**CFW**), live weight (**LW**), and reproductive performance are important traits in Merino flocks. This study estimated the genetic parameters for a range of production traits and ewe reproductive performance. Data from approximately 5,700 mixed-sex yearling lambs and 2,000 mixed-age ewes born in a single Uruguayan Merino flock were analyzed. There were generally favorable (positive) genetic correlations between LW and reproduction traits. The genetic relationships between FD and reproduction traits were generally negligible. In addition, moderate unfavorable (negative) genetic correlations were found between adult CFW and ewe reproduction traits. This study indicates that selecting finer fleeces will yield little to no change in ewe reproduction traits, whereas heavier fleeces are related to reduced ewe reproductive performance. On the other hand, genetically heavier yearling ewes will display greater reproductive performance.

Abbreviations: A_CFW, adult clean fleece weight; A_FD, adult fiber 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; ERA, ewe rearing ability; FAT, fat thickness; FD, fiber diameter; 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; 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 fiber diameter; Y_GFW, yearling greasy fleece weigh; Y_LW, yearling live weight at shearing; Y_SL, yearling staple length

Introduction

In the Australian and New Zealand fine-wool Merino sheep industries, breeding objectives typically include fiber diameter (**FD**), clean fleece weight (**CFW**), live weight (**LW**), and repro-duction 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 mo 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). A recent Uruguayan study showed that simultaneous genetic improvements in FD, CFW, and LW resulted in phenotypically heavier ewes, that produced slightly more weight of lamb over their lifetime (Ramos et al., 2021b). 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, 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 indexes 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 indexes 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 indexes resulted in greater genetic improvements in profit. With the exception of fly strike, the above-mentioned traits are relevant in Uruguayan Merino sheep (Ramos et al., 2021b; 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 indexes 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 analyzed. 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, 2021). 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 analyzed. The establishment, genetic selection objectives, nutritional conditions, and management of this flock have previously been reported by Ramos et al. (2021a, 2021b). 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 and New Zealand) 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 (Ramos et al., 2021a). During the first 10 yr, 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 (Ramos et al., 2021a).

Production traits

Wool and growth traits were measured at different stages throughout the animals' life utilizing the procedures described by Ramos et al. (2021a, 2021b). Briefly, traits recorded at yearling age (298 to 432 d) included fiber 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 yr (2010, 2011, and from 2013 to 2019) after shearing. Lambs were body condition scored (**Y_BCS**) after shearing from 2016 to 2020 according to a five-point scale (Jefferies, 1961), whereas all other production traits were variously measured over the whole study period (2001 to 2020, ewe LWM information was missing in 2001).

Reproduction traits

Adult ewe reproduction traits analyzed 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 (Ramos et al., 2021b). 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 1–3 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 yr old, and 7 yr or older) as fixed effects. For all yearling traits, age at the time of measurement was fitted as a covariate in the model.

Table 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_BCS, Y_EMA, and Y_FAT correspond to yearling fiber diameter, clean fleece weight, greasy fleece weight, staple length, live weight at shearing, body condition score, eye muscle area, and fat thickness, respectively.

Table 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 fiber 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.

Table 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. 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 calculated 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 d of age) of all lambs each ewe had in her life.

Table 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	Records
Yearling	Fiber 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), cm²	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	Fiber 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)[4]	58.4	48.17	0	286.5	1,931

[1]SD, standard deviation.
[2]Body condition score: scale 1 to 5.
[3]ERA was calculated as the number of lambs weaned per number of fetuses scanned.
[4]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 d of age) of all lambs each ewe had in her life.

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 yr 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 analyzed 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 et al., 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 relevant.

Results

A summary of the data is shown in Table 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 yr 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 the Supplementary material (Tables 2 to 8).

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 and 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. The genetic

Table 5. Estimates of heritability (posterior mean, bold on diagonal), genetic (below diagonal), and phenotypic (above diagonal) correlations among wool and growth traits at yearling age

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)**

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

Table 6. Estimates of heritability (posterior mean, bold on diagonal), genetic (below diagonal), and phenotypic (above diagonal) correlations among wool and growth traits in mixed-age ewes

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)**

Posterior standard deviations are in parentheses. A_FD, A_CFW, A_GFW, and A_SL refer to adult fiber 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.

Table 7. Genetic and phenotypic correlations (posterior mean) among production traits at yearling age and adult ewes

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)

Posterior standard deviations are in parentheses. Y_FD, Y_CFW, Y_GFW, Y_SL, Y_LW, Y_BCS, Y_EMA, and Y_FAT correspond to yearling fiber 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 fiber 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.

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 6 summarizes the correlations between wool and growth traits in mixed-age ewes (2 to 10 yr 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.

Correlations between yearling and adult traits

Genetic and phenotypic correlations between yearling and adult traits are presented in Table 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 8. The genetic relationships between reproduction traits and A_FD were not different from zero (see Tables S5 and S6 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 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.

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

Table 8. Genetic and phenotypic correlations (posterior mean) between reproductive performance and production traits in adult ewes

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)

Posterior standard deviations are in parentheses. A_FD, A_CFW, A_GFW, and A_SL correspond to adult fiber 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 d of age) of all lambs each ewe had in her life.

Table 9. Genetic and phenotypic correlations (posterior mean) between reproductive performance and production traits at yearling age

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)

Posterior standard deviations are in parentheses. Y_FD, Y_CFW, Y_GFW, Y_SL, Y_LW, Y_BCS, Y_EMA, and Y_FAT correspond to yearling fiber 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 repeated 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 d of age) of all lambs each ewe had in her life.

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 mo 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 (Ramos et al., 2021a, 2021b). 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 (Ramos et al., 2021b). 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-yr 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 indexes.

Predictions of selection response for standard MERINOSELECT indexes 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; Walkom and Brown, 2017; 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 yr. 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 indexes 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.

Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

Acknowledgments

Conflict of Interest Statement

The authors declare no real or perceived conflicts of interest.

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