Journal of Animal Breeding and Genetics

WILEY

Journal of Animal Breeding and Genetics

ORIGINAL ARTICLE OPEN ACCESS

Genetic Trends for Production and Reproduction Traits in Ultrafine Merino Sheep of Uruguay

Zully Ramos[1,2] | Dorian J. Garrick[2] | Hugh T. Blair[2] | Ignacio De Barbieri[3] | Gabriel Ciappesoni[4] | Fabio Montossi[3] | Paul R. Kenyon[2]

[1]Centro Universitario de Tacuarembó, Tacuarembó, Uruguay | [2]School of Agriculture and Environment, Massey University, Palmerston North, New Zealand | [3]Estación Experimental INIA Tacuarembó, Instituto Nacional de Investigación Agropecuaria, Tacuarembó, Uruguay | [4]Estación Experimental INIA Las Brujas, Instituto Nacional de Investigación Agropecuaria, Canelones, Uruguay

Correspondence: Paul R. Kenyon (p.r.kenyon@massey.ac.nz)

Received: 8 June 2024 | **Revised:** 22 February 2025 | **Accepted:** 11 March 2025

Funding: This study was supported by European Union's Horizon 2020, 772787, National Institute of Agricultural Research of Uruguay (INIA_CL_38: Rumiar) and National Agency for Investigation and Innovation of Uruguay Massey University.

Keywords: breeding objectives | breeding programmes | genetic changes | ovine | realised responses

ABSTRACT

Genetic trends were estimated for production and reproduction traits in an Uruguayan Merino genetic nucleus. Two consecutive 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 shifted and then focused on maintaining FD, while increasing both CFW and live weight (LW). Data from approximately 5380 yearling lambs and 2000 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 (−0.210 μm/year, corresponding to −1.28% of the mean of the trait for that period). Before 2010, yearling lambs showed reductions of −0.013 kg/year (−0.62%) in CFW, whereas from 2011 to 2018, this trait increased by 0.052 kg/year (1.88%). The annual genetic gain for Y_LW was greater in the second period than in the first period (0.286 vs. 0.091 kg/year). The genetic trends for FD, CFW and LW were affected by period ($p < 0.001$), indicating that the change in the selection index applied in the genetic nucleus 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 programme utilised in the genetic nucleus improved the traits under selection (FD, CFW and LW) and had a marginal impact on 2-yo_BCSM and NLWEJ. To also achieve relevant genetic gains in ewe reproductive performance, in the future, reproduction traits 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.

1 | 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 programme. Numerous studies have reported the success of breeding schemes within Merino sheep populations (Taylor et al. 2007; Swan et al. 2009; Ciappesoni et al. 2014; Di et al. 2014).

In Uruguay, the current selection indexes for Merinos include yearling fibre diameter (FD), clean fleece weight (CFW) and live weight (LW) as traits. 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. Phenotypic responses for reproduction and BCS in mixed-age ewes to a long-term experimental breeding programme have been reported by Ramos et al. (2021b). It is of interest to know to what extent those phenotypic responses for wool, growth and reproduction traits can be explained by the Uruguayan long-term selection programme.

Data from a long-term selection Merino nucleus 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 (Ramos et al. 2023). From 2011 to 2018, the breeding objective was focused on maintaining reduced FD (< 15.5 μm), while increasing both CFW and LW (Ramos et al. 2023). The selection criteria included yearling expressions of fibre diameter, greasy fleece weight and live weight. 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 selection strategies used in the whole period 1999–2018.

2 | Materials and Methods

2.1 | Location and Data

This study was conducted at the Glencoe Experimental Unit of the Instituto Nacional de Investigación Agropecuaria (INIA, 32°00′21′′ S and 57°08′06″115 W). Information on the region and details of the flock analysed were provided by Ramos et al. (2021a, 2021b). This work was carried out with the approval of the INIA Animal Ethics Committee (INIA_2018.2).

2.2 | Merino Nucleus: Genetic Selection

At approximately 1 year of age, male and female offspring born in the Merino genetic nucleus were selected as replacement animals. The number of selected animals per year is shown in Table 1. Selection decisions were based on phenotypic and genetic criteria as described in Ramos et al. (2021a). During the first 10 years (1999–2010), the selection index utilised combined FD and CFW. Predicted genetic responses from this index included improvements of −0.25 μm/year for FD, whereas CFW was predicted to remain unaltered (De Los Campos et al. 2000). During the CRILU (Uruguayan Regional Consortium for Innovation in Ultrafine Wool) phase (2011–2018), the selection index utilised included FD, CFW and LW. The annual predicted improvements in this index were −0.13 μm, 0.04 and 0.49 kg for FD, CFW and LW, respectively.

Data analysed in this study were a subset of the data presented in Ramos et al. (2023) and included 5381 mixed-sex yearling lambs born between 1999 and 2018 and subsequent records on 2000 of these animals as ewes. The complete pedigree included 7168 animals, 83 sires and 2223 dams. More than 99% of the animals with records had a full pedigree.

TABLE 1 | Total annual number of ewes and rams and number of animals selected over the study period.

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

[a]Selected lambs: Number of offspring who became parents.

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 utilised for fibre diameter, clean fleece weight, greasy fleece weight and staple length were A_FD, A_CFW, A_GFW and A_SL, respectively. Live weight and BCS at mating were measured in ewes aged 2 years (2-yo_LWM and 2-yo_BCSM, respectively). 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 all traits were described by Ramos et al. (2021a, 2021b).

2.3 | Statistical Analysis

Descriptive statistical analyses, outlier detection and definition of fixed effects were performed as described by Ramos et al. (2023). Estimated breeding values (EBVs) for production

(FD, CFW, SL, LW and BCS) and reproduction (NLWEJ) traits were predicted using an animal model implemented in Julia for Whole-Genome Analyses Software (JWAS, Cheng et al. 2018).

TABLE 2 | Descriptive statistics for wool traits, live weight, body condition score and reproduction traits in yearling and adult animals over the entire study period (1999–2020).

Trait	Mean	SD[a]	Min	Max	Records
Y_FD (μm)	15.8	1.61	12.4	22.7	5381
A_FD (μm)	16.6	1.75	11.7	24.5	7079
Y_CFW (kg)	2.35	0.68	0.78	4.86	5381
A_CFW (kg)	2.80	0.51	1.40	4.50	6288
Y_GFW (kg)	3.16	0.91	1.15	6.16	5381
A_GFW (kg)	3.50	0.63	1.90	5.80	6812
Y_SL (cm)	8.4	1.84	3.5	14.0	5381
A_SL (cm)	8.7	1.29	4.5	13.0	6403
Y_LW (kg)	45.2	10.6	18.5	76.5	5674
2-yo_LWM (kg)	43.3	4.50	30.0	58.5	1821
2-yo_BCSM (kg)	3.4	0.62	2.0	4.75	1776
Number of lambs weaned per ewe joined (NLWEJ)	0.71	0.64	0	3	6376

Abbreviation: NLWEJ, number of lambs weaned per ewe joined.
[a]SD, standard deviation. 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.

A multi-trait model was applied to derive EBVs for FD, CFW, GFW, SL and LW. Single-trait models were utilised 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 fitted only significant fixed effects as described by (Ramos et al. 2023; Tables 1–3). Age at the time of sharing (298–432 days of age) and days between consecutive shearing dates (268–399 days) were fitted as covariates for yearling and adult wool traits, respectively (Ramos et al. 2021a, 2021b).

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 were defined based on the flock of origin), 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 effects and X, Q, Z and W are incidence matrices relating records to fixed effects, expected fractions relating individuals to 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 (Blasco 2017).

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). The genetic parameters utilised in the analysis were reported by Ramos et al. (2023). Annual genetic gains were calculated via the linear regression of the EBVs for each trait on the birth year utilising the regression procedure of the SAS software package (version 9.4, SAS Institute Inc., Cary, NC, USA). The slopes of the linear

TABLE 3 | Genetic trend estimates (b) with respective standard errors (SE) and percent change for yearling and adult traits by period.

	First period (1999–2010)[a]		Second period (2011–2018)[b]		
Trait	b ± SE	Percent (%)[c]	b ± SE	Percent (%)[c]	Interaction b* period
Y_FD (μm)	−0.210 ± 0.004*	−1.28	−0.082 ± 0.006*	−0.54	*
A_FD (μm)	−0.282 ± 0.07*	−1.64	0.116 ± 0.01*	0.75	*
Y_CFW (kg)	−0.013 ± 0.0008*	−0.62	0.052 ± 0.002*	1.88	*
A_CFW (kg)	−0.011 ± 0.002*	−0.39	0.023 ± 0.003*	0.82	*
Y_LW (kg)	0.091 ± 0.012*	0.21	0.286 ± 0.02*	0.62	*
2-yo_LWM (kg)	0.021 ± 0.03[NS]	0.05	0.309 ± 0.05*	0.71	*
2-yo_BCSM	0.002 ± 0.0015[NS]	0.06	0.007 ± 0.0016*	0.23	NS
NLWEJ	−0.010 ± 0.0006*	−1.47	0.010 ± 0.001*	1.30	*

Note: 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.
Abbreviations: NLWEJ, number of lambs weaned per ewe joined; NS, non-significant.
[a]First period (1999–2010): The selection objective focused on reducing FD (as finer as possible), while allowing for a slight loss in CFW.
[b]Second period (2011–2018): The breeding objective was focused on maintaining FD (< 15.5 μm), while increasing both CFW and LW.
[c]Percent (%): Corresponds to the annual genetic change as a percentage of the mean of the trait for each period.
*Significant effect at $p < 0.001$.

regression of the EBVs on year of birth as well as the period were tested for significance. Genetic progress was expressed as a percentage of the mean of the trait of each period (FMP and CRILU).

3 | Results and Discussion

3.1 | Descriptive Statistics

Summary statistics for yearling and adult traits are shown in Table 2. The dataset contained 5381 records for each yearling wool trait, which includes both female and male lambs. The number of records ranged from 1776 to 1821 for 2-year-old ewe traits, and from 6288 to 7079 for mixed-age ewes (2–10 years old).

The mean of 2.35 for Y_CFW was similar to that previously reported by Swan et al. (2016; 2.38 kg), but lower than the value observed by Mortimer et al. (2017; 2.79 kg), and slightly higher than Walkom and Brown (2017; 2.06 kg). The mean of 8.4 for Y_SL agreed with the reports of Swan et al. (2016; 8.4 cm) and Walkom and Brown (2017; 8.5 cm), but was longer than Brown and Swan (2016; 7.3 cm). However, it was shorter than reported by Mortimer et al. (2017; 8.9 cm). Adult clean fleece weight found in the present study was consistent with that previously reported in mixed-age ewes of an ultrafine Merino flock (Wuliji et al. 1998; 2.89 kg), but higher values have been reported by Walkom and Brown (2017; 3.96 kg) in fine Merino ewes. The mean of 8.7 for A_SL was longer than the value of 7.6 reported by Wuliji et al. (1998) in ewes of an ultrafine Merino flock, but shorter compared to that earlier reported by Walkom and Brown (2017; 9.8 cm).

Coefficient of variation (CV) expresses the standard deviation as a percentage of the mean; the higher the CV, the greater the variability. The coefficient of variation of FD found in the present study agreed with the value of 10% reported by Daetwyler et al. (2010), Swan et al. (2016) and Mortimer et al. (2017) in fine-wool Merino sheep, but lower values have been reported by Safari et al. (2005; 7%) and Brown and Swan (2016; 7%). The coefficient of variation for Y_CFW was high (29%) which is consistent with previously reported studies (Cloete et al. 2007 [23%–35%]; Swan et al. 2016 [0.31%]; and Mortimer et al. 2017 [0.34%]). In the present study, the number of lambs weaned per ewe joined had a very high coefficient of variation, which agreed with earlier findings (Safari et al. 2005 [63.5%]; Walkom and Brown 2017 [109%]).

3.2 | Genetic Trends for Wool Traits and Live Weight

Long-term responses in individual traits will vary depending on the selection programme 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 (Ramos et al. 2023). The regression coefficients of mean annual EBV on birth year for each trait over both the selection strategies are given in Table 3. The genetic trends are shown graphically in Figures 1–5.

From 1999 to 2010, yearling lambs showed significant reductions in FD (−0.210 μm/year; Table 3). This is consistent in size and sign to responses predicted for the index utilised in this period (−0.25 μm/year), and the high heritability of this trait (Ciappesoni et al. 2010; Fozi et al. 2012; Swan et al. 2016; Mortimer et al. 2017; Dominik and Swan 2018; Ramos et al. 2023). This genetic gain can also be explained by reproductive technologies utilised in the flock, including multiple ovulation and embryo transfer (Ramos et al. 2021b). 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 and 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 (Wuliji et al. 1998; Cloete et al. 2007; Taylor et al. 2007; Di et al. 2014). For example, selection over 10 years using an index that emphasised reduced FD, while maintaining fleece weight showed a reduction in FD of −0.24 μm/year (Taylor et al. 2007).

During the current study, the genetic gain of Y_FD was almost three times greater in the first period than in the second period

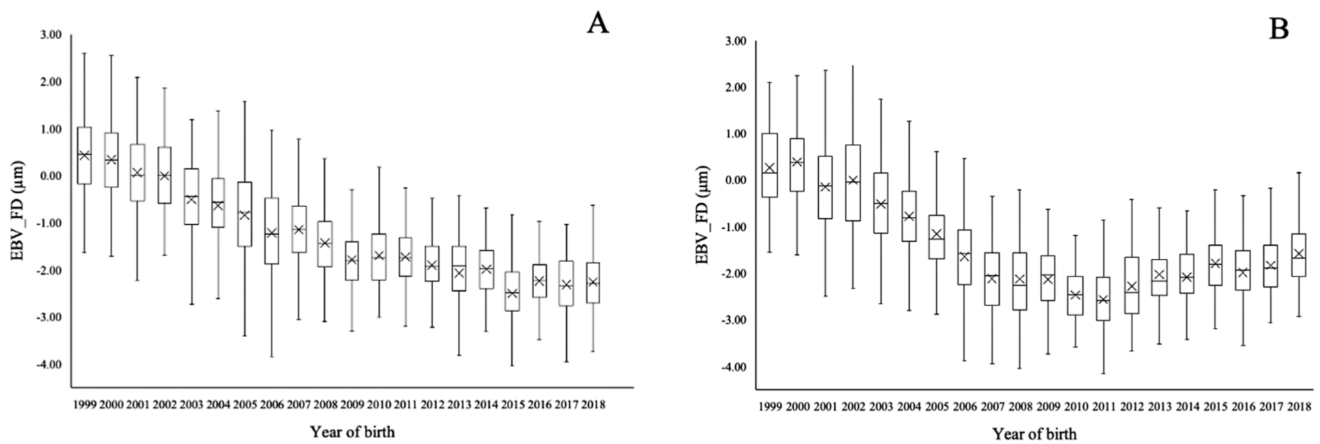

FIGURE 1 | Boxplot graph of estimates of breeding value (EBV) for yearling (A) and adult (B) fibre diameter by year of birth. Mean values are represented by a cross. The fixed genetic base was the average of animals born in 2002 Ciappesoni et al. (2007).

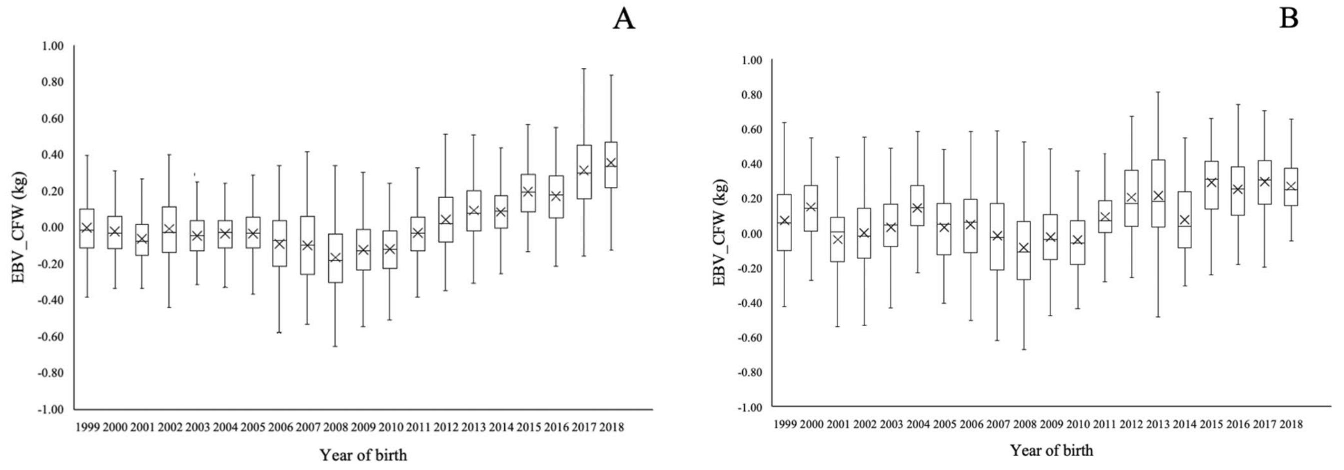

FIGURE 2 | Boxplot graph of estimates of breeding value (EBV) for yearling (A) and adult (B) clean fleece weight by year of birth. Mean values are represented by a cross. The fixed genetic base was the average of animals born in 2002 Ciappesoni et al. (2007).

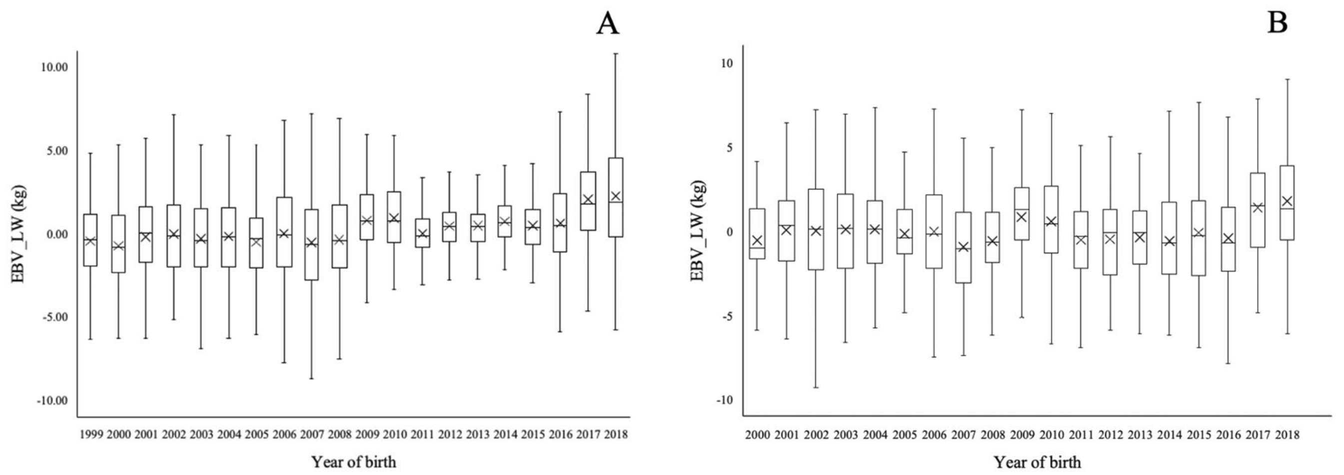

FIGURE 3 | Boxplot graph of estimates of breeding value (EBV) for yearling live weight (A) and 2-year-old ewe live weight at mating (B) by year of birth. The fixed genetic base was the average of animals born in 2002 Ciappesoni et al. (2007).

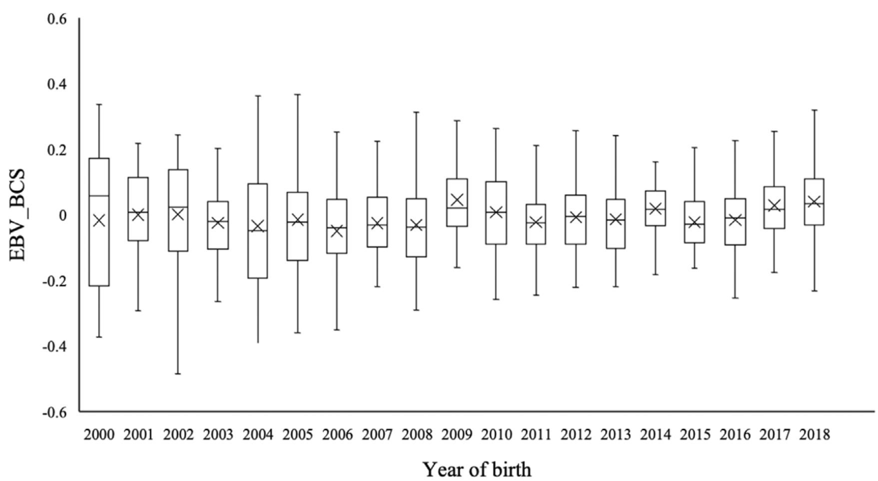

FIGURE 4 | Boxplot graph of estimates of breeding value (EBV) for 2-year-old ewe body condition score by year of birth. Mean values are represented by a cross. The fixed genetic base was the average of animals born in 2002 Ciappesoni et al. (2007).

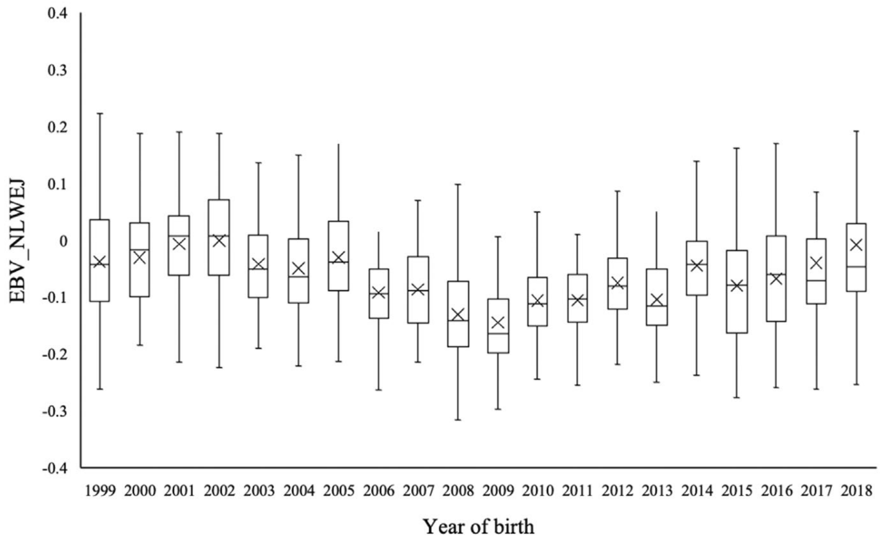

FIGURE 5 | Boxplot graph of estimates of breeding value (EBV) for the number of lambs weaned per ewe joined by year of birth. Mean values are represented by a cross. The fixed genetic base was the average of animals born in 2002 Ciappesoni et al. (2007).

(−0.210 vs. −0.082 μm/year, Table 3). This result reflected the change in trait emphasis in the selection index utilised in the second period, which focused on maintaining already reduced FD, while increasing both CFW and LW. Overall, the genetic progress of Y_FD agreed well with the phenotypic trend of this trait reported by Ramos et al. (2021a).

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 repeatability of this trait (0.76, 0.74 and 0.67, Manson et al. 1998; Murray et al. 2001; Hatcher et al. 2005, respectively). This pattern was also observed in the genetic trends for the MERINOSELECT analysis (Sheep Genetics consultant, personal communication).

The genetic trends for Y_CFW and A_CFW are given in Table 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 prioritised selection for reduced FD due to the unfavourable genetic correlation between the two traits (Safari et al. 2007; Ciappesoni et al. 2006; Ciappesoni et al. 2013). From 2011 to 2018, the genetic trend of Y_CFW showed a steady increase (0.052 kg/year, corresponding to 1.88% 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, which is a moderately heritable trait and has a large phenotypic variation (CV of 29%, Table 2). It could also be due to selection pressure being placed on LW, which is positively genetically correlated with CFW (0.27, 0.23, 0.54; Safari et al. 2007, Ciappesoni et al. 2013, Mortimer et al. 2017). The genetic trends of 0.052 kg/year for Y_CFW during the CRILU period agreed with the results reported by Cloete et al. (2007) in a South African Merino resource flock.

During the entire study period (1999–2018), 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 that fleece weight is medium to highly repeatable (Manson 1998). Overall, the genetic progress of yearling and adult fleece weight is consistent with the phenotypic trend of these traits reported by Ramos et al. (2021a, 2021b).

The regression coefficients of mean annual EBVs on birth year for Y_LW and 2-yo_LWM are shown in Table 3. The annual genetic gain for Y_LW was greater in the second period than in the first period (0.286 vs. 0.091 kg/year). This result is consistent with the selection index utilised 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, https://www.geneticaovina.com.uy/percentiles.php). Increases in Y_LW have been accompanied by increases in 2-yo_LWM (Figure 3). This result is supported by Huisman and Brown (2008) who reported that selection for increased LW at a given age will increase LW at all ages. In general, the genetic gain of Y_LW agreed with the phenotypic change of this trait presented by Ramos et al. (2021a).

In the present study, total genetic responses for FD, CFW and LW were in the desirable direction. During the study period, genetic progress achieved in the selection indexes for Uruguayan Merino sheep resulted in an increase of approximately 25 USD per ewe joined (https://www.geneticaovina.com.uy/tendencias.php). These findings indicate that breeding programmes applied during the study period resulted in increased productivity and profitability.

3.3 | Genetic Trends for Body Condition Score at Mating and Reproduction Traits

As shown in Table 3, a non-significant genetic trend for 2-yo_BCSM was observed in the first period. This result suggests that the reduction in phenotypic ewe BCS reported by Ramos et al. (2021b) was due to non-genetic effects. Post-2011, this trait had a small increase of 0.007 points/year ($p < 0.001$), 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 (Ramos et al. 2023). The genetic responses for 2-yo_BCSM were of a very low magnitude and would have minimal impact on phenotype.

From 1999 to 2010, the regression coefficient for NLWEJ was negative (Table 3). This result is consistent with a positive and unfavourable genetic correlation between adult FD and NLWEJ (0.33) reported by Chapman et al. (2021). Post-2011, the annual genetic gain for NLWEJ was positive (0.010 lambs/ewe joined per year). This could be due to selection pressure being placed on Y_LW, which is positively genetically correlated with NLWEJ (0.58; Safari et al. 2007). The annual genetic gains in NLWEJ achieved in this study are consistent with the results reported by Cloete et al. (2004) in Merino lines divergently selected for multiple rearing ability (−0.0105 and 0.0158 for low and high line, respectively). Over the entire study period (1999–2018), the total response indicated no genetic change for NLWEJ. This is consistent with previous research, which found that predictions of genetic gain for an index rewarding reduced FD and increased CFW in Merino sheep resulted in unchanged NLWEJ (Brown and Swan 2016).

Achieving substantial genetic gain in reproduction traits is difficult due to their low heritability and the direct measurement is limited to females only (Brien et al. 2011). However, high coefficients of variation allow substantial progress in reproduction traits (Cloete et al. 2004). Previous studies have suggested that to achieve relevant genetic gains in ewe reproductive performance, reproduction traits should be included in Merino breeding objectives (Swan et al. 2007; Brown and Swan 2016; Chapman et al. 2021). In Australia, the Genetic Evaluation system MERINOSELECT provides selection indexes with varying emphases on wool traits, LW at yearling and adult age, worm egg count and NLWEJ (Sheep Genetics 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 traits such as ultrasound carcass measures, ewe body condition score and other resilience traits into MERINOSELECT indexes (Walkom and Brown 2014; Brown and Swan 2016). Based on these findings and the results obtained in the present study, the current breeding objectives and selection indexes for Uruguayan Merino sheep should be refined to improve farm profitability and sustainability, and this would require other production traits to be included in selection programmes.

4 | Conclusion

This study estimated genetic trends for production and reproduction traits in an Uruguayan Merino genetic nucleus after 20 years of selection, which consisted of two distinct periods with different selection emphases. The results indicate that the breeding programme was effective in achieving its aims and efficacious in improving genetic gain in the traits under selection (FD, CFW and LW). The increase in LW during the second phase suggests a higher mature ewe weight, which likely implies greater maintenance requirements. Overall, the selection programmes applied in the flock resulted in only marginal net genetic changes in 2-yo BCSM and NLWEJ, reflecting the lower selection pressure on these traits. Generally, the breeding strategy successfully enhanced targeted production traits while maintaining reproductive performance.

Acknowledgements

We gratefully acknowledge contributions from all staff of Glencoe Experimental Unit, INIA Tacuarembó, SUL, SCMAU, INIA and CRILU. Also, we thank Melissa Stephen and Rhiannon Handcock for their assistance in the statistical analysis. Thanks to the National Institute of Agricultural Research of Uruguay (INIA) for the conduct of the field data collection, which received funding from the European Union's Horizon 2020 research and innovation programme under the Grant Agreement 772787 (Smarter) and from the National Institute of Agricultural Research of Uruguay (INIA_CL_38: Rumiar). The first author acknowledges the financial support for her PhD provided by Massey University, New Zealand and the National Agency for Investigation and Innovation of Uruguay (ANII). Open access publishing facilitated by Massey University, as part of the Wiley - Massey University agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data presented in this study are available within the article.

References

Blasco, A. 2017. *The Linear Model: II. The 'Mixed' Model in Bayesian Data Analysis for Animal Scientists: The Basics*. Springer. https://doi.org/10.1007/978-3-319-54274-4.

Brien, F. D., G. N. Hinch, J. H. J. Van der Werf, D. J. Brown, and A. A. Swan. 2011. "Selection Strategies for the Genetic Improvement of Reproductive Performance in Sheep." Proceedings of the Association for the Advancement of Animal Breeding and Genetics 19, 151–158.

Brown, D. J., and A. A. Swan. 2016. "Genetic Importance of Fat and Eye Muscle Depth in Merino Breeding Programs." *Animal Production Science* 56: 690–697. https://doi.org/10.1071/an14645.

Chapman, J. A., M. L. Hebart, and F. D. Brien. 2021. "Growth, Body Composition and Body Wrinkle Are Favourably Correlated With Reproductive Performance in 2-8-Year-Old Merino Sheep." *Animal Production Science* 61: 1873–1883. https://doi.org/10.1071/AN21101.

Cheng, H., R. L. Fernando, and D. J. Garrick. 2018. "JWAS: Julia Implementation of Whole-Genome Analysis Software." Proceedings of the World Congress on Genetics Applied to Livestock Production. Auckland. New Zealand. 859.

Ciappesoni, G., D. Gimeno, I. tablarbieri, F. Montossi, M. Grattarola, and A. Mederos. 2007. "Evaluación Genética Poblacional: Caracterización de los Animales del Núcleo que se Entregan." Boletín de Divulgación INIA 90. INIA. 71–93. https://crilu.org.uy/docs/2016/INIA%20boBd%2090.pdf.

Ciappesoni, G., D. Gimeno, and F. Coronel. 2014. "Progreso Genético Logrado en las Evaluaciones Ovinas del Uruguay." *Archivos Latinoamericanos de Producción Animal* 22: 73–80.

Ciappesoni, G., D. Gimeno, and O. Ravagnolo. 2010. "Genetic Relationships Between Faecal Worm Egg Count and Production Traits in Merino Sheep of Uruguay." Proceedings of the World Congress on Genetics Applied to Livestock Production. Leipzig. Germany. 384.

Ciappesoni, G., V. Goldberg, and D. Gimeno. 2013. "Estimates of Genetic Parameters for Worm Resistance, Wool, and Growth Traits in Merino Sheep of Uruguay." *Livestock Science* 157: 65–74. https://doi.org/10.1016/j.livsci.2013.07.011.

Ciappesoni, G., O. Ravagnolo, D. Gimeno, F. Montossi, and I. De Barbieri. 2006. "Estimation of Genetic Parameters and Genetic Trends for Wool Production and Quality for the Uruguayan Merino." Proceedings of the World Congress on Genetics Applied to Livestock Production. Belo Horizonte- MG. Brazil. 1392–1395.

Cloete, S. W. P., A. R. Gilmour, J. J. Olivier, and J. B. Van Wyk. 2004. "Genetic and Phenotypic Trends and Parameters in Reproduction, Greasy Fleece Weight and Liveweight in Merino Lines Divergently Selected for Multiple Rearing Ability." *Australian Journal of Experimental Agriculture* 44: 745–754. https://doi.org/10.1071/EA02225.

Cloete, S. W. P., J. J. Olivier, and W. J. Olivier. 2007. "Genetic Change in South African Merino Resource Flocks." Proceedings of the Association for the Advancement of Animal Breeding and Genetics 17, 320–323.

Daetwyler, H. D., J. M. Hickey, J. M. Henshall, et al. 2010. "Accuracy of Estimated Genomic Breeding Values for Wool and Meat Traits in a Multi-Breed Sheep Population." *Animal Production Science* 50: 1004–1010. https://doi.org/10.1071/AN10096.

De Los Campos, G., D. De Mattos, F. Montossi, R. San Julián, and J. Frugoni. 2000. "Incorporación de las Señales de Mercado a la Toma de Decisiones en Mejora Genética. Serie Actividades de Difusión 246. INIA. 43–53." http://www.ainfo.inia.uy/digital/bitstream/item/9711/1/SAD-246p43-53-Glencoe.pdf.

Di, J., L. Ainiwaer, X. M. Xu, Y. H. Zhang, L. J. Yu, and W. C. Li. 2014. "Genetic Trends for Growth and Wool Traits of Chinese Superfine Merino Sheep Using a Multi-Trait Animal Model." *Small Ruminant Research* 117: 47–51. https://doi.org/10.1016/j.smallrumres.2013.12.001.

Dominik, S., and A. A. Swan. 2018. "Genetic and Phenotypic Parameters for Reproduction, Production and Bodyweight Traits in Australian Fine-Wool Merino Sheep." *Animal Production Science* 58: 207–212. https://doi.org/10.1071/AN15738.

Fozi, M. A., J. H. J. Van der Werf, and A. A. Swan. 2012. "Modelling Genetic Covariance Structure Across Ages of Mean Fibre Diameter in Sheep Using Multivariate and Random Regression Analysis." *Animal Production Science* 52: 1019–1026. https://doi.org/10.1071/an12139.

Hatcher, S., K. D. Atkins, and K. J. Thornberry. 2005. "Age Changes in Wool Traits of Merino Sheep in Western NSW." In Proceedings of the Association for the Advancement of Animal Breeding and Genetics. Queensland. Australia. 25–28. 314–317.

Huisman, A. E., and D. J. Brown. 2008. "Genetic Parameters for Bodyweight, Wool, and Disease Resistance and Reproduction Traits in Merino Sheep. 2. Genetic Relationships Between Bodyweight Traits and Other Traits." *Australian Journal of Experimental Agriculture* 48: 1186–1193. https://doi.org/10.1071/ea08120.

Manson, D. A. 1998. "Repeatability of Performance Rankings and Wool Production Characteristics of Merino Ewes in a Semi-Arid Farming Environment." M.Sc. Thesis submitted to University of Adelaide. Australia. https://digital.library.adelaide.edu.au/bitstream/2440/78622/2/02whole.pdf.

Mortimer, S. I., S. Hatcher, N. M. Fogarty, et al. 2017. "Genetic Parameters for Wool Traits, Live Weight, and Ultrasound Carcass Traits in Merino Sheep." *Journal of Animal Science* 95: 1879–1891. https://doi.org/10.2527/jas2016.1234.

Murray, W. K., S. I. Mortimer, K. D. Atkins, P. J. Taylor, and S. L. Anderson. 2001. "Style and Production Changes Across Ages in Merino Sheep." In Proceedings of the Association for the Advancement of Animal Breeding and Genetics. Queenstown. New Zealand. 493–496

Ramos, Z., H. T. Blair, I. De Barbieri, G. Ciappesoni, F. Montossi, and P. R. Kenyon. 2021a. "Phenotypic Responses to Selection for Ultrafine Wool in Uruguayan Yearling Lambs." *Agriculture* 11, no. 2: 179. https://doi.org/10.3390/agriculture11020179.

Ramos, Z., H. T. Blair, I. De Barbieri, G. Ciappesoni, F. Montossi, and P. R. Kenyon. 2021b. "Productivity and Reproductive Performance of Mixed-Age Ewes Across 20 Years of Selection for Ultrafine Wool in Uruguay." *Agriculture* 11, no. 8: 712. https://doi.org/10.3390/agriculture11080712.

Ramos, Z., D. Garrick, H. T. Blair, et al. 2023. "Genetic and Phenotypic Relationships Between Ewe Reproductive Performance and Wool and Growth Traits in Uruguayan Ultrafine Merino Sheep." *Journal of Animal Science* 101: skad071. https://doi.org/10.1093/jas/skad071.

Safari, E., N. M. Fogarty, and A. R. Gilmour. 2005. "A Review of Genetic Parameter Estimates for Wool, Growth, Meat and Reproduction Traits in Sheep." *Livestock Production Science* 92: 271–289. https://doi.org/10.1016/j.livprodsci.2004.09.003.

Safari, E., N. M. Fogarty, A. R. Gilmour, et al. 2007. "Genetic Correlations Among and Between Wool, Growth and Reproduction Traits in Merino Sheep." *Journal of Animal Breeding and Genetics* 124: 65–72. https://doi.org/10.1111/j.1439-0388.2007.00641.

Sheep Genetics. 2019. "MERINOSELECT Indexes. A Ram Breeder's Guide." https://www.sheepgenetics.org.au/globalassets/sheep-genetics/resources/brochures-and-fact-sheets/19mla-breeder-merino.pdf.

Swan, A. A., D. J. Brown, and R. G. Banks. 2009. "Genetic Progress in the Australian Sheep Industry." Proceedings of the Association for the Advancement of Animal Breeding and Genetics. Barossa Valley. South Australia. 326–329.

Swan, A. A., D. J. Brown, and J. H. Van der Werf. 2016. "Genetic Variation Within and Between Subpopulations of the Australian Merino Breed." *Animal Production Science* 56: 87–94. https://doi.org/10.1071/AN14560.

Swan, A. A., J. H. J. Van der Werf, and K. D. Atkins. 2007. "Developments in Breeding Objectives for the Australian Sheep Industry." Proceedings of the Association for the Advancement of Animal Breeding and Genetics. Armidale. New South Wales. Australia. 483–490.

Taylor, P., T. Bird-Gardiner, S. Mortimer, and K. Atkins. 2007. *Selection Indexes Work for All Merino Strains and Breeding Objectives*. Department of Primary Industry.

Van der Werf, J., D. Brown, S. Walkom, and P. Bradley. 2022. "Orientación y rol Futuro del Mejoramiento Genético en la Competitividad del Sector Lanero." University of New England. Australia. https://www.youtube.com/embed/CiR36t-YZRY.

Walkom, S. F., and D. J. Brown. 2014. "Breeding for Resilience and Resistance in Merino Sheep." In *Breeding Focus 2014: Improving Resilience*, edited by S. Hermesch and S. Dominik, 141–156. Animal Genetics and Breeding Unit.

Walkom, S. F., and D. J. Brown. 2017. "Genetic Evaluation of Adult Ewe Bodyweight and Condition: Relationship With Lamb Growth, Reproduction, Carcass and Wool Production." *Animal Production Science* 57: 20–32. https://doi.org/10.1071/AN15091.

Wuliji, T., K. G. Dodds, R. N. Andrews, and P. R. Turner. 1998. "Mature Merino Ewe Performance in an Ultrafine Fibre Diameter Selected and a Control Flock." *Proceedings of the New Zealand Society of Animal Production* 58: 284–287.