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Breeding for resilience and resistance in Merino sheep

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Abstract

Resilience is poorly defined in the Australian sheep industry. However, there are a number of traits available to the industry which provide scope to understand an individual's potential resilience and resistance to environmental stressors. These traits include body condition score, body weight and condition change throughout the year and reproduction. The parasite resistance traits of worm egg count and fly strike resistance are also of interest. Currently, genetic improvement programs are focussed on improving the quality and quantity of wool growth, reproduction and lean meat production. However, significant phenotypic and genetic correlations between production and resilience and resistance traits could be leading to unintentional changes in the performance of the national flock when faced with differing environmental and disease challenges. These relationships are not always favourable making it a complex area for breeders to easily resolve, in particular how much emphasis to place on each of these traits. Furthermore, the Australian sheep industry is located across a range of variable environments and thus the importance of these resilience and resistance traits is likely to vary across those environments. We combined the current knowledge of the relationships between traits and evaluated the impact of various measurement and index selection scenarios to compare the impact of both production, resilience and resistance traits on current breeding strategies available to the Merino industry. The results suggest that selection purely on production traits has and may continue to influence the resilience of the Merino component of the national sheep flock. At this point in time breech wrinkle is the only trait that is predicted to change in an undesirable direction when using the standard MERINOSELECT indexes made available by Sheep Genetics. More desirable gains can be achieved in the additional resilience and resistance traits when they are valued in the indexes, with generally little impact on the standard production traits. When more accurate economic values for resilience and resistance traits can be derived, breeding objectives should be revised and appropriate selection traits identified, and accommodated into the selection indices used by breeders.

Defining resilience in the Australian sheep industry

The Australian sheep industry is economically significant with annual incomes from the wool industry and lamb industries at just under $1.8 billion each (Rowe, 2010). The sheep industry has transitioned from a primarily wool based industry, prior to 2000, to an industry with increased emphasis on reproduction, growth rates and lean meat yield of lambs. Along with development of dual purpose Merino indexes in response to market changes, producers are also faced with costly environmental factors that limit the sheep's performance. High temporal variation in rainfall (Nicholls *et al.,* 2012) and the prevalence of drought across Australia mean pasture supply is highly variable. As a result, costly supplementation of feed is required to maintain live weight and condition during periods when pasture quality, quantity or both are below the nutritional requirements of the ewe. Other limiting factors include internal and external parasites. Fly strike, which is infestation of the skin of sheep by blowfly larvae, is a major disease affecting wool-producing sheep which in 2006 was estimated at $280 million annual cost to the industry with breech strike, which is fly strike that occurs on the backside of the sheep, accounting for just over half, at an annual cost of $147 million (Meat and Livestock Australia, 2006). The cost of breech strike has the potential to increase as animal welfare lobbyists push to ban the current mulesing practices before alternative humane techniques or breeding programs have been implemented (Davidson *et al.,* 2006, Greeff *et al.,* 2014). Internal parasites have been estimated at an annual cost of $369 million to the Australian sheep industry (Meat and Livestock Australia, 2006). The costs associated with environmental variation and disease in particular external parasites suggest that solutions should be identified to reduce those costs, but a breeding solution will only be beneficial if there is genetic variation in those traits to be exploited and it is cost-effective.

This highlights the question of how selection can be used to limit the impact of environmental stressors and improve the consistency of production across years and environments. To breed for an animal that can maintain production levels across multiple environments ram breeders will need to improve the animal's robustness, resilience and/or resistance (de Goede *et al.* 2013):

- Robustness is considered to relate to the ability to combine high production potential with some resilience to environmental stressors, which allows unproblematic expression of a ewe's production potential across a variety of environmental conditions (Knap, 2005, Star *et al*., 2008, de Goede *et al*., 2013)
- Disease resilience has been defined as the ability of the host to maintain a reasonable level of productivity when challenged by infection (Albers *et al*., 1987). This would lead to a resilient ewe being an individual that shows superior performance under environmental stress (Bissett and Morris, 1996, de Goede *et al*., 2013)
- Resistance to animal disease is considered as the ability of the animal to exert control over the parasite or pathogen lifecycle (Bishop, 2012). Consequently, resistance is a direct measure of the individual's susceptibility to environmental stressors, eg. Worm egg count (Bishop, 2012, de Goede *et al*., 2013).

Current Sheep Genetics evaluations do not describe an individual's ability to respond to environmental stressors with the current approach to breed for animals with high genetic merit averaged across the range in environments in which they are evaluated, by adjusting for the production level and its variance, across environments. Breeding flocks contributing to the Sheep Genetics data are traditionally better managed and probably not entirely representative of extreme commercial conditions, genotype by environment (G x E) interaction effects are considered to be small, with sire by flock fitted to account for some small amounts of G x E interaction.

This chapter firstly, explores if based on current knowledge the current MERINOSELECT indexes provided by Sheep Genetics are leading to unfavourable responses in the resilience and resistance traits. We then explored the inclusion of these traits and their economic values into the breeding objective. Several traits have recently become available to provide producers with an understanding of how animals are responding to environmental stressors. These include potential indicator traits of the ewe's energy reserves and the nutritional stress on the ewe as assessed by body condition score and change in weight and condition throughout the production cycle (Russel *et al.,* 1969, Young *et al.,* 2011). Traits such as levels of worm egg count (Karlsson and Greeff, 2006) and fly strike (Greeff *et al.,* 2014) are indicator traits of an animal's resistance to internal and external parasites. Reproduction is a key production trait but can also be used as an indicator of an animal's wellbeing or fitness as ewes will only partition energy into reproduction if maintenance demands are met (Freer *et al.,* 1997). Using the resilience and resistance traits, we will evaluate the responses to selection using the three standard MERINOSELECT indexes and the correlated responses in resilience and resistance traits over a ten year period. Before doing this, we will briefly review current knowledge of the genetic variation in these traits and their relationship with production traits. Among the sources of genetic parameter estimates used for this review is the Sheep CRC Information Nucleus Flock (INF) program (van der Werf *et al.,* 2010). The INF was set up as a progeny testing scheme where progeny of selected industry sires were measured for a large range of existing and novel traits relevant to wool and meat production, with many of the novel traits not commonly measured in stud flocks, but considered to have potential economic value. Animals were born within the INF from 2007 to 2011, with Merino ewes and Merino and first cross wether progeny providing three assessments of production (fleece and carcase) and reproductive performance (yearling and twice as adults). The INF database provided weight and condition data for 13,698 adult ewes (approx. six expressions per ewe) which were used to estimate genetic variation in body condition and weight change and the genetic relationship of these traits with the fleece and carcase production traits recorded within the INF.

Current resilience and resistance traits and their relationship with production traits

Body condition

Body condition score is a subjective measure of the "wellbeing" or condition of the ewe. Body condition is scored from 1 (emaciated) to 5 (obese) based on the fat and muscle coverage over the anterior lumbar vertebrae (Russel *et al.,* 1969). Lifetime Wool guidelines advise producers to maintain an average body condition score of 3 on a scale of 1 – 5 at mating (Curnow *et al.,* 2011; Young *et al.,* 2011), and not allow body condition score to fall below 2.5 during gesta-

Table 1. Heritabilities (bolded on the diagonal), genetic standard deviations, and phenotypic (above diagonal) and genetic (below diagonal) correlations between key production traits used in the MERINOSELECT indexes and resilience and resistance traits. Estimates presented are current Sheep Genetic parameters from the MERINOSELECT database, updated to include estimates calculated using the INF data set (underlined) or sourced from literature (italics, Δ Estimates sourced from Greeff et al., (2014), ∞ Estimates sourced from Brown et al., (2010)

Trait	ywt	wt	fat	emd	fw	fd	cv	ss	wec	nlw	cs	fs	ebwr	wtc
Genetic standard deviation	3.29	4.00	0.73	1.02	9.43	1.10	1.32	5.20	1.26	0.16	0.17	0.61	0.50	0.22
Yearling weight (kg, ywt)	**0.35**	0.60	0.20	0.26	0.28	0.14	-0.06	-0.01	0.06	0.10	0.20	-	*0.00* $^{\infty}$	-
Mature weight (kg, wt)	0.80	**0.40**	0.02	0.07	0.25	0.17	-0.14	0.00	0.00	0.10	0.46	-	*0.00* $^{\infty}$	-
Fat depth (mm, fat)	0.31	-0.00	**0.20**	0.23	-0.09	0.04	-0.02	-0.11	-0.04	0.02	0.13	-	-	-
Eye muscle depth (mm, emd)	0.30	0.15	0.49	**0.30**	-0.11	0.07	-0.07	0.02	-0.05	0.01	0.14	-	-	-
Fleece weight (%, fw)	0.15	0.14	-0.36	-0.29	**0.46**	0.31	0.07	-0.01	0.04	-0.05	0.04	*0.02* $^{\Delta}$	-	-0.03
Fibre diameter (µm, fd)	0.15	0.20	0.11	0.15	0.36	**0.60**	-0.11	0.23	-0.00	-0.02	0.13	*0.04* $^{\Delta}$	-	0.02
CV diameter (%, cv)	-0.05	-0.14	-0.18	-0.24	0.25	-0.14	**0.35**	-0.48	0.08	-0.04	-	*0.05* $^{\Delta}$	-	-
Staple strength (N/Ktex, ss)	-0.00	0.00	0.00	0.00	0.00	0.31	-0.59	**0.30**	-0.05	-0.01	0.06	*-0.01* $^{\Delta}$	-	0.00
Worm egg count (egg/g$^{0.33}$, wec)	0.10	0.00	-0.15	-0.15	0.05	-0.05	0.15	-0.05	**0.20**	-0.05	-	*0.01* $^{\Delta}$	-	-
Number of lambs weaned (lambs / ewe joined, nlw)	0.15	0.15	0.19	0.19	-0.10	-0.00	-0.00	-0.00	-0.00	**0.06**	0.02	-	*-0.30*	0.05
Condition score (scores, cs)	0.70	0.70	0.80	0.68	-0.02	0.33	-	0.23	-	0.10	**0.19**	-	-0.12	-
Breech fly strike (%, fs)	-	-	-	-	*0.06* $^{\Delta}$	*0.14* $^{\Delta}$	*-0.27* $^{\Delta}$	*0.15* $^{\Delta}$	*0.04* $^{\Delta}$	-	-	***0.51*** $^{\Delta}$	*0.20* $^{\Delta}$	-
Early breech wrinkle(scores, ebwr)	*-0.13* $^{\infty}$	*-0.20* $^{\infty}$	-	-	*0.30* $^{\infty}$	*-0.22* $^{\infty}$	-	*0.02* $^{\infty}$	*0.12* $^{\infty}$	*-0.30*	-0.42	*0.18* $^{\Delta}$	**0.39**	-0.03
Weight change (kg, wtc)	-	-	0.10	-	-0.16	0.10	-	-0.03	-	0.77	-	-	-0.20	**0.07**

tion (Edwards *et al.,* 2011). The Lifetime Wool premise is that body condition score provides a good indicator of the wellbeing, nutritional status and available body reserves of the ewe and that through regular measurement of body condition score producers have a clear and reliable indicator of the potential impact environmental and health stressors are having on the flock and/ or ewe's health and wellbeing.

Adult body condition has been estimated to be moderately to highly heritable in the INF (h^2=0.19, Table 1) and across literature (h^2=0.21 – 0.37, Shackell *et al.,* 2011, Brown and Swan, 2014a, Walkom *et al.,* 2014ab). Body condition measurements across the production cycle have been reported to be highly genetically correlated and can be considered the same trait (Shackell *et al.,* 2011, Brown and Swan, 2014a, Walkom *et al.,* 2014a, b). Analysis of the INF data showed that adult body condition is strongly genetically correlated with weight (r_G=0.70), fat depth (r_G=0.80) and muscle depth (r_G=0.68) at post-weaning age (Table 1). Body condition score was also found to have low unfavourable genetic correlation with fibre diameter (r_G=0.33, Table 1). Analysis of the INF data indicated that genetic relationship with number of lambs weaned was lowly favourable (r_G=0.10, Table 1).

Weight and condition change

Young *et al.* (2011) has estimated that managing fluctuations in the live weight profile of ewes throughout the production cycle has the potential to improve the overall profitability of the system through reduced feed costs and increased reproductive performance. It has been proposed that through the use of weight and condition change traits producers can breed for a ewe that requires less inputs (supplementary feed) and is resilient to weight/condition loss when faced with an increased seasonal variability in pasture supply (Young *et al.,* 2011, Rose *et al.,* 2013).

Whilst the premise to select against changes in weight and condition seems promising, the practicality of achieving desired weight and condition profiles of ewes through breeding appears to be limited. Weight and condition measurements across ages and the production cycle have been found to be very highly genetically correlated and in some cases statistically not different to one (Shackell *et al.,* 2011, Brown and Swan, 2014a, Walkom *et al.,* 2014a, b). With genetic variation differing very little between measurements across the production cycle, the heritability of change between measurements will be very low. Analysis of the INF data found the heritability of weight change to range from h^2=0.02 to 0.11, with condition change ranging from h^2=0.02 to 0.08. Previous heritability estimates range from very low (Walkom *et al*., 2014a, b) to low (Rauw *et al.,* 2010, Rose *et al.,* 2013) in Merino and Merino cross ewes.

Whilst genetic variation in weight change is small, weight change during the period between joining and mid-pregnancy has a weak positive genetic correlation with fibre diameter (r_G=0.10) and weak negative genetic correlation with greasy fleece weight (r_G=-0.16, Table 1). Condition change during the same period in the INF data however had a weak negative genetic correlation with both fibre diameter and greasy fleece weight (r_G=-0.13 and -0.30, respectively). Weight and condition gain from joining to mid-pregnancy were lowly to moderately correlated with post-weaning fat depth (r_G=0.10 and 0.21, respectively). Body condition change from joining to mid-pregnancy was weakly genetically correlated to number of lambs weaned (r_G=0.11, Table 1).

Worm egg count

Current management practices rely heavily on chemical treatments for controlling worm egg counts that are increasingly becoming less efficient as parasite resistance too many chemical groups occur. Currently, genetic selection within the Australian sheep industry is based around selection against worm egg counts (Karlsson and Greeff, 2006, Ingham *et al.,* 2007, Afolayan *et al.,* 2008, Brown *et al.,* 2010), with a small negative selection pressure placed on worm egg count within some Sheep Genetics indexes.

By selecting against worm egg count, through using rams with superior breeding values for reduced worm egg count, producers can improve the profitability of their production system. Karlsson and Greeff (2006) reported an annual genetic improvement of 2.7% in worm egg count over 15 years in the Rylington Merino flock. Heritability of worm egg count in young ewes (between weaning and 12 months of age) under sufficient worm burden was reported to be low (h^2=0.10, Ingham *et al.,* 2007), though Afolayan *et al.* (2008) reported a slightly higher heritability of 0.18 based on more data collected from the same source. Analysis of more recent industry data suggests a moderate to high heritability for WEC, with heritabilities in Merino yearlings and hoggets ranging from h^2=0.29 to 0.41 (Brown *et al.,* 2010) with Sheep Genetics using a heritability of h^2=0.20 (Table 1). Worm egg count is moderately positively genetically correlated with post-weaning growth (r_G=0.36), but lowly positively correlated with fleece weight (r_G=0.12) and fibre diameter (r_G=0.02, Ingham *et al.* 2007). Whilst WEC is lowly negatively correlated with carcase fat depth (r_G=-0.15) it has a moderate positive genetic correlation with carcase muscle depth (r_G=0.46, Ingham *et al.,* 2007). The genetic correlation between WEC and both fat and eye muscle depths in the analysis of Sheep Genetic data is negligible and lowly negative ranging between r_G=-0.04 to -0.20 across ages (Brown and Swan, 2014b). The relationship between WEC and NLW is negligible, with Afolayan *et al.* (2008) reporting genetic and phenotypic correlations of zero. Worm egg count is currently used within Sheep Genetics MERINOSELECT indexes and parameter estimates have been estimated from the Sheep Genetics data (Table 1).

Fly strike - breech

Fly strike, which is infestation of the skin of sheep by blowfly larvae, is a major problem in wool-producing sheep, which results in production losses and death if not treated in a timely fashion (Greeff *et al.,* 2014). Breech fly strike is still largely being controlled by surgical mulesing of the breech area of the sheep, regular crutching, and treating struck sheep with chemicals. Mulesing is increasingly becoming socially unacceptable as a result of a push by animal welfare groups. Consequently, the wool industry has looked towards genetic solutions to improve fly strike resistance (Greeff *et al.,* 2014). Breech wrinkle, dags, urine stain, neck wrinkle, breech cover and face cover traits are potential indicator traits for indirect selection for breech strike resistance (Bird-Gardiner *et al.,* 2014, Greeff *et al.,* 2014). By selecting against breech strike and for plainer bodied animals ram breeders are breeding for an animal that is resistant to fly strike.

Analysis of a sub-set of the INF data (Bird-Gardiner *et al.,* 2014) found that yearling breech wrinkle was highly heritable (h^2=0.58) with body and neck wrinkle slightly less heritable (h^2=0.26 and 0.51, respectively). Heritability estimates for breech wrinkle in the INF data align with heritability estimates within the literature which range from h^2=0.25 to 0.73 (Smith *et al.,* 2009, Brown *et al.* 2010, Greeff *et al.,* 2014). Greeff *et al.* (2014) found low genetic correlations (r_G=0.18 to 0.27) between breech wrinkle and flystrike with less accurate but moderate (r_G=0.47 to 0.66) genetic correlations reported by Bird-Gardiner *et al.* (2014). Because selection directly on fly strike is dependent on the prevalence of fly strike within the flock, selection on wrinkle is more attractive as a means of selecting for a resistant sheep as selection for a plainer bodied sheep can be based on scores recorded as early as marking.

Greeff *et al.* (2014) found that fly strike is very lowly positively genetically correlated with fleece weight (r_G=0.06) and fibre diameter (r_G=0.14, Table 1). Breech wrinkle has a low to moderate positive genetic correlation with fleece weight (r_G=0.30) and low negative genetic correlation with fibre diameter (r_G=-0.22, Brown *et al.,* 2010). Breech wrinkle has a weak negative genetic correlation with bodyweight (r_G=-0.20, Brown *et al.,* 2010). A similar genetic relationship was derived from the INF data, with moderate negative genetic correlations with body condition (r_G=-0.42) and a very weak genetic relationship with body weight change (Table 1). The genetic correlation between breech wrinkle and NLW estimated from Sheep Genetic data (Brown and Swan, 2014b) was low and negative (r_G=-0.30, unpublished, Table 1).

Reproduction

Reproduction (number of lambs weaned per ewe joined) is a key production trait within the Australian sheep industry accounting for between 2 to 26% of current selection emphasis within MERINOSELECT indexes (Sheep Genetics, 2014).

Number of lambs weaned per ewe (NLW) is a composite trait that has components of fertility, litter size and lamb survival to weaning. Heritability estimates reviewed by Fogarty (1995) and Safari *et al.* (2005) indicated average estimates of heritability for NLW to range from h^2=0.05 to 0.07. Data from first-cross Merino ewes have suggested, however, that it may be more heritable with an estimate of h^2=0.13 (Afolayan *et al.,* 2008). Analysis of the INF data resulted in an estimated heritability of h^2=0.04 for number of lambs weaned. The review of NLW by Safari *et al.* (2005) presented weak negative genetic correlations with growth (r_G=-0.05 to -0.09) and fleece weight (r_G=-0.10). Recent analysis by Brown and Swan (2014b) showed low positive genetic correlations with fat (r_G=0.05 to 0.33) and muscle depths (r_G=0.18 to 0.33) in Merino industry data. As previously reported NLW has weakly favourable genetic relationships with body condition, body weight change and condition change and negligible relationships with worm egg count and breech wrinkle. Number of lambs weaned is currently used within Sheep

Genetics MERINOSELECT indexes and parameter estimates have been estimated from the Sheep Genetics data (Table 1).

How current MERINOSELECT indexes are influencing resilience and resistance

To understand the relationship between resilience and resistance traits and production traits, ram breeders and producers need to move from consideration of relationships among individual traits and focus on the potential impact of current selection indexes and the advantages of incorporating resilience and resistance traits into breeding objectives to improve productivity and profitability. To provide this understanding, we have examined responses to selection using the three standard MERINOSELECT indexes, Fibre Production (FP+), Merino Production (MP+) and Dual Purpose (DP+) (Sheep Genetics, 2014):

- The FP+ index places a large premium on micron and aims to reduce fibre diameter and hold fleece weight constant, and also has a small negative emphasis on worm egg count (Table 2)
- The MP+ index places a moderate premium on micron and aims to reduce fibre diameter and increase fleece weight (Table 2)
- The DP+ index places a small emphasis on micron with the aim to hold fibre diameter while increasing fleece weight with an additional emphasis on lamb production (Table 2).

The relative economic values for these indexes were as reported by Brown and Swan (2014) and are shown in Table 2. As there are no economic values available for fly strike, condition score, weight and condition score change, additional indexes (R) were constructed using economic values derived for these three resilience and resistance traits (Table 2). The economic values were approximated as follows:

- Condition Score: The economic value used was $12.50 per ewe per year per condition score. This was calculated from the cost of grain feeding ($300/t) a ewe to change 1 condition score over a 3 month pre-joining period and based on a 50kg ewe when feed is limited and the assumptions of http://www.lifetimewool.com.au/Tools/dryfeedbud.aspx.
- Fly Strike: The economic value used was -$0.60 per ewe per year per 100% reduction in flystrike. This was derived using the results of Horton (2013) who described a benefit of a 50% reduction in the risk of strike would be $0.23–0.27 per sheep per year.
- Weight Change: The economic value used was $1.50 per ewe per year per kg. This was calculated from the cost of grain feeding ($300/t) a ewe to change 1 kg in body weight over a 3 month post-joining period and based on a 50kg ewe and the assumptions of http://www.lifetimewool.com.au/Tools/dryfeedbud.aspx.

Response to selection were predicted using the genetic parameter estimates presented in Table 1, which were based on current Sheep Genetics parameters, including recent updates from Brown and Swan (2014b), resilience and resistance trait parameter estimates available from analysis of the INF database and published literature (Brown *et al.,* 2010 and Greeff *et al.,* 2014, Table 1).

The breeding program assumed for the index calculations had generation intervals of 3 years for males and 4 years for females. The proportion of males selected was 5% and 50% for females giving selection intensities of 2.06 and 0.80 respectively. It was also assumed that 65% of the selection emphasis was placed on index values and the remaining 35% on other information sources such as visual assessments. It was also assumed that records were available on 30 half sibs for weaning weight (wwt), and at yearling age weight (ywt), clean fleece weight (ycfw), fibre diameter (yfd), coefficient of variation of fibre diameter (yfdcv), ultrasound fat depth (yfat), ultrasound muscle depth (yemd) worm egg count (ywec) and breech wrinkle (ebwr) and 15 half sib records for yearling staple strength (yss). Seven half sib records were collected as adults for clean fleece weight (acfw), fibre diameter (afd) and coefficient of variation of fibre diameter (afdcv), and further 5 records for number of lambs weaned (nlw), body condition score (cs) and weight change (wtc).

Selection criteria used by ram breeders within the industry is highly variable. Selection scenarios used within this analysis were based on the traits measured by a typical Merino breeder with a focus on wool production (1). Alternative scenarios were included to incorporate ram breeders who have an interest in lamb and reproduction traits (2) and also resilience and resistance traits (3).

1. wwt, ywt, ycfw, yfd, yfdcv, yss, acfw, afd and afdcv
2. 1 + yfat, yemd, ywec and nlw
3. 2 + cs, wtc and ebwr

Impact of MERINOSELECT indexes on resilience

Predicted responses from the MERINOSELECT indexes suggest that selection on current indexes is likely to be having a small unfavourable influence on only one of the resilience and resistance traits. Averaged over the three measurement scenarios and standard indexes in Table 2, condition score and wrinkle are predicted to increase by 0.08 and 0.10 scores respectively after 10 years of selection. Flystrike and weight change are predicted to decline by 2% and 0.04 kg respectively. However, when these traits were measured and valued in the resilience index, slightly more desirable changes in condition score and wrinkle, by 0.18 and -0.07 scores respectively, and fly strike and weight changes declining by 5% and 0.03kg respectively (Table 2) were predicted.

The impact on the other production traits of including selection pressure on the resilience traits using the MP+ R vs. the MP+ index was generally small in trait terms with more in-

Table 2. Economic value ($/unit increase) and proportion of genetic gain (%) to traits within MERINOSELECT indexes

	Economic value ($/unit increase)						Proportion of economic gain (%)					
Trait	**FP+**	**FP+R**	**MP+**	**MP+R**	**DP+**	**DP+R**	**FP+**	**FP+R**	**MP+**	**MP+R**	**DP+**	**DP+R**
Yearling weight (kg)	-	-	-	-	0.94	0.94	-	-	-	-	30.81	28.95
Mature weight (kg)	-0.03	-0.03	-0.58	-0.58	-0.25	-0.25	-0.02	-0.07	-15.13	-19.45	-7.33	-7.05
Fat (mm)	-	-	-	-	-	-	-	-	-	-	-	-
Eye muscle depth (mm)	-	-	-	-	3.14	3.14	-	-	-	-	-	-
Fleece weight (%)	1.55	1.55	0.46	0.46	0.82	0.82	18.52	19.23	64.62	57.94	36.88	29.05
Fibre diameter (µm)	-13.74	-13.74	-2.52	-2.52	-3.44	-3.44	64.82	61.12	25.97	12.54	2.27	-2.26
CV diameter (%)	-1.10	-1.10	-	-	-	-	1.90	1.95	-	-	-	-
Staple strength (N/Ktex)	1.57	1.57	0.52	0.52	0.42	0.42	17.81	19.34	9.04	10.31	3.71	3.90
Worm egg count (egg/g$^{0.33}$)	-5.39	-5.39	-	-	-	-	-1.43	-1.59	-	-	-	-
Number of lambs weaned (lambs / ewe joined)	126.96	126.96	69.51	69.51	126.18	126.18	-1.92	-0.13	6.19	12.21	25.37	25.97
Condition score (scores)	-	12.50	-	12.50	-	12.50	-	0.08	-	16.03	-	13.93
Fly strike (%)	-	-0.60	-	-0.60	-	-0.06	-	0.03		0.23	-	0.16
Early breech wrinkle(scores)	-	-	-	-	-	0.00	-	-	-	-	-	-
Weight change (kg)	-	1.50	-	1.50	-	1.50	-	-0.40	-	-0.73	-	-0.33

Table 3. Trait and economic gain after 10 years of index selection (using updated genetic parameters)*

	FP+			FP+R	MP+			MP+R	DP+			DP+R
Trait	**1#**	**2**	**3**	**3**	**1**	**2**	**3**	**3**	**1**	**2**	**3**	**3**
Yearling weight (kg)	0.70	0.33	-0.02	0.24	2.44	1.77	1.41	1.79	3.56	1.86	1.10	1.32
Mature weight (kg)	0.20	-0.55	-1.31	-1.11	1.93	0.99	0.29	0.59	3.23	0.89	-0.39	-0.15
Fat (mm)	-0.14	-0.03	-0.13	-0.07	0.00	0.02	-0.07	0.04	0.16	0.22	0.04	0.10
Eye muscle depth (mm)	-0.17	0.08	0.03	0.11	0.02	0.30	0.23	0.38	0.21	0.60	0.43	0.50
Fleece weight (%)	2.49	1.92	1.91	1.97	5.79	4.46	4.34	4.04	4.45	2.50	2.26	2.19
Fibre diameter (µm)	-0.77	-0.67	-0.60	-0.52	-0.34	-0.29	-0.22	-0.07	-0.05	-0.05	0.01	0.09
CV diameter (%)	-0.3	-0.46	-0.59	-0.60	0.03	-0.16	-0.28	-0.31	0.06	-0.25	-0.46	-0.46
Staple strength (N/Ktex)	1.47	1.16	0.78	0.78	0.73	0.62	0.26	0.27	0.52	0.27	-0.21	-0.16
Worm egg count (egg/ $g^{0.33}$)	0.06	-0.24	-0.37	-0.39	0.13	0.03	-0.12	-0.18	0.12	-0.11	-0.32	-0.33
Number of lambs weaned (lambs / ewe joined)	0.00	0.05	0.08	0.08	0.01	0.06	0.09	0.10	0.02	0.09	0.12	0.12
Condition score (scores)	-0.02	0.01	0.06	0.09	0.06	0.07	0.12	0.18	0.12	0.12	0.18	0.21
Fly strike (%)	-0.01	0.01	-0.03	-0.04	-0.03	0.00	-0.05	-0.06	-0.04	0.01	-0.05	-0.06
Early breech wrinkle(scores)	0.22	0.24	0.14	0.11	0.11	0.13	0.00	-0.07	0.03	0.12	-0.05	-0.09
Weight change (kg)	-0.06	-0.06	-0.05	-0.04	-0.04	-0.04	-0.03	-0.02	-0.03	-0.03	0.00	0.00
Total Economic ($/ewe)	24.41	29.09	31.53	32.46	10.01	12.32	13.40	15.29	12.02	19.45	23.59	26.05

Criteria measured; 1=wwt, ywt, ycfw, yfd, yfdcv, yss, acfw, afd and afdcv, 2 = 1 + yfat, yemd, ywec and nlw, 3 = 2 + cs, wtc and ebwr

* Traits averaged across stages of measurement

crease in yearling weight (0.38kg), fat depth (0.12mm), muscle depth (0.15mm), fibre diameter (0.15um), staple strength (0.01 N/Ktex) and number of lambs weaned (1%) and less in fleece weight (-0.7%), fibre diameter CV (0.10%), and worm egg count (-0.06 eggs/g) gain after 10 years of selection (Table 3). Minimal changes in the genetic progress of production traits, suggest including resilience and resistance traits into breeding objectives will not significantly harm production gains. The impact of measuring and having an economic value on resilience traits for the FP+ and DP+ indexes was smaller than observed with the MP+ for both production and resilience/resistance traits. By using the MP+ R index producers could achieve a 14% increase in economic gain ($/ewe/yr) for the MP+ index compared to only 3% and 10% improvement in FP+ R and DP+ R indexes respectively. A two fold increase in the economic value of resilience traits would lead to approximately a twofold change in the magnitude of the impact of resilience traits on index gains.

These results suggest that if resilience and resistance traits are not among the breeding objective traits, then breech wrinkle is the only trait that is predicted to change very slightly in an undesirable direction when using the Sheep Genetics indexes (Table 3). Strong selection for heavy and finer fleeces is bringing about the increase in wrinkle due to a low to moderate unfavourable genetic correlations (Table 1). By measuring breech wrinkle and placing an economical value on body weight as occurs with the DP+ index the undesirable change toward a wrinklier body can limited or halted (Table 3). Desirable gains can be achieved with the addition of resilience and resistance traits, with generally little impact on the standard production traits. Measuring carcase traits, worm egg count and reproduction (selection criteria 2 vs. 1) lead to increased improvement in these traits but also small increases in condition score, flystrike and breech wrinkle (Table 3).

The most economic gain was achieved by measuring all traits, as shown when using scenario 3 (Table 3). Measuring reproduction traits had the biggest impact on economic gain in all indexes (Table 3). Measuring the additional resilience traits of condition score, weight change and early breech wrinkle score resulted in 8%, 9%, 21% and 14% additional economic gain for the fine (FP+), medium (MP+), dual purpose (DP+) and medium with resilience (MP+ R) indexes respectively when compared to scenario 2 (Table 3). The larger impact in the dual purpose index is due to the fact this is the only index in which yearling and body weight and eye muscle depth have a direct economic value (Table 2). Measuring reproduction traits directly resulted in 17%, 27% and 45% additional economic gain across the three standard indexes (Table 3).

The future of "resilience traits" in the Merino production systems

Though in the past resilience and often resistance traits have been at worst not defined and at best poorly defined, better identification and definition of these traits is now occurring. This in turn is stimulating development of economic values and genetic parameters for these traits, offering ram breeders and producers the opportunity to include these traits in their breeding programs. This analysis shows that when resilience and resistance traits are measured and included within the MERINOSELECT standard indexes greater genetic improvements in profit occurred. In the short term, the biggest limitation facing the industry is getting accurate information on the size and economic impact of the environmental stressors faced during the production cycle. The ram breeders who currently contribute to the Sheep Genetics database are traditionally better managed and probably not entirely representative of extreme commercial conditions, this consequently limits the ability to quantify any potential G x E interaction effects and could lead to rams being over valued for some environments as environmental stressors have been avoided. Consequently, under extreme commercial environments the assumptions made in this study may be underestimating the economic value of the resilience and resistance traits and therefore their importance to the breeding objective.

Genotyping of reference populations run under extreme commercial conditions will assist to quantify G x E interaction and accuracy of breeding values for resilience and resistance traits. Until there are more accurate economic values for these traits and information on the environment in which phenotypes are measured, selection for animals with high genetic merit averaged across the range in environments will remain the norm. Additionally, future inclusion of resilience and resistance traits in breeding objectives would be advantageous in addressing increased environmental variability expected due to climate change and other industry issues such as the banning of mulesing to control breech strike. Improved measurement technology may also lead to better phenotyping of key traits related to resilience in production and disease resistance and subsequently expanded performance recording and parameter estimation for these traits to support their inclusion in Sheep Genetics. If coupled with genotyping in appropriately challenged reference flocks, improved phenotyping would also enable associations of SNPs with the traits of interest to be identified and the genomic information used to increase genetic gains.

Summary

The current approach of Sheep Genetics is successfully producing animals with high genetic merit in the traits for which they are evaluated. Selection purely on production traits will continue to influence the resilience and disease resistance of Merino sheep flocks. However, the current predictions of selection response from standard MERINOSELECT indexes suggest that breech wrinkle is the only trait that might change slightly in an undesirable direction. The inclusion of resilience and resistance traits had very little effect on changes in production traits and was found to improve the profitability when they are valued and included among the breeding objective traits. It is concluded that when more accurate economic values and genetic parameter estimates for these traits can be derived, breeding objectives should be revised to appropriately accommodate these traits into the selection indices used by breeders.

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