

Breeding for sheep parasite resistance in extensive production systems in Uruguay: From phenotype to genotype

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Abstract

Gastrointestinal parasites (GIP) are one of the main causes of economic losses for sheep farmers worldwide. The need for alternative control measures comes from increasingly critical anthelmintic resistance. One alternative is to include genetic resistance to GIP in breeding programmes, by selecting for worm faecal egg count (FEC). Using this selection criterion since 1994, Uruguay has included genetic resistance to GIP in the genetic evaluation of Australian Merino and Corriedale

breeds. Although FEC has been the most used selection criterion to evaluate resistant animals, data recording is time-consuming and costly and requires a nematode infection challenge. Selecting parasite resistance without the need for nematode challenge would be a less expensive alternative approach without compromising the wellbeing of the animals. Moreover, other indicator traits such as packed cell volume (PCV), FAMACHA[®] score, body condition score (BCS) could be included to increase genetic improvement. This paper describes the current selection programmes for GIP-resistant sheep,

data recording, new criteria evaluation, selection nuclei, development and use of molecular tools, projects, as well as further approaches to enhance and improve genetic progress in Uruguay. Current databases enabled various estimations and demonstrated that genetic progress can be achieved. We can highlight the following results: (i) FEC heritability values ranging from 0.15 to 0.21; (ii) high genetic correlation between FEC in ewes at spring rise and FEC in lambs at post-weaning (0.81 ± 0.11); (iii) genetic selection by FEC is effective in different environments (low or high worm environments) and the genetic correlation between environments is high (0.87 ± 0.04); (iv) there is a moderate favorable genetic correlation between FEC and FAMACHA[®]; (v) the Corriedale susceptible line had up to 3.3 times higher average of FEC than resistant line; (vi) INIA Corriedales showed better genetic merit for twinning rate, greasy fleece weight, fibre diameter, and body weight at shearing in comparison with the resistant line of SUL; and (vii) in Australian Merino, it has been possible to generate heavier progeny producing more and finer wool, and also more resistant to GIP. Moreover, generating reference populations for molecular studies and selection nuclei is also very important. All strategies described in this study aim at improving the genetic resistance of sheep to GIP.

Keywords

Corriedale, FEC, *Haemonchus contortus*, Merino, SNP

1. Introduction

Worldwide, gastrointestinal (nematodes) parasites (GIP) generate numerous productive and economic losses in sheep production and Uruguay does not escape from this problem. Gastrointestinal parasites inhabit the digestive system and can trigger chronic conditions that jeopardize productive potential (Radosits *et al.*, 2006). A wide variety of domestic animals are affected, and small ruminants are among the most susceptible. Although some mortality is observed, subclinical diseases are frequent, with poorer growth rate, fertility, milk, and wool production and body condition; resulting in large losses for farmers (Castells *et al.*, 1995; Jackson *et al.*, 2009). Due to the serious situation of anthelmintic resistance for all commercial drugs available, the use of non-chemical alternative strategies is essential to address the problem of GIP. For this reason, the inclusion of genetic resistance to GIP as one selection objective in a comprehensive breeding goal is being considered by commercial farmers and stud breeders who raise their sheep in temperate and subtropical areas under extensive production systems. By improving sheep GIP resistance, animal productivity increases (Castells *et al.*, 1995) and the use of anthelmintic drugs can be reduced (Byrne *et al.*, 2012), leading to lower environmental chemical

contamination and less drug residue in tissues. Another benefit of selection for GIP resistance is improving animal welfare through more resilient sheep, that are better adapted to the environment (Bishop, de Jong and Gray, 2003).

In Uruguay, since 1994, genetic resistance to GIP has been included in the genetic evaluation systems of the Australian Merino and Corriedale breeds. The selection criterion is faecal worm egg count (FEC), according to a protocol based on the Australian experience (Cardellino, Peñagaricano and Castells, 1994). The FEC is recorded in lambs after weaning in two independent natural challenges separated by an effective anthelmintic treatment. Faecal samples are collected from the animal's rectum and after identification they are sent to the parasitology laboratory for FEC determination within 72 hours. The FEC is determined using a modified McMaster technique (Whitlock, 1948). Under this natural uncontrolled challenge, the most prevalent nematode is *Haemonchus sp.* followed by *Trichostrongylus sp.* (Castells, 2009, Goldberg, Ciappesoni and Aguilar, 2012, own data surveyed in the stud-flocks since 2017). Depending on the epidemiological conditions, the first and second FEC records are made at 8-9 and 10-12 months of age of the lambs (Ciappesoni, Goldberg and Gimeno, 2013). This corresponds to the months from May to June and from July to September, respectively, and thus to the end of the autumn and the winter in Uruguay. The weather conditions in Uruguay are characterized by an average annual temperature of about 17.7 °C and average annual accumulated rainfall between 1 200 and 1 600 mm with a great interannual variability (Castaño *et al.*, 2011). For example, in extreme years, minimum and maximum values are lower than 20 and greater than 250 mm/month respectively (Castaño *et al.*, 2011).

Stud-breeders (supported by the Rural Association of Uruguay) provided genealogical information and performance data recorded at stud level through the SULAR software developed by the Uruguayan Wool Secretariat (SUL). The genetic evaluation is performed by a repeatability animal model adjusting the FEC data through natural logarithms $\text{Log}_e(\text{FEC} + 100)$ to normalize the residual distribution (Ciappesoni, Goldberg and Gimeno, 2013). Animal genetic merit is published as the expected progeny difference (EPD) for FEC. The genetic trends are presented as estimated breeding values ($\text{EBV} = \text{EPD} \times 2$). National genetic evaluations (NGE) of wool and meat quality and production traits are routinely carried out by SUL and the National Agricultural Research Institute (INIA) (www.geneticaovina.com.uy).

Although FEC has been the most used method to evaluate the resistance of animals to GIP, there are other indicator traits such as packed cell volume (PCV), FAMACHA[®] score, and body condition score (BCS),

among others. The protocol for recording these traits is described in Marques, Goldberg and Ciappesoni (2020). All these traits are recorded by INIA trained technicians. To determine the PCV, blood samples collected from the external jugular vein in tubes containing anticoagulant were subjected to hematologic analysis. Values were determined using the routine microhematocrit method reported by Schalm (1986). For the BCS analysis, scores ranged from 1 to 5, where higher numbers indicate increasing amounts of fat cover (Jefferies, 1961).

Selecting for GIP resistance without the need for nematode challenge could be a less expensive and laborious alternative approach that does not compromise the animal wellbeing and may thus lead to greater adoption by stud breeders. The national approach has been to contribute to the selection of genetically resistant animals within integrated management of GIP, in which genetic resistance can play a very important role. However, because it is a difficult trait to record, the adoption of this selection criterion in the main breeding programmes has been low. Hence, different strategies have been pursued at the country level to increase the genetic improvement of resistance to GIP. The aim of the present work is to describe the current selection programmes for GIP-resistant sheep, as well as projects and the main strategies to enhance genetic progress in Uruguay.

All the studies were conducted in accordance with the current Uruguayan laws for the care and management of experimental animals (cnea.gub.uy, law 18611). All applied protocols were approved by INIA Animal Ethics Committee (Approval numbers INIA_2018.2, INIA_2018.3 and INIA.2020.17).

1.1 Supporting data recording and evaluation of new criteria

Given the reluctance of breeders to collect FEC data, different projects are underway to support the expansion of the recording. All projects use the same protocol described above. As an example, we can mention the initiative for the development of recording for Corriedale (2002) and Australian Merino (2004) funded by INIA and the Inter-American Bank. More recently, coordination and registration have been done directly at Corriedale (2018) and Merilin (2020) stud flocks, as part of an INIA project in collaboration with the breed societies. Merilin breed is the first synthetic breed developed in Uruguay crossbreeding between Merino Rambouillet (75 percent) and Lincoln (25 percent) (Merilin, 2022). Additionally, Dohne Merino lambs have been recorded at INIA (2008) and SUL (2015) experimental stations and some commercial stud flocks. Currently, the genetic evaluation of the Australian Merino breed is consolidated and growing for the Corriedale and Dohne Merino breeds. A stud-flock of the Merilin breed began the FEC genetic evaluation with the 2019 progeny.

In the last six years, regardless of the breed, the number of stud flocks presenting FEC data has increased, as has the number of lambs evaluated (Table 1 and Table 2). Among the progeny of 2014, 882 lambs from 9 stud flocks were evaluated, while in 2019, 4 105 lambs from 25 stud flocks were evaluated (Table 1 and Table 2). Collection of data is performed by INIA's technicians (i.e. Corriedale and Merilin breeds) or by stud breeders trained, coordinated and advised by INIA's or SUL's technicians (i.e. Merino breeds). The accuracy of FEC EPD in the first genetic evaluation (lambs with own data) ranges between 0.65 and 0.70.

Table 1: Number of stud-flocks with FEC records by breed per year of birth

Breed	Birth year					
	2014	2015	2016	2017	2018	2019
Corriedale	4	7	7	9	11	15
Australian Merino	4	5	6	6	7	7
Dohne Merino	1	1	1	2	3	3
Total	9	13	14	17	21	25

Source: Authors' own elaboration.

Table 2: Number of lambs with FEC records by breed per year of birth

Breed	Birth year					
	2014	2015	2016	2017	2018	2019
Corriedale	121	1 079	1 301	1 451	1 778	1 634
Australian Merino	726	1 298	1 400	1 397	1 906	2 039
Dohne Merino	35	58	95	285	391	432
Total	882	2 435	2 796	3 133	4 075	4 105

Source: Authors' own elaboration.

With the current databases it has been possible to estimate the heritability of FEC for the main breeds in production systems under natural infections. The methods to estimate genetic parameters and breeding values at the national level are described in detail in the cited papers (Castells, 2009; Goldberg, Ciappesoni and Aguilar, 2012; Ciappesoni, Goldberg and Gimeno, 2013). In brief, a multivariate animal model was used to estimate genetic parameters and breeding values with the BLUPF90 family of programs (Misztal *et al.*, 2018). Variance components were estimated using a Bayesian methodology (GIBBS2F90 software). Heritability estimates range between 0.15 ± 0.01 for Merino (Ciappesoni, Goldberg and Gimeno, 2013) and 0.21 ± 0.02 for Corriedale (Castells, 2009). These estimates are in agreement with international studies (i.e. review by Safari, Fogarty and Gilmour, 2005), which indicate moderate FEC heritability in lambs (0.2 to 0.4), thus enabling genetic progress by selection. The association between nematode resistance in periparturient ewes and post-weaning lambs in Australian Merino sheep was also investigated (Goldberg, Ciappesoni and Aguilar, 2012). Lambing season in the studied flocks was Spring (most births taking place in September and October) and weaning occurs generally between December and January (late Spring, early Summer). Two repeated post-weaning FEC records in lambs were registered in these flocks in June and from August to September for FEC 1 and 2, respectively. These flocks were in the northern part of Uruguay, characterized by warm and wet climate, with a

mean annual temperature of 18–19 °C, relative humidity of 70–72 percent and an average annual rainfall of 1 400 – 1 500 mm (Castaño *et al.*, 2011). Animals are kept outdoors all year around and graze mostly native grasslands and have access to improved pastures or are supplemented with grains or commercial rations when nutrient requirements are high (e.g. twin bearing ewes) or when native grasslands growth is low (late Winter, dry Summer). This study found a high genetic correlation (0.81 ± 0.11) between the two traits: FEC at spring rise in ewes and FEC in lambs at post-weaning. In addition, this study found that selection based on lamb FEC is twice as efficient as selection based on ewe FEC (Goldberg, Ciappesoni and Aguilar, 2012). In other words, using lamb FEC for indirect selection will be more effective than direct selection on ewe FEC, producing ewes that eliminate less worm eggs resulting in less pasture contamination. Currently, the study of the spring rise phenomenon continues in different breeds and others grazing production systems (Del Pino *et al.*, 2019).

Furthermore, different studies have been carried out looking for new, easy-to-measure, or complementary selection criteria such as FAMACHA[®] (Ciappesoni and Goldberg, 2018), faecal occult blood test (FOB) (Rodríguez *et al.*, 2015), control of IgA levels (Escribano *et al.*, 2019) and Dag score (RUMIAR project, INIA). Descriptive statistics for traits related to GIP of the total data included in the national database (SULAR) used for the NGE of INIA-SUL (lambs born from 1994 to 2019) are shown in Table 3.

Table 3: Descriptive statistics for traits related to GIP resistance included in the national database (SULAR) from progeny 1994 to 2019

Breed	Trait	<i>n</i>	Mean	Standard deviation
Corriedale	BCS at FEC (score)	4 901	3.27	0.76
	FAMACHA (score)	6 577	2.14	0.74
	FEC (count)	25 183	1 525	2 467
	PCV (%)	2 494	35.27	4.75
Australian Merino	BCS at FEC (score)	853	2.85	0.39
	FAMACHA (score)	2 213	2.13	0.86
	FEC (count)	29 645	1 295	1 948
	PCV (%)	1 356	32.05	5.41
Dohne Merino	BCS at FEC (score)	867	3.19	0.47
	FAMACHA (score)	1 171	1.91	0.73
	FEC (count)	1 684	1 314	1 688
	PCV (%)	221	33.85	4.71

Source: Authors' own elaboration.

Note: *FEC: post-weaning Faecal Egg Count. PCV: Packed cell volume. BCS: Body condition score.

Marques, Goldberg and Ciappesoni (2020) estimated a moderate favourable genetic correlation between FEC and FAMACHA[®]. In addition, the genetic correlation between FEC measured at low and high worm environments was high (0.87 ± 0.04). This indicates that genetic selection by FEC is effective in different environments. Research is

also being carried out to understand the trade-offs of the selection by FEC on other economically relevant traits. The first studies indicate that breeding resistant animals for GIP may not present negative effects on intake or feed conversion efficiency regardless of the level of parasitism (Ferreira *et al.*, 2021). This study evaluated the differences

in feed conversion ratio and residual feed intake in 1-year old lambs (fed ad libitum with a high-protein forage diet) of Corriedale divergent selection lines (see section 2.1).

2. Genetic resistance to GIP in selection nucleus

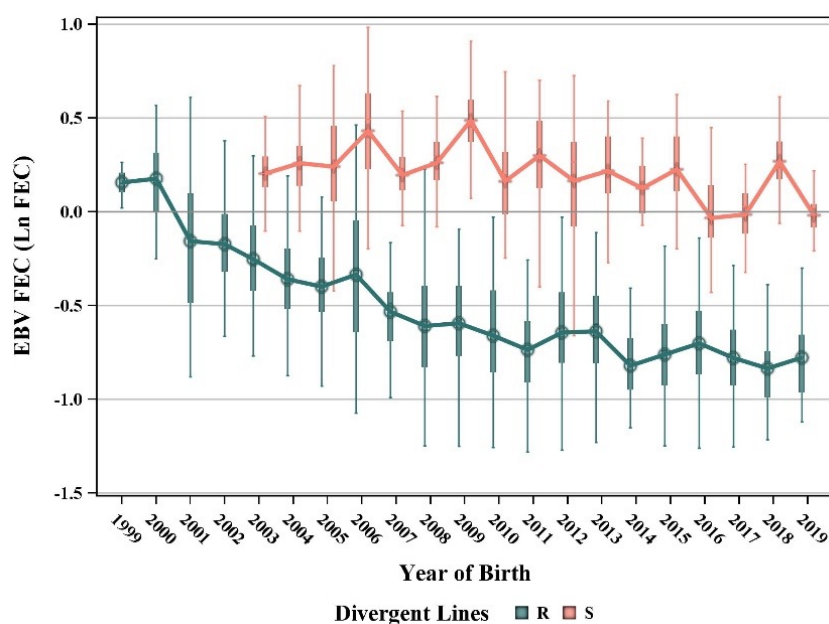
As a strategy for the generation of genetically resistant breeding stock and the dissemination of genetic tools (i.e. EPD), selection nuclei are in place in experimental stations: (1) Corriedale: divergent selection lines by FEC EPD; (2) Australian Merino: selection by FEC EPD and production; (3) Corriedale and Australian Merino: selection by production and FEC EPD.

2.1 Corriedale: divergent selection lines

Corriedale divergent breeding lines ewes were selected for low (Resistant line, R-Line) or high (Susceptible line, S-Line) FEC after natural mixed infection and grazing native pastures at *Dr Alejandro Gallinal* Experimental Research Centre of SUL since 1998 (Castells and Gimeno, 2011). After screening for low or high FEC EPD of 3 545 progeny lambs, the nucleus flock was established. More than 150 ewes were annually mated in the R-Line and 120 ewes in the S-Line, and at least five sires were used in each line per mating. Three FEC measurements (FEC1, FEC2, and FEC3) were recorded post-weaning and after natural nematode challenge of different cycles: summer (between 21 December and 20 March), autumn (between 20 March and 21 June) and winter (between 21 June and 22 September). Post-weaning and production traits and complete pedigree were also recorded each year.

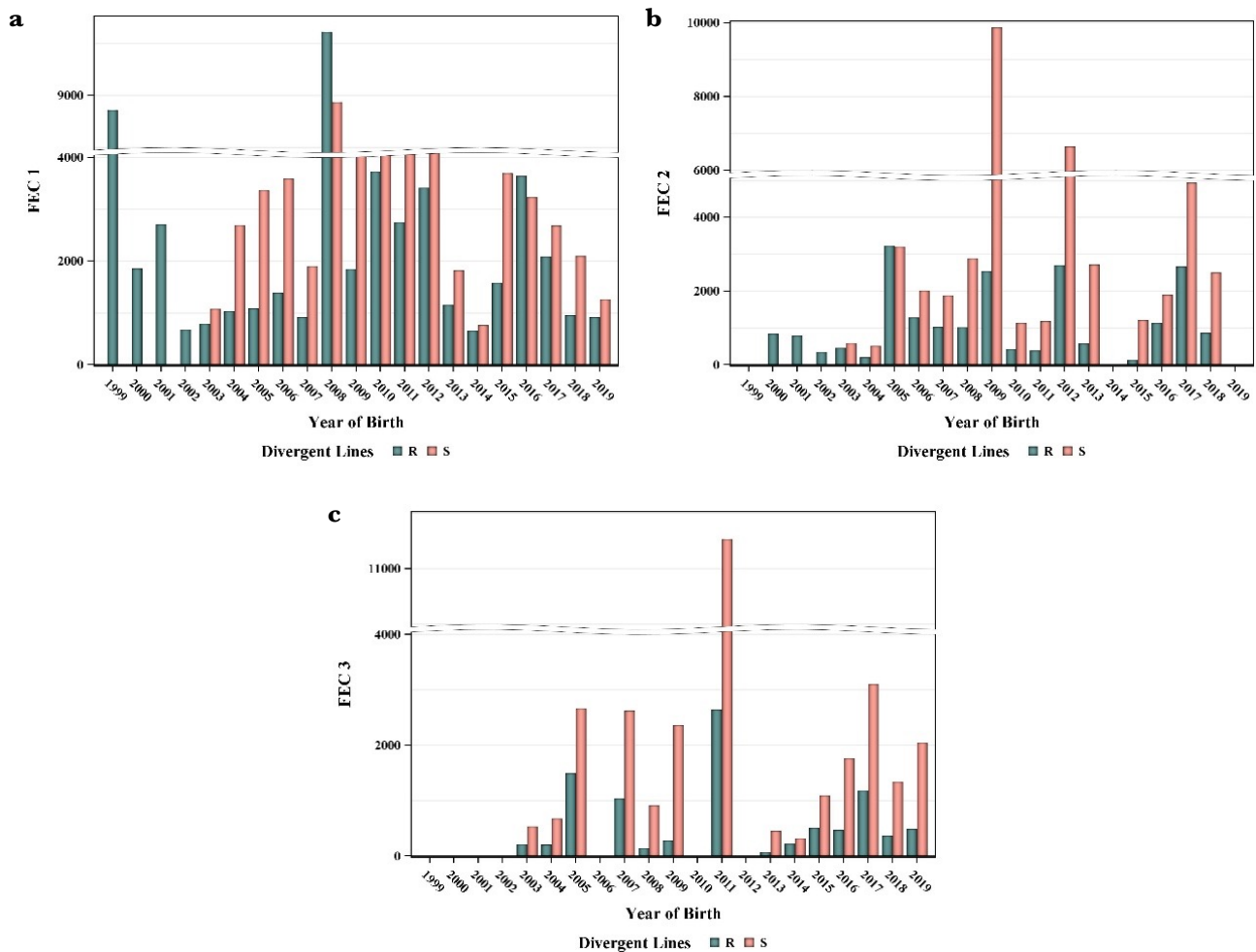
The genetic trend of the S-line shows a small reduction. From 2014 progeny, this line has become more like a

control line due to the complexity of maintaining a high number of susceptible animals (low longevity or stayability) and because of animal welfare issues. The average number of lambs registered per year were 40 and 80 for the S-Lines and R-Lines, respectively. Additionally, for R-Line some rams from stud-flocks were used. The difference in average breeding values between the first (2000) and last generation (2019) of the R-line represented genetic progress of 15 percent (Figure 1), indicating annual genetic progress of -0.71 percent per year. When analysing R-line FEC average breeding values of the progeny 2019 in comparison with the rest of the Corriedale population in 2019, a genetic difference of 11 percent was observed. This distance between the R-line and the rest of the Corriedale population would be between 5 to 10 years of selection. Considering means of the three records FEC1, FEC2, and FEC3 (at 210 ± 33 , 298 ± 43 and 391 ± 53 days of age respectively) for the last five years (from 2015 to 2019) the values for the S-Line were 1.31, 2.47, and 3.26 times higher than the R-Line, respectively (Figure 2). Marked differences were observed between years depending on climatic and epidemiological conditions. Additionally, those phenotypic responses were also observed on lactating ewes during the spring rise 73 days after lambing. The FEC means of R-Line ewes was 395, and 660 for the S-Line (Castells and Gimeno, 2011). It is concluded that by selecting for decreased FEC EPD it is possible to achieve considerable progress, which is reflected, in addition to the genetic trends, in lower infestations in lambs and ewes at spring rise. This experimental flock represents a valuable demonstration population where breeders can see the genetics in practice.



Source: Authors' own elaboration.

Figure 1: Genetic trends of FEC EBV in Corriedale divergent lines (Resistant -R and Susceptible -S) from the Uruguayan Wool Secretariat



Source: Authors' own elaboration.

Figure 2: Phenotypic average for Faecal Egg Count (FEC) 1 (a), 2 (b), and 3 (c) of Resistant (R) and Susceptible (S) lines from 1999 to 2019 progeny from the Uruguayan Wool Secretariat

2.2 Australian Merino: selection by FEC EPD and production

Breeders are reluctant to include genetic resistance to GIP in their breeding programmes because recording FEC is complex and labour-intensive. In 2015, an Australian Merino flock was established at the *Estación Experimental Facultad de Agronomía Salto* (EEFAS, *Universidad de la República*) to intensively select sheep for GIP resistance and thus give access to farmers to high rams with genetic merit for GIP resistance (FEC EPD) without the need for data collection. The selection flock at EEFAS is also a research platform for quantitative and molecular genetics in collaboration with INIA and SUL. The first years of selection were funded by the INNOVAGRO research project (described in acknowledgements) and semen from Australian studs renowned for their resistance to GIP was purchased. High selection pressure on FEC has been applied to the flock resulting in fast genetic progress-producing animals ranking in the top 1 percent of the Australian Merino population in Uruguay in this trait.

The foundation ewes for the GIP resistance flock came from the existing flock at EEFAS which was complemented by ewes from three regional Australian Merino studs (*La*

Magdalena, Los Arrayanes and Los Manantiales). In 2015 and 2016, semen from *Rylington Merino* (WA, Australia) was used. The *Rylington Merino* flock was founded in 1988 as an experimental flock by wool farmers and agricultural institutions, firstly by selecting sheep on phenotypic data and from 1994 on by estimated breeding values and became highly resistant to worms (Karlsson and Greeff, 2006). *Rylington Merino* sires have been widely used in flocks participating in Sheep Genetics Australia (www.sheepgenetics.org.au). From 2017 to 2019, semen from the commercial stud *Anderson Rams* (www.andersonrams.com.au/index.html), also located in Western Australia, was utilized. In collaboration with the *Talitas* stud, rams from this stud were used either in a timed artificial insemination programme or in single sire matings with allocated ewes. *Talitas* has been selecting sheep for GIP resistance for more than two decades and produces high-ranking sires in the Uruguayan Genetic Evaluation of Australian Merino. Furthermore, through collaboration with the *Consortio Regional de Innovación en Lana Ultrafina* (CRILU, Regional Consortium for Innovation in Ultrafine Wool), rams selected for reduced fibre diameter were obtained. Other rams were selected directly from the EEFAS flock based

on their FEC EPD. Table 4 describes the contribution sires and progeny from these studs the FEC EPD data for the animals. Procedures followed to estimate FEC EPD and management practices, and statistical analyses are similar to those previously indicated.

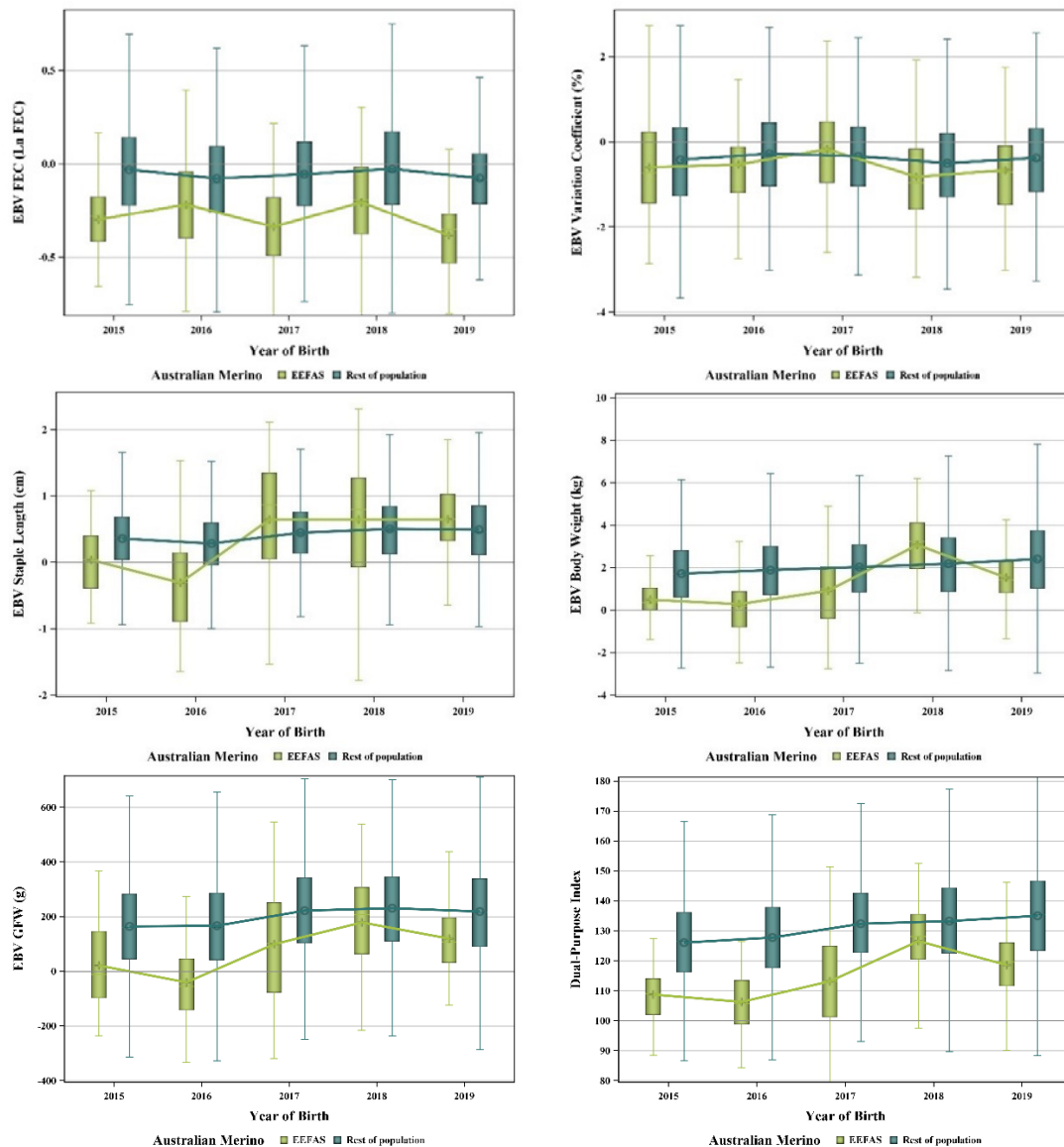
From the beginning, the main breeding goal has been to rapidly increase GIP resistance (reducing FEC EPD). This activity has been a success since the genetic trend for this trait is well below the population trend (Figure 3). One sire from *Rylington Merino*, used in 2015, has produced

Table 4: Number of sires, progeny and expected progeny difference (EPD) of faecal egg count (FEC) data for the studs contributing to the EEFAS flock from 2015 to 2019

Stud	Rylington	Anderson	Talitas	CRILU	EEFAS
Sires (n)	3	4	4	7	7
Progeny (n)	31	174	62	159	111
FEC EPD *					
Mean	-0.16	-0.11	-0.16	-0.12	-0.20
Std Dev	0.17	0.11	0.10	0.10	0.12
Minimum	-0.45	-0.45	-0.48	-0.39	-0.43
Maximum	0.20	0.15	0.02	0.10	0.25

Source: Authors' own elaboration.

Note: * FEC EPD data according to the 2020 genetic evaluation results (max = -0.54; 1% = -0.30; 5% = -0.20; 10% = -0.15).

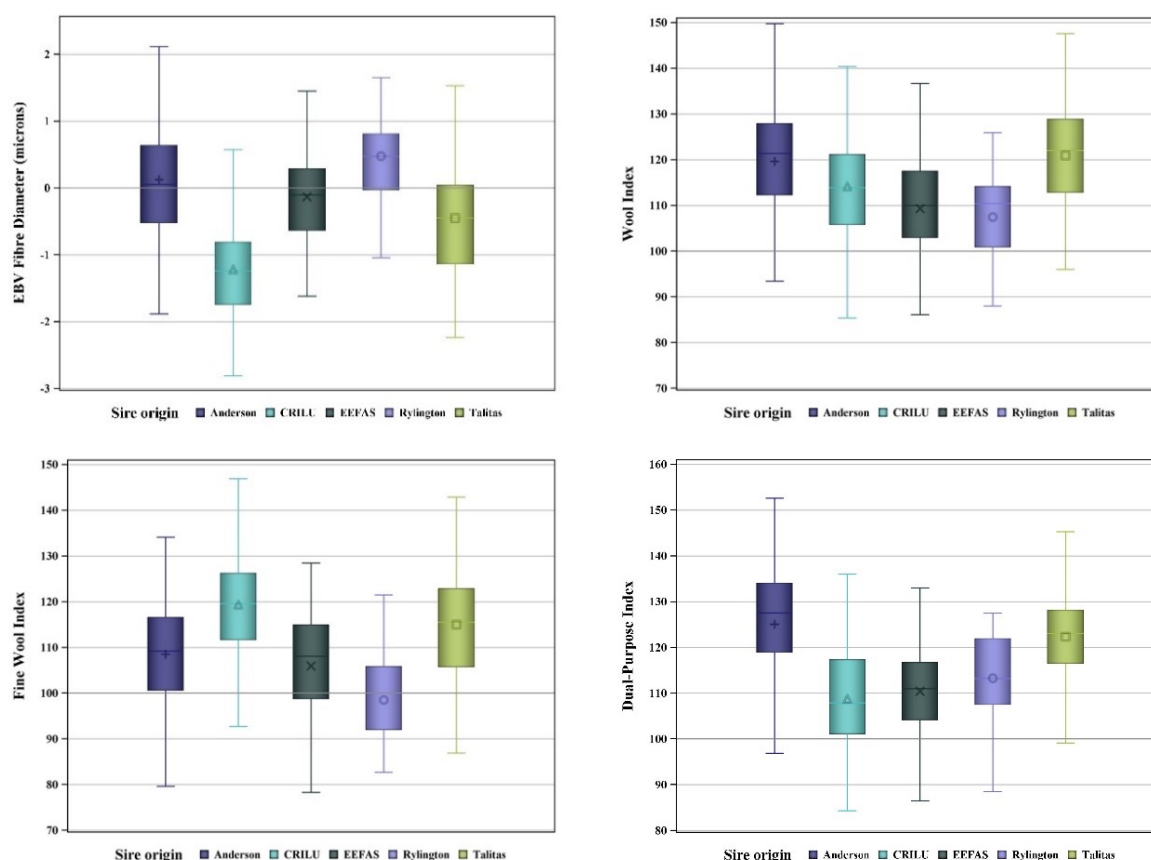


Source: Authors' own elaboration.

Figure 3: Five-year genetic trends for Faecal Egg Count (FEC), Variation Coefficient of Fibre Diameter, Staple Length, and Body Weight, Greasy Fleece Weight (GFW) and Dual-Purpose Index of the EEFAS flock and the general Australian Merino population according to the 2020 National Genetic Evaluation; the 2020 drop is not included in the evaluation

the top 1 percent ranking ewes from which several of the EEFAS sires were bred, leaving a long-lasting effect on GIP resistance in the flock. The combination of origins of *Rylington Merino* with *Talitas* has been particularly powerful in delivering top 1 percent ranking EEFAS sires for GIP resistance. Other traits that have improved over time, in comparison with the general population, are the variation coefficient of fibre diameter, staple length, and body weight (Figure 3). The selected sires from *Anderson Rams* have highly contributed to staple length and body weight, as well as greasy and clean fleece weight, while *Talitas* and *CRILU* sires used have contributed to the reduction of fibre diameter (Figure 4). The genetic evaluation of Australian Merino in Uruguay includes three selection

indexes to aid producers in deciding which sire to purchase according to their breeding or production goals; focus on reducing fibre diameter and moderate increases in fleece and body weight (Fine Wool Index), focus on increasing fleece and body weight with moderate reductions on fibre diameter (Wool Index) or a strong focus on increasing fleece and body weight with low reductions in fibre diameter (Dual-Purpose Index) (https://geneticaovina.com.uy/catalogo/catalogo_merino.pdf). Although, the EEFAS flock has not reached top ranks in greasy fleece weight EPD or selection indexes, progress has been made (Figure 3). The step forward is to keep on improving the overall wool quality traits of the progeny and to disseminate correct sires with high genetic merit for GIP resistance.



Source: Authors' own elaboration.

Figure 4: Estimated breeding values for the progeny according to the origin of their sires for Fibre Diameter, Wool Index, Fine Wool Index, and Dual-Purpose Index, based on the 2020 National Genetic Evaluation

2.3 Corriedale and Australian Merino: selection by production and FEC EPD

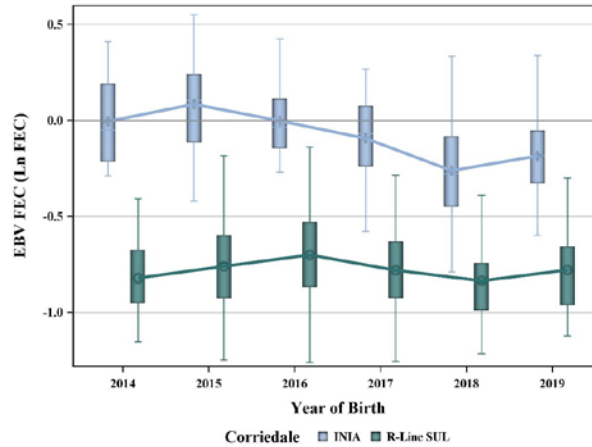
The development of the Corriedale nucleus began in 2014 at the Experimental Unit *Glencoe* of INIA to explore the productive and reproductive potential of the breed in extensive grazing conditions. The first ewes came from the Progeny Test Centre *Dr Pedro A. Narbondo*. They were selected mainly by the twinning rate EPD and the A-selection index of the breed, which aims to genetically decrease the fibre diameter and increase the clean fleece weight and body weight. The FEC EPD has been just recently included in the breeding programme.

Progeny born between 2014 and 2016 came from 120 original ewes and 17 hoggets born in *Glencoe*. This nucleus is genetically connected with the Corriedale stud-flocks in NGE. Every year connection rams are used from elite Corriedale stud-flocks. The objective is to search for a balanced flock, in terms of health, reproductive and productive aspects. In the last three years, the reproductive performance of the nucleus, grazing native grasslands, has been excellent for Uruguay, obtaining values of 134 percent lambing (lambs born/ewes joined), 93 percent survival (lambs marked/lambs born) to marking and 120 percent for weaning rate (lambs weaned per ewe joined).

For experimental purposes, in the last two years (from 2019 to 2021), resistant and average rams (negative and close to zero FEC EPD, respectively) for the FEC EPD trait have been used. This contrast is carried out to evaluate the effect of genetic resistance to GIP on other traits such as feed intake, residual feed intake and methane emissions.

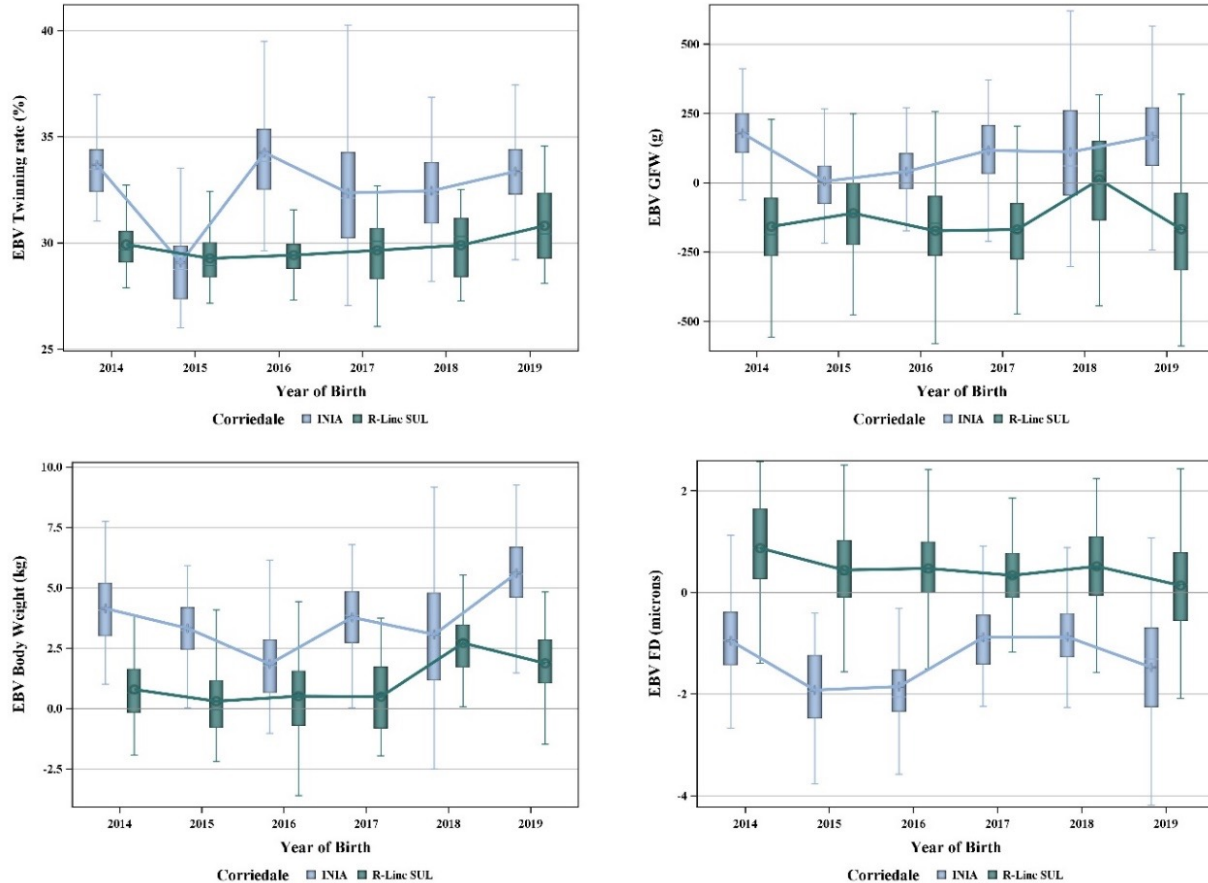
When comparing the genetic trends for FEC EBV between the INIA Corriedale nucleus and the SUL

resistant line (mentioned in section 2.1), lambs from the later are markedly more resistant (FEC EBV more negative) than the Corriedale of INIA (Figure 5) due to a stronger selection for this trait at SUL. In contrast, INIA animals showed better genetic merit for reproductive and productive traits that are included in the productivity selection indices (Figure 6).



Source: Authors' own elaboration.

Figure 5: Genetic trends (EBV) for Faecal Egg Count (FEC) of the INIA Corriedale flock in comparison with the resistant line of the Uruguayan Wool Secretariat

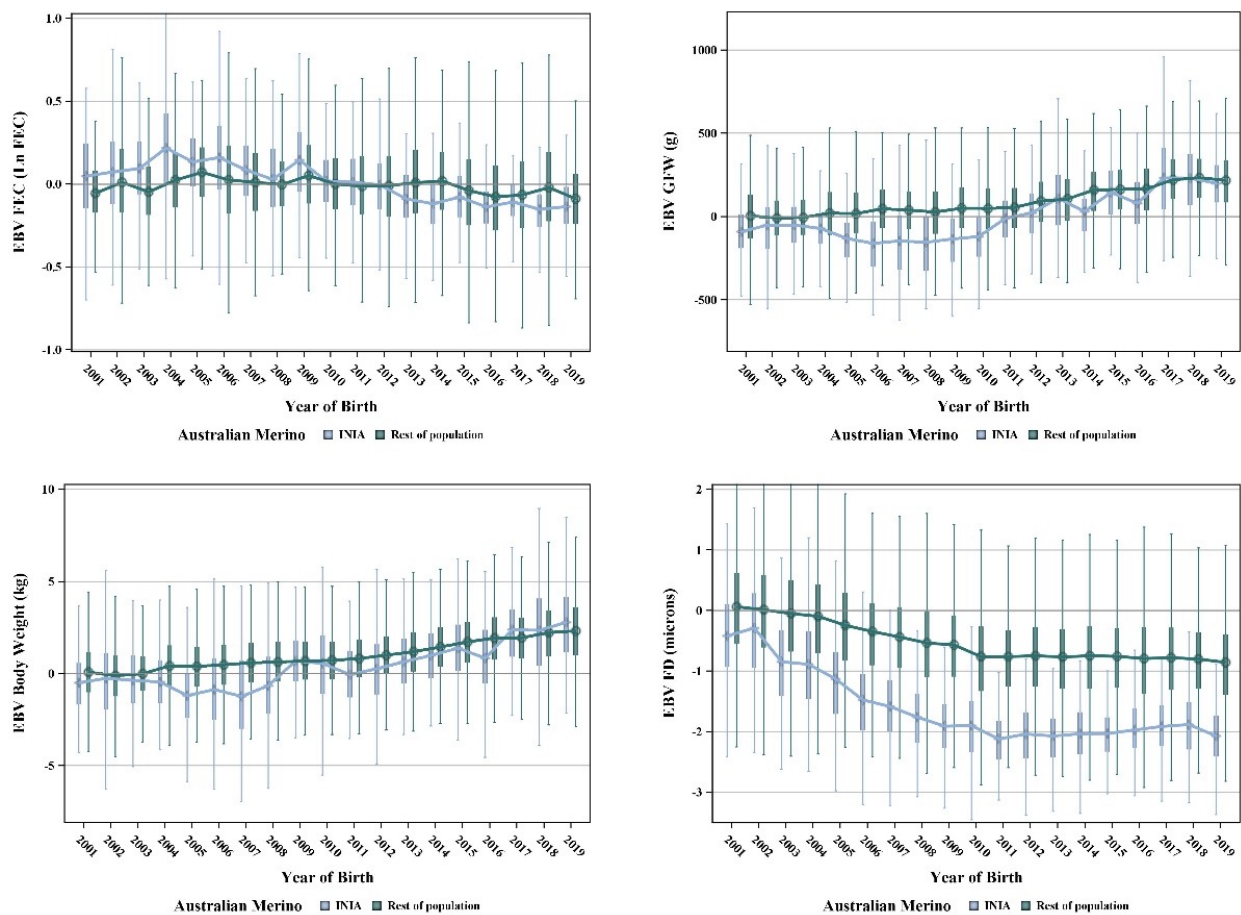


Source: Authors' own elaboration.

Figure 6: Genetic trends (EBV) for productive and reproductive traits: twinning rate, greasy fleece weight (GFW), fibre diameter (FD), and body weight at shearing of the INIA Corriedale flock in comparison with the resistant line of SUL

An Australian Merino nucleus was created at the Glencoe Experimental Unit of INIA in 1999. This nucleus was part of the Fine Merino Project of Uruguay (from 1999 to 2010) and CRILU (from 2011 until present) as described by Ramos *et al.* (2021). The main objective of this nucleus has been to identify and generate genetically superior animals and then disseminate them among commercial farmers and stud breeders of Uruguay. Since 1999 the main selection objective has been to produce super- to ultrafine wool without compromising other economically relevant traits such as fleece and body weight, FEC, staple length, wool colour, conformation, and coefficient of variation of fibre diameter, among others. Therefore, the focus during the first years of the nucleus was to drastically reduce fibre diameter (Figure 7). Once wool diameter was in the range of super- to ultrafine

wool (2011), the emphasis of selection switched to fleece and body weights and then to FEC. By using the genetic tools available (EPDs), pedigree information, phenotypic records, controlled mating, and visual assessment of the animals, it has been possible to generate progeny that produce more and finer wool, are heavier and more resistant to GIP than previous generations of animals in the nucleus and when compared with the average of the evaluated Merino population (Figure 7). Finally, as mentioned before, the dissemination of superior genetics was an objective. In this sense, from 2000 to 2020, 1 000 superior rams and more than 20 000 doses of semen have been disseminated among farmers and breeders. Thus, it can be considered that the superior genetics generated have been spread across the Merino population of Uruguay.



Source: Authors' own elaboration.

Figure 7: Genetic trends (EBV) for faecal egg count (FEC), fibre diameter (FD), greasy fleece weight (GFW), and bodyweight (BW) at shearing of the Glencoe Merino nucleus in comparison with the rest of the evaluated Merino population in Uruguay

3. Development and use of molecular tools

Initially, many countries aimed to use genetic markers to identify alleles associated with resistance to GIP and to select for breeding young animals carrying these alleles. Marker association studies were carried out in

Uruguay using microsatellite molecular markers (STR) in Corriedale (Nicolini, 2006) and Australian Merino breeds (Ciappesoni *et al.*, 2010) and paternity tests were performed in the Corriedale breed (Peraza *et al.*, 2013). Recently, with the development of technologies for data storage and processing and lower costs of equipment and reagents, single nucleotide polymorphism (SNP)

markers have generally outperformed microsatellites for genomic analysis and breeding applications worldwide. A low-density panel of 507 SNP, which includes a subset of markers shared between commercial platforms, was developed in Uruguay (Macedo *et al.*, 2014; Ciappesoni *et al.*, 2016). This panel allows breed genetic identification among populations, paternity assignment (Macedo *et al.*, 2014) and includes markers associated with GIP resistance identified in Australian Merino and Corriedale to improve the prediction of breeding values for genetic resistance to GIP (Grasso *et al.*, 2014).

Nowadays, feasible genomic selection is the preferred approach for genetic improvement, particularly for expensive or difficult to measure traits such as FEC. By using SNP information provided by low/high-density panels, in combination with phenotypic and pedigree information, it is possible to increase EPD accuracy in young animals. Several countries are implementing genomic selection in sheep, such as New Zealand (Auvray *et al.*, 2014), Australia (Daetwyler *et al.*, 2010), and France (Duchemin *et al.*, 2012). In Uruguay, particularly in the Australian Merino breed, progress has been made in the design of the reference population. As of mid-2021 the reference included 2 231 animals with FEC phenotypes and genotypes with either 50K (85 percent) and 15K (15 percent) panels. The first results of genomic evaluation

have already been obtained, with the aim of publishing the first FEC the genomic EPD in 2021.

Genomic data provided by SNP panels with various densities have been used for breed genetic characterization and population structure analysis. Several studies considering different breeds or origins have been carried out, such as the genomic comparison of Australian Merino, Corriedale and Creole breeds (Grasso *et al.*, 2014), and Australian Merino with other related Merino breeds (Ceccobelli *et al.*, 2019; Vera *et al.*, 2019). Additionally, metabolic mechanisms and pathways involved in genetic resistance to GIP in the Corriedale breed were identified by using RNA sequencing technology in several tissues (Peraza *et al.*, 2016). Genomic regions associated with FEC have also been identified in the Australian Merino breed in chromosomes 6, 11, 12, and 21, which are consistent with international studies in other sheep breeds (Benavides *et al.*, 2015). In the near future, we plan to undertake selection signature or genome-wide association studies in the Corriedale breed, based on the divergent selection lines by FEC to identify new regions associated with this trait.

INIA's DNA Genomic Bank supports all these research initiatives, with more than 18 000 DNA samples stored from Australian Merino, Corriedale, Dohne Merino, and Creole breeds (Carracelas *et al.*, 2019). From these, more than 6 700 animals have been genotyped with different SNP arrays (Table 5).

Table 5: DNA samples stored at INIA's DNA genomic bank, total number of genotyped samples and samples genotyped by panel

Breed	DNA samples	Genotyped samples	IAEA ¹	UY panel ²	50K panel ³	Other panel ⁴
Australian Merino	9 597	4 198	0	1 866	1 896	436
Corriedale	6 061	2 369	499	1 446	388	36
Dohne Merino	1 726	0	0	0	0	0
Creole	680	199	0	0	10	189

Source: Authors' own elaboration.

Note: ¹170 SNP; ²507 SNP UY panel; ³50K panels included: Affymetrix 54K, Illumina 50K and GGP50K; ⁴Other panels included: 15K, 60K and 700K SNP.

4. Conclusions

Genetic resistance to GIP is a high relevance trait to stud breeders and commercial farmers. However, to implement a registration system that allows genetic evaluations, initial support from the institutions is needed (i.e. developing protocols, recording support, training, etc.). Several strategies have been developed to improve sheep genetic resistance to GIP, and further research is ongoing to increase their effectiveness and contribute to greater economic benefits and more sustainable production systems.

Thus, inter-institutional (academy, research, technology transfer) and breeder association's coordinated work and commitment are crucial. In addition, the generation

of selection nuclei in experimental stations can play a very important role as demonstration centers, besides the genetic contribution to the commercial flocks. Researchers and institutions need to be up-to-date in the latest procedures such as molecular techniques, in order to provide the best selection tools. Therefore, training people at the local level is very important to achieve this task.

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