Unpublished Report

Document ID:	SheepCRC_13_30
Title:	A science-based approach to breeding the future Merino
Author:	Hatcher, S.; Gardner, G.E.; Gill, S.; Lee, S.; Swan, A.A.; van der Werf, J.H.H.
Key words:	sheep; breeding; wool; meat; pedigree; genomics

Sheep CRC Report 13_30

A science-based approach to breeding the future Merino

S. Hatcher[AB]*, G.E. Gardner*[AC]*, S. Gill*[D]*, S.Lee*[AE]*, A.A. Swan*[AF] *and J.H.J. van der Werf*[AG]

[A]CRC for Sheep Industry Innovation, Homestead Building, UNE, Armidale, NSW 2351
[B]NSW Department of Primary Industries, Orange Agricultural Institute, Forest Road, Orange NSW 2800
[C]School of Veterinary and Life Sciences, Murdoch University, Murdoch WA 6150
[D]Meat and Livestock Australia, Armidale NSW 2351
[E]School of Animal and Veterinary Sciences, The University of Adelaide, Roseworthy SA 5371
[F]Animal Genetics and Breeding Unit[1], University of New England, Armidale NSW 2351
[G]School of Environmental and Rural Science, University of New England, Armidale NSW 2351

Introduction

Over the past decade Australian Merino production systems and Merino breeding objectives have moved from a traditional focus on heavy fleeces of high value to include aspects of sheepmeat production, both lamb growth rates and meat quality, as well as reproduction in a bid to increase weaning rates. This has been a response to a period of relatively high sheep and lamb prices compared to wool returns in the Australian wool, lamb and mutton markets. In the late 1980s and early 1990s wool accounted for about 85% of the gross value from sheep, however, by the mid to late 2000s the gross value of meat and wool was evenly balanced (Curtis, 2009). At the same time there has also been a significant increase in the number of Merino flocks located in areas where there is a high risk of internal parasites selecting for resistance. More recently there has also been increased selection against breech wrinkle to reduce the risk of flystrike.

Each of these changes has extended the range of traits that are important to Australian Merino breeders and bring added complexity to the assessment, measurement and selection of animals in breeding programs. Not all traits are able to be measured phenotypically at a time conducive to the demands of genetic evaluation systems or at the time of the year or wool growth that ram buyers demand. These 'hard-to-measure' traits include carcase and meat quality, parasite resistance and reproduction. This means that new approaches, such as genomic selection, are required to adequately improve these traits in breeding programs. Furthermore, an extended range of traits with varying genetic relationships between them both favourable and unfavourable must be combined into selection strategies that maximise rates of genetic gain, while improving management efficiency.

It is against this background of change and complexity that science can provide Merino breeders with the means to meet these challenges. This paper highlights a number of technologies and information, developed through the Cooperative Research Centre for Sheep Industry Innovation[2] (Sheep CRC), that highlight the role of science in Merino breeding programs. These technologies include:

i. Pedigree Matchmaker and the SNP-based parentage test which will enable syndicate mating while recording full pedigree;
ii. development of genomic tests to increase accuracy of estimated breeding values and decrease the generation interval and increase the accuracy of selection;
iii. the Poll/Horn test to increase the ease of management of rams through decreasing injury and flystrike;
iv. a greater understanding of meat production from Merinos;
v. estimates of correlations both within and between wool, meat, reproduction and disease traits to ensure the required balance is maintained in Merino breeding objectives and selection systems and;

---

[1] A joint venture of NSW Department of Primary Industries and the University of New England

[2] Operating as part of the Australian Government's Industry Cooperative Research Centres Program, the Sheep CRC is a collaboration of industry, government and the commercial sector. It is working to increase the productivity and profitability of the Australian sheep industry through adoption of new technologies in both the meat and wool supply chains.

vi. development of improved wool processing technologies to open up new markets for wool.

The Sheep CRC's Information Nucleus (IN) flock is a unique genetic resource that was designed to estimate genetic parameters for new traits that could potentially be added to breeding program. The flock also served as a reference population to predict the breeding values of young industry sires, both for existing and new traits using conventional and genomic technologies. The IN was essentially a large progeny testing scheme, where progeny of a diverse range of industry sires were measured and assessed for a large range of traits, most of them not commonly measured on commercial studs (van der Werf *et al.*, 2010). IN progeny were the result of an annual mating of 100 sires (40 Terminal, 20 Maternal and 40 Merino) to approximately 4,500 dams (Merino or Border Leicester x Merino 1st cross) spread across the major sheep production regions of Australia from 2007 to 2012 (Table 1).

Table 1. Geographical location and climate of the eight Sheep CRC IN flocks

Flock ID	Location	Climate
IN01	Kirby, NSW 30.50S 151.66E	Summer rainfall. High rainfall zone
IN02	Trangie, NSW 31.99S 147.95E	Non-seasonal rainfall. Temperate zone
IN03	Cowra, NSW 33.81S 148.70E	Winter rainfall (average 625 mm). Mediterranean climate
IN04	Rutherglen, VIC 37.10S 140.79E	Winter rainfall (average 583 mm).
IN05	Hamilton, VIC 37.83S 142.06E	Winter rainfall (average >600mm). High rainfall zone.
IN06	Struan, SA 37.10S 140.48E	Winter rainfall (average 556mm). Mediterranean climate
IN07	Turretfield, SA 34.55S 138.8E	Winter rainfall (average 468mm) Mediterranean climate
IN08	Katanning, WA 33.69 117.55E	Winter rainfall (400 mm). Mediterranean climate

Detailed protocols for the measurement and assessment of a large number of traits were developed and implemented ensuring that all progeny born into the IN were extensively evaluated for a wide range of traits including: i. wool production, wool quality and a full range of visual sheep scores (Australian Wool Innovation and Meat and Livestock Australia, 2013); ii. growth and meat quality, iii. reproduction and lamb survival and; iv. disease traits. This extensive range of measurements on both existing and new traits provided the necessary resource material for scientists across Australia working in many areas of biology and genetics such as:

i. . implementation of precision sheep management principles on a large scale,
ii. development of new breeding values for a wide range of traits as well as increasing the accuracy of existing breeding values,
iii. developing the capacity to use genomic information to predict breeding values as well as parentage and pollness
iv. improving the understanding of the biology of meat production and quality
v. estimating genetic correlations both within and between trait groups to understand all key elements of sheep production and their interrelationships.

Accurate pedigree – for accurate genetic evaluation and prediction of genetic progress

Reliable genetic evaluation of animals and estimation of genetic trends in studs requires accurate pedigree information. Most Merino breeding flocks have either little (i.e. sire only) or no record of pedigree (Richards and Atkins, 2007). A typical scenario involves either artificial insemination (AI) or single sire joining followed by lambing ewes down in sire groups and recording the dam of each lamb during lambing rounds or mothering up at perhaps 2 to 6 weeks after birth. This process is laborious, relatively expensive and time consuming. The actual cost of such systems of pedigree reporting has been reported to be in the vicinity of $10 per lamb (Russell *et al.*, 2006).

Development of alternative technologies and systems for accurate determination of pedigree will allow wider use of syndicate mating within Merino breeding programs. This has the potential to provide significant efficiencies in terms of labour, as ewes will not need to be drafted into single sire groups for joining and lambing, and capital as fewer paddocks (and fencing) will be required. Low labour systems will have the added advantage of improved Work Health and Safety (WHS) for the stockman and animal welfare benefits for the flock as less hands-on animal husbandry (i.e. mustering and yarding) will be required.

Determining pedigree by association - Pedigree MatchMaker

Pedigree MatchMaker uses a walk-over-weighing system which records the order of movement of ewes and lambs as they pass a radio-frequency identification (RFID) panel or portable reader on the way to food, water or between paddocks (Richards *et al.*, 2006). It works on the principle that lambs follow their mothers closely. The RFID tag of each ewe and lamb, previously tagged at lamb marking for example, is captured by the reader in a time-ordered list as they pass. The walk-through records are then processed by software, based on a list that codes each RFID as belonging to a ewe or lamb, to determine which ewe and lamb combinations appear in the data. The result is a matrix of frequency counts for each ewe/lamb combination which is then further processed by the software to provide the dam pedigree. The association process relies on finding a dam for each lamb, which allows for pedigreeing of twins as well as single lambs (Richards and Atkins, 2007).

The Pedigree MatchMaker system has been shown to be 85 - 96% accurate in predicting pedigree from the association between ewes and lambs over a period of 3 – 4 weeks (Richards and Atkins, 2007). This compares to once daily lambing rounds which have potential pedigree error rates of 9, 15 and 24% for single, twin and triplet lambs (Alexander *et al.,* 1983). While it is possible that some of the ewe lamb pairs identified by Pedigree MatchMaker could be the result of cross- or mis-mothering, this would also occur during traditional mothering up of ewes and their lambs. The Pedigree Matchmaker system also provides useful information about the environment in which a lamb was raised (i.e. as a single or a twin) as well as the maternal behaviour of the dam (Richards and Atkins, 2007).

Determining pedigree by association using Pedigree MatchMaker is much less labour-intensive and lower cost than traditional mothering up techniques, having been estimated at as little as $3 - 4 per lamb (Richards and Atkins, 2007). In Australia, the analysis of data provided by the Pedigree Matchmaker system is undertaken by a network of private providers (currently numbering about 12 but growing). Breeders and commercial producers submit their data to these providers and receive a dam pedigree for each lamb. NSW DPI, through *Advanced Breeding Services*, currently provides a Pedigree MatchMaker service to 25 clients which are a mix of stud and commercial enterprises with mob sizes ranging from 50 up to 800 ewes.

The Pedigree MatchMaker system provides other data which can be incorporated into genetic improvement programs or used for animal management. A lamb survival record is simultaneously provided for each ewe in the mob, this can be used to derive the number of lambs reared by each ewe allowing selection on net reproduction rate (number of lambs reared per ewe joined). If the information from Pedigree MatchMaker is combined with that from pregnancy scanning it is possible to derive birth type and rearing type, which are necessary parameters to quantify the early life environment of each lamb for genetic evaluation. It is also possible to combine other data from the Pedigree MatchMaker system such as the number of times each day an animal is recorded by the system, the compatibility between a lamb and its assigned dam or the average time between readings for lamb and its dam (Brown *et al.,* 2011) with other measures such as lamb growth rate and mothering ability which can then be correlated with subsequent ewe and lamb performance (Richards and Atkins, 2004).

SNP-based parentage test

The Pedigree MatchMaker system provides an accurate dam pedigree but does not provide the sire pedigree. However, another new development, the SNP-based parentage test can be used in conjunction with Pedigree MatchMaker to provide the additional paternal parentage information. The SNP-based parentage test is based on recent research conducted by the Sheep CRC, Meat & Livestock Australia and the International Sheep Genomic Consortium (ISGC). A SNP, single-nucleotide polymorphism, is a variation at a single site in the DNA sequence that occurs when a single nucleotide (i.e. A, T, C or G) differs between a pair of chromosomes and is the most frequent type of variation in the genome. SNPs are now the most widely used class of genetic marker in genetics (Kijas *et al.*, 2009). The ISGC identified and prioritised a number of markers for use in assigning parentage in sheep (Kijas *et al.*, 2012; Kijas *et al.*, 2009). Recently Bell *et al.* (2013) confirmed that the design of the SNP used to assign parentage in sheep are technically robust and recommended that a 3 panel test (or 190 SNP) be used. This SNP-based parentage test is suitable for use with all breeds, not just Merinos, and is currently available in Australia at a cost of $17 per sample.

The challenge for breeders is to determine the most cost effective means of incorporating the test into their breeding program. The parentage test can be used to assign a 'full' pedigree to an individual animal, which links a lamb to both its sire and dam. However this will require collection of blood samples from all rams, ewes and lambs that need to be matched up. Failing to sample one or two rams can make it difficult to assign all of the lambs to their sires. If only the sire pedigree is required, in situations where Pedigree MatchMaker has used to assign dam pedigree, it would be necessary to sample all rams used in a flock as well as a groups of targeted progeny that need to be matched to the rams – such as all of the ram lambs. As the SNP-based parentage test is compatible with other SNP-based tests, rams that have already been genotyped using a 12K chip will not need to be re-sampled for determining their progeny.

Increasing rates of genetic gain with genomic selection

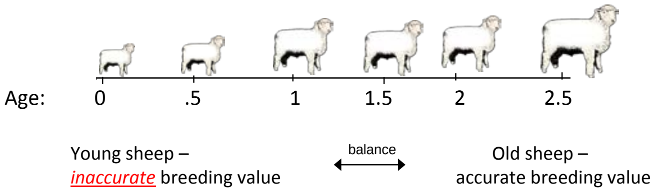
Genetic improvement requires four key ingredients: i. *selection intensity* – so only the very best animals are selected; ii. *selection accuracy* – so that the best animals are picked more often; iii. *generation interval* – so the best animals are bred from as soon as possible and; iv. *variation* – animals must be different enough to pick from.

Genomic selection allows Merino breeders to select rams earlier in life with more confidence, thus decreasing the generation interval while increasing the accuracy of prediction of genetic merit for their breeding objective. Commercial sheep producers benefit through better informed ram purchases as ASBVs containing genomic information will have higher accuracy. The main benefits of genomic selection arise for those traits that are usually difficult or expensive to measure (i.e. carcass and eating quality traits, parasite resistance), cannot be measured early (i.e. adult wool production, or number of lambs weaned) or have low heritability (i.e. reproduction traits) (Swan *et al.*, 2012).

Genomic information requires phenotypic measurements and DNA collection from a large number of sheep along - called the reference population. Ram breeders then collect DNA from their rams and a computer centre uses this information and a 12K SNP chip to predict the breeding value for young rams based on the genomic relationship combined with other information. Genomic prediction is based on many small genomic relationships in the DNA of each animal and does not require 'direct' relatives to be tested. While it can be based on more distant relatives, this requires greater numbers for accurate prediction as well as a higher genetic relationship to the reference population to ensure genomic accuracy (Clark *et al.*, 2012).

Merino breeding programs can benefit from genomic selection by increasing rates of genetic change through increasing the accuracy of selection and decreasing the generation interval as an animal's breeding value can be estimated earlier in life (Moghaddar *et al.*, 2014). Traditional selection means that young sheep have relatively inaccurate breeding values compared to older sheep as it is not until older ages that traits such as wool production, wool quality or reproduction can be accurately measured (Figure 1). Genomic selection increases the accuracy of breeding values in young sheep by combining genomic information with pedigree and performance data in a genetic evaluation system (Swan *et al.*, 2012) as the genetic relationships in the genome can be used to predict performance at later ages.

Traditional Selection



Genomic Selection

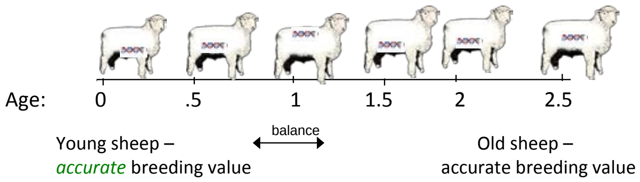


Figure 1. A diagrammatic comparison of the change in relative accuracy of an animals breeding value with age for traditional and genomic selection.

(Breeding value accuracy is depicted by the size of the sheep, smaller sheep being more inaccurate than larger sheep).
Source: Sheep CRC 12K Information Sheet www.sheepcrc.org.au

For traditional selection, where traits can be measured cheaply, on both sexes and before first selection at 18 months of age, such as clean fleece weight and fibre diameter, the accuracy of an ASBV can be high (Table 2). In this situation, even though the additional accuracy gained from genomic testing for some traits is small, there is still substantial accuracy added for several traits that are an important component of the selection index (Table 2). However if selection was to occur at 6 months, the ASBV accuracy is much lower, particularly for traits with lower heritabilities (i.e. staple strength) or those that are expressed at older ages (i.e. adult body weight). In this scenario, adding genomic information to the ASBV prediction substantially increases the accuracy of the ASBV to a level similar to or even higher that of traditional selection at 18 months of age (Table 2). Adding genomic selection to ASBV prediction at 6 months of age is predicted to increase the rate of genetic gain achieved from using a Merino Production index by 12%. The extra rate of genetic gain is a result of higher selection accuracy and reduced generation interval which is associated with more young animals being selected as the ASBV accuracy increases. The benefit of genomic selection is clearly highest for traits that are more difficult to measure and have low heritability and is the greatest for traits that cannot be measured at all (i.e. carcase traits), unless these traits have very high correlations with measured traits.

Table 2. Including genomic selection information into an ASBV can improve the accuracy of an early life ASBV (i.e. at 6 months) to a level similar to that of an ASBV at 18months of age

Ram age at first use	6 months		18 months	
Trait	ASBV	+ Genomics	ASBV	+ Genomics
Yearling clean fleece weight	0.43	0.63	0.67	0.75
Yearling mean fibre diameter	0.54	0.71	0.80	0.84
Yearling staple strength	0.29	0.48	0.46	0.56
Adult body weight	0.51	0.69	0.59	0.72
MP Index	**0.28**	**0.40**	**0.38**	**0.45**

Source: Sheep CRC Genomics tests for Merinos – taking genetic gain to the next level www.sheepcrc.org.au

However the potential to increase the rate of genetic gain via genomics must be balanced against the costs and benefits for individual breeders who invest in the required genotyping and the additional trait measurements. The 12k SNP test, available for $50 with support from the Sheep CRC, can provide genomic information for Australian ram breeders now for a range of economically important traits (Table 3). The predicted benefit from incorporating genomic selection into a Merino breeding program will depend on the variation in genetic merit for profit (measured as the SD of the breeding objective) and the selection accuracy that is being achieved with current (non-genomic) measurement strategies. An important factor is whether breeders are able to mate their young rams within the first year (i.e. at

7 months of age) as genomic information is relatively more beneficial for increasing the breeding value accuracies of younger animals.

Table 3. Trait list for the 12K SNP test to predict genomic breeding values

Trait	Name	Unit
BWT	Birth weight	kg
WWT	Weaning weight	kg
PWT	Post weaning weight	kg
PEMD	Post weaning eye muscle depth	mm
PFAT	Post weaning GR fat	mm
GFW	Greasy fleece weight	%
FD	Fibre diameter	µm
FDCV	Fibre diameter coefficient of variation	%
SL	Staple length	mm
SS	Staple strength	N/ktex
EBWR	Early breech wrinkle	score
FEC	Worm egg count	%
HCWT	Hot carcase weight	kg
CEMD	Carcase eye muscle depth	mm
CFAT	Carcase fat depth	mm
LMY	Lean meat yield	%
IMF	Intra muscular fat	mm
SHEAR5	Shear force at 5 days	kg
DRESSPERC	Dressing percentage	%
POLL/HORN	Poll horn	PP, PH or HH

Source: Sheep CRC 12K Information Sheet www.sheepcrc.org.au

For individual breeders, there are various ways to save on genotyping costs. Firstly, genotyping of females is less efficient due to the lower selection intensity in females. In a Merino dual purpose index, genotyping only males gave 18% more response, while genotyping both males and females gives 22% additional response. Therefore, while genotyping costs are relatively expensive, it is not efficient to genotype females unless some are selected for intensive use via reproductive technologies. Secondly, breeders can apply two-stage selection. At current levels of breeding value accuracy being achieved by Australian Merino ram breeders, genotyping only about 20% of a young sire crop, would give more than 80% of the additional benefits of genomic selection when genotyping all males. If the information added by genomic selection is small, then a smaller proportion should be genotyped. However if traits in the breeding objective are antagonistic or there is low initial selection accuracy a higher proportion of rams would need to be tested to achieve comparable gains. This is particularly true for multi-trait breeding objectives where there are unfavourable correlations between traits in the first stage of selection and the information added in a second stage. It is important to test a larger group than you want to select, as well as choosing rams that represent all sire groups in the flock.

Evaluating the costs and benefits for individual breeders can result in break-even figures for genotyping young males. A critical factor in a cost benefit analysis is the proportion of the benefits that can be recovered by the breeder, as this is typically very low in animal breeding. Under modest assumptions, the break-even price of genotyping did not exceed the actual cost if the breeder recovered only 5-20% of the extra benefit, although these results depend heavily on the efficiency of the operation (i.e. the proportion of young males sold). Modelling of 2- and 3-tier breeding systems, has confirmed that the optimal proportion of males genotyped to be typically around 20%, where the genotyping cost in the nucleus did not exceed 5% of the total additional benefits of genomic selection (Horton *et al.*, 2014).

It is important to remember that the genomic predictions do not replace the need for performance and pedigree information. The three sources of information need to be used together to drive genetic improvement and rates of genetic gain. Research in the next 5 years will focus on enhancing the genomics tests and on developing breeding programs that are cost effective and make the best use of genomics.

The SNP-based Poll Test

The move by Merino breeders towards running poll sheep has been one of the most significant changes in the breed's history. Traditionally, selection for horns in Merino sheep took place on the male side as it provided the animal with a more impressive phenotype (Dominik *et al.*, 2012), however most studs today have pollness as a breeding objective. Horns pose significant animal husbandry, product quality, animal welfare and work health and safety issues. Horned rams are predisposed to a higher incidence of flystrike on their head which can lead significant decreases in production. There is also an increased risk of horned rams being caught up in fences and or having difficulty traversing a race potentially injuring themselves or the attending stockman.

Polledness in sheep is an example of a trait that is controlled by genes at a single locus on the chromosome (Turner and Young, 1969). These types of traits are not affected by either the environment in which the animal lives or by genes at other loci and tend to be discrete in nature – a ram is either polled or horned (Turner and Young, 1969). There are three possible genotypes for poll status in Merino sheep: i. PP – polled; ii. PH – half poll; and iii. HH – horned. An analysis of horn data from a population of Australian Merino sheep mapped the *Horns* locus to a small region on chromosome 10 and identified a SNP in the region that was highly predictive for the polled phenotype (Dominik *et al.*, 2012). This work lead to the development of the SNP-based test by the Sheep CRC that provides *predicted* breeding values for poll status in Merinos. However, as the SNP is not the direct marker or the actual gene causing polled status, these breeding values are predictive only and do not provide an absolute indication of an animal's poll status. Nevertheless, the breeding values can be used to can be used to understand the probabilities of different outcomes when mating PP and HH rams to either horned or polled ewes (Table 4).

Table 4. Probability of progeny phenotype based on predicted sire breeding values for horn status

	Male progeny		Female progeny	
	Horned	Polled	Horned	Polled
When mated to PP 'polled' dams				
PP sire	0.03	0.82	0.01	0.92
PH sire	0.03	0.65	0.01	0.87
HH sire	0.04	0.49	0.01	0.82
When mated to HH 'horned dams				
PP sire	0.03	0.49	0.01	0.82
PH sire	0.37	0.27	0.05	0.50
HH sire	0.70	0.06	0.08	0.18

Source: Sheep CRC Poll Test Information Sheet www.sheepcrc.org.au

Animals with knobs or scurs have been classified as neither polled nor horned and probabilities do not add to 1.0.

Estimates are based on 2,300 Merino progeny in the Sheep CRC IN

Identification of polledness using the SNP-based test only requires sampling of individuals of interest. In most cases this requires sampling of rams and possibly some ewes being selected for the breeding program. The SNP-based Poll Test is suitable for use with all breeds, not just Merinos, and is currently available in Australia at a cost of $17 per sample, however it is also compatible with other SNP-based tests which can reduce the cost of testing if SNP-based parentage or genotyping is also undertaken on rams or lambs within the flock.

Increasing Merino enterprise profitability through improved meat production

Current estimates put the size of the Australian sheep flock at approximately 71.6 million head (ABARES, 2014) which indicates a continuing slow recovery from the historical low levels of the previous decade. When considered with MLA's positive demand projections for the Australian lamb industry for 2014 and beyond, it is clear that meat production from Merinos will remain an important contributor to the profitability of Merino enterprises. In this context a greater understanding of the production and quality of meat produced by Merinos will provide Merino breeders with the required knowledge on how to best include key meat production or quality traits into their breeding objectives.

Limitations of the Merino for meat production

Although an optimal wool producing breed, Merino's do have their limitations in a prime lamb enterprise. They have long been known as a slower-growing smaller mature size breed when compared to terminal breeds such as the Poll Dorset, Texel or White Suffolk. Recent data collected by the Sheep CRC in their Information Nucleus flock has quantified this differential in an Australian context, recording detailed lightweights from birth through to slaughter. When compared to Terminal sired lambs, Merino sired lambs were 0.48 kg lighter at birth, and then 8.29, 9.56 and 14.69 kg lighter at 100, 150 and 240 days of age (Kelman *et al.*, 2014). These lambs were slaughtered across a range of different ages, however when the breeds were slaughtered at the same time the live weight of the Merino lambs (43.2 ± 0.28 kg) was 16 % lighter than Terminal sired lambs (51.4 ± 0.18 kg) (Gardner *et al.*, 2014). The other important limitation of the Merino breed is their dressing percentage (carcase weight/liveweight). Within the same lambs at slaughter Merino's (42.7 ± 0.20 %) were between 3 - 4 dressing percentage units lower than Terminal sired lambs (46.8 ± 0.10 %). These combined differences of lightweight and dressing percentage result in markedly lower carcass weights, with Merino's 5.5 kg lighter than Terminal sired lambs (18.5 ± 0.22 kg compared to 24.0 ± 0.11 kg) (Gardner *et al.*, 2014).

In contrast to the Terminal sire breeds, selection for growth has not been a main focus in the Merino breed. The Australian industry uses breeding values for yearling and post weaning weight (PWT) to select for growth, and this represents a clear opportunity to address the key limitation of the Merino breed, particularly given that selecting for PWT not only increases live weight, but also increases dressing percentage. Thus lambs from high PWT sires had an increased dressing percentage, and this effect was particularly marked in Merino lambs (coefficient = 0.127 ± 0.029 % per unit increase in PWT), with the magnitude being 3 times that of Terminal lambs (coefficient = -0.042 ± 0.040 % per unit increase in PWT) (Gardner *et al.*, 2014).

Merinos have good mean eating meat quality

Although Merinos produce less meat quantity, they have a marked advantage in terms of quality of meat. This was well characterised by Pannier *et al.* (2014a) who assessed the meat quality of 1,086 lambs that were the progeny of Merino (n sires = 61) or Terminal (n sires = 65) sires. Untrained consumers were offered medium cooked samples from the *m. longissimus lumborum* (loin) and *m.semimembranosus* (topside) muscles. Across these two cuts the Merino sired lambs had higher sensory scores than the Terminal sired lambs, with differences of 5.2, 3.9, 3.3 and 2.9 for tenderness, overall liking, juiciness and flavour scores (Pannier *et al.*, 2014a). Selection for rapid lean growth within Terminal sired lambs is likely to explain part of this effect, impacting heavily on eating quality-linked traits such as intramuscular fat (Pannier *et al.*, 2014b). Thus when compared at the same weight Merino sired lambs had more intramuscular fat than Terminal sired lambs (Pannier *et al.*, 2014b). One potential down-side to their meat quality is that Merinos are particularly prone to high ultimate pH meat (Gardner *et al.*, 1999), resulting in darker meat colour which is dry and tough when eaten. This also impacts on retail colour stability making the meat turn brown more rapidly (Calnan *et al.*, 2014). For this reason meat from Merino lambs has reduced retail display time. However, with adequate nutrition, and careful pre-slaughter management, the incidence of high ultimate pH can be minimised.

Genetic correlations – an indicator of intended and unintended consequences of selection

Most traits of economic importance to Merino production systems are quantitative traits - they are controlled by many genes at many loci on the chromosome. Quantitative traits are also affected by the environment in which the animal lives. Therefore differences between geographical locations in factors such as pasture type and availability, seasonal conditions, the incidence of internal and external parasites and disease will result in variation, both between flocks and between animals within a flock, in the phenotypic expression of that trait (Turner and Young, 1969). Genetic correlations provide us with the means to quantify the genetic relationships between traits. They provide us with information on how a second trait is likely to change in time when a first trait is under selection and are therefore a valuable tool for use in Merino breeding programs.

Identifying alternative selection criteria

Genetic correlations allow the identification of alternative selection criteria for expensive or difficult to measure traits. One example is the use of the coefficient of variation in fibre diameter (FDCV) as an alternative selection criterion for staple strength (SS). Measurement of SS is relatively expensive, in Australia the current cost is $11.66 when done in conjunction with a yield test[3]. While it is cost effective to directly measure SS as part of a two-stage selection program for rams, it is generally not cost effective to measure all breeding ewes. Therefore it is necessary to use cheaper, yet effective alternative selection criteria for SS. The genetic relationships between an extensive suite of visual wool quality scores, liveweight and measured wool production and quality traits were estimated for all of the Merino progeny born into the Sheep CRC's IN flock (Table 5). The high negative genetic correlations between CVFD and SS (between -0.61 and -0.70) indicate that these two traits have common genes that control their expression. Therefore FDCV, which is effectively received at no cost as part of the standard FD measurement, is a useful alternative selection criterion for SS.

Table 5 Genetic correlations* between SS, visual wool quality traits, off-shears liveweight & wool production and measured wool quality traits (2008 – 2012 IN shearings)

Visual Wool Quality Scores	YSS	ASS	Liveweight & wool production	YSS	ASS	Measured wool quality	YSS	ASS
Colour	*-0.03*	*-0.09*	OSLWT	*0.19*	*0.16*	FD	0.36	**0.54**
Character	-0.32✓	-0.22✓	GFW	*0.10*	*0.01*	FDSD	**-0.42✓**	-0.29✓
Dust	-0.37✓	-0.21✓	Yield	**0.45✓**	0.36✓	CVFD	**-0.70✓**	**-0.61✓**
Weathering	-0.36✓	-0.33✓	CFW	0.28✓	*0.13*	Curve	*0.15*	*0.06*✓
Fleece rot	-0.22✓	*-0.13*				RTOC	*0.09*	*0.15*
Staple structure	*-0.01*	*0.11*				SL	*0.19*	*0.19*
Handle	-0.25✓	*-0.09*				MID	*-0.17*	*-0.14*
						Y	0.37✓	*0.05*
						(Y-Z)	*0.14*	**0.68**

Source: (Hatcher and Preston, 2013)

* Negligible correlations (i.e. <0.2) are in *italics* text, low correlations (i.e. 0.2 – 0.4) are in normal text, medium correlations (i.e. 0.4 -0.6) are in bold text and high correlations (i.e. >0.6) are shaded. A ✓ indicates a favourable genetic relationship.

Quantifying correlated responses in other traits

Genetic correlations also allow us to predict the consequences of selection for one trait on other traits of interest. SS is only one of a suite of wool quality traits that impact on the price paid for wool, so selection decisions must be made on the full array of traits that impact on Merino enterprise profitability. It is therefore, important to take into account the genetic relationships with other traits including liveweight, wool production and both visual and measured wool quality. The genetic correlations estimated from the Sheep CRC's IN between YSS and YFD and YSS and AFD were both low (0.36 and 0.23 respectively), while those between ASS and YFD and ASS and AFD were both moderate (0.48 and 0.54 respectively). These estimates are indicative of an unfavourable genetic relationship between SS and FD such that *genetic selection for increased staple strength will lead to broader fibre diameter*. However, such unfavourable or antagonistic genetic relationships can be effectively accounted for through the use of an appropriate selection index.

With the exception of FD and clean colour (Y-Z), all of the significant genetic correlations between SS and other wool production and quality traits were favourable (Table 5). Selection for increased SS will generate:

i. little to no correlated improvements in greasy wool colour (i.e. whiter wool), staple structure (i.e. finer staple bundles), off-shears liveweight, GFW, fibre curvature (Curve), resistance to compression (RTOC), staple length (SL) or the percentage of midbreaks (MID);
ii. small improvements in character (i.e. better defined and more consistent crimp frequency), dust penetration (i.e. less penetration of dust along the staple), fleece rot (i.e. decreased incidence of bacterial staining) and CFW,
iii. moderate improvements in staple weathering (i.e. reduction in visible weathering at the tip of the staple and deterioration of fibre structure), yield, FDSD and Y (i.e. brightness) and;
iv. large correlated improvements in CVFD (as discussed previously).

---

[3] AWTA Raw Wool Testing Fees 2012/13

Merino breeding objectives are currently being expanded to include a wider range of traits. Breeders are looking to simultaneously improve the wool production, wool quality, growth and meat production of their flock as well as aspects of reproduction including both ewe and lamb traits. In this context, quantifying the genetic correlations between trait groups becomes increasingly important. Examples of other key correlations identified by scientists working with the Sheep CRC's IN and their implications for Merino breeding programs include those between:

i lamb survival and meat traits
  - positive *favourable* genetic correlations have been estimated between indicators of carcase lean meat yield (tissue depth at the GR site and eye muscle depth, 0.34 ± 0.05 and 0.17 ± 0.07 respectively) with lamb survival
  - *unfavourable* genetic correlations exist between lamb survival and both lean meat yield (-0.33 ± 0.06) and shear force (i.e. tenderness) (0.27 ± 0.07)
  - this means that selection programs that enhance lean meat yield and increase tenderness will need to consider the possibility of small correlated genetic losses in lamb survival (Brien *et al.*, 2013). Although this risk could be managed through appropriate index selection as the unfavourable correlations were low.

ii feed intake and growth rate
  - there are low positive *unfavourable* genetic correlations between feed intake (measured as relative digestible dry matter intake rDDMI) and birth weight (0.12 ± 0.08), weaning weight (0.12 ± 0.08) and hogget weight (0.18 ± 0.08)
  - these low genetic correlations between growth traits and feed intake mean that feed intake can be included as a component of a selection index to achieve simultaneous improvement in both traits thus reducing the feed costs required to maintain the ewe flock and replacements without compromising lamb growth rates (Safari *et al.*, 2007).

iii flystrike indicator traits and production traits
  - genetic correlations between flystrike indicator traits and Merino production traits range from moderately *unfavourable* (eg early breech wrinkle and yield -0.38) to moderately *favourable* (eg early breech cover and yearling liveweight -0.33)
  - this range in genetic correlations between flystrike indicator traits and Merino production traits indicate that selection to reduce flystrike through indirect selection criteria (including wool cover, skin wrinkle, dags, wool colour and fleece rot) needs to be carefully applied through appropriate selection indexes which improve flystrike resistance and production simultaneously (Brown *et al.*, 2010).

iv feed intake and production traits
  - genetic correlations between feed intake (rDDMI) and various wool (greasy fleece weight, clean fleece weight and fibre diameter), reproduction (litter size and number of lambs born per ewe joined), carcase (hot carcase weight, ultrasound fat and muscle depth, dressing percentage) and meat quality traits were close to zero
  - these genetic correlations suggest that feed requirements of ewes can be reduced by selection, although ewe weight and growth would also decline unless accounted for in a selection index (Fogarty *et al.*, 2009).

v carcase, wool, internal parasites and reproduction traits
  - fat and eye muscle depth had small to moderate genetic correlations with most traits, with positive correlations with liveweight, fibre diameter, fibre curvature and ewe reproduction and negative correlations with fleece weight, fibre diameter coefficient of variation, worm egg count and breech wrinkle
  - these genetic correlations indicate that desirable genetic progress can be made in wool, carcase, internal parasite resistance and numbers of lambs born and weaned simultaneously however multiple selection approaches are required to account for the mix of favourable and unfavourable correlations between these traits (Brown and Swan, 2014).

vi lamb survival and wool production and quality
  - lamb survival at birth, to 3 days of age and to weaning was negatively genetically associated with lower greasy and clean fleece weights measured as yearlings and adults

- selection for whiter greasy colour, consistent well defined crimp and a decreased incidence of fleece rot as yearlings (i.e. lower scores) will lead to correlated improvements in lamb survival due to *favourable* genetic correlations between these traits
- selection for finer yearling fibre diameter will lead to correlated decreases in lamb survival to both 3 days of age and weaning while selection for decreased variation in yearling fibre diameter (i.e. lower FDCV) will generate correlated increases in lamb survival at birth and to both 3 days of age and weaning
- the genetic correlations between wool production and quality traits and lamb survival vary from *unfavourable* to *favourable* therefore as per the correlations reported above between the various trait groups multiple selection approaches will be necessary to achieve overall genetic progress in the key traits of interest (Hatcher *et al*., *unpublished data*)

These examples of key genetic correlations between traits groups are a key resource to enable a greater understanding of the relationships between all key elements important to Merino production systems – wool production, wool quality, reproduction, lamb survival and growth, carcase weight and meat quality as well as resistance to both internal and external disease. It is clear that the genetic relationships between these key elements are a combination of both favourable and unfavourable genetic correlations and all must be taken account of in a Merino breeding program. A common theme of all the cited research is that multiple selection approaches, such as combining traits in a selection index, are required to adequately account for the mix of favourable and unfavourable genetic correlations and ensure that genetic progress is made in the key traits of economic interest without compromising the ‘fitness’ of the Merino.

When and how often to measure a trait to maximise genetic gain

Genetic correlations between repeated measures of a trait across ages, such as those between early age measurements and later performance provide reliable information as to when it is best to measure a trait and how often measurement is required. (Brown *et al.*, 2013) found that assessments for greasy fleece weight made on young animals (i.e. at yearling stage) are good predictors of adult performance as the genetic correlations between greasy fleece weight from yearling to 6 years of age were all high (i.e. 0.62 to 0.81). In fact, as the genetic correlations between the adult expression of greasy fleece weight were all higher than 0.8, they could be treated as the same trait. The same conclusions were made for fibre diameter measurement at different ages. (Swan and Brown, 2013) used these correlations between early age measurements and later performance in three different selection indexes and adding a single adult measurement of both fleece weight and fibre diameter increased the economic gain compared to measuring yearling expressions of the traits alone. The increase in gain for fibre diameter was lower about 35% lower because the genetic correlations between yearling and adult fibre diameter were higher than those for fleece weight. As MERINOSELECT, the Australian Merino industry’s genetic evaluation service, already accommodates one adult measurement most of the gains possible could be realised by breeders (Swan and Brown, 2013).

However, Swan and Brown (2013) identified that there was a limitation on the genetic gain that could be made in adult wool traits due to the fact that measurement takes place *after* the most intense selection point (i.e. the selection of young rams) and only on females selected for breeding. Therefore genomic selection of young rams can result in further increases in genetic gain when combined with adult measurement, particularly for fleece weight (Swan and Brown, 2013).

Novel wool traits to increase global demand for wool

The growing casual markets for trans-seasonal knitwear, sports and leisurewear present a key opportunity to increase the global demand for wool. However, these market segments require bright, white and pastel shade products (Millington *et al.*, 2012) and wool’s major competing fibres in these markets, cotton and polyester, are both significantly brighter and whiter than wool (Fleet *et al.*, 2010). Therefore, wool destined for use in white or pastel shade garments is always bleached during processing (Millington *et al.*, 2012) which can have detrimental effects on both the handle (softness) (Millington and King, 2010) and photostability (Millington *et al.*, 2012) of the finished fabric. The Sheep CRC has developed improved processing technology to improve both the whiteness and photostability (colour fastness of the final garment). The EverWhite Wool process allows new light-stable wool products in bright whites and pastel shades to be processed and manufactured by the application of a UV absorber using a novel application method that maintains the initial whiteness of wool and confers highly improves photostability during exposure to sunlight (Millington, 2013).

An alternative to the processing solution is genetic selection for brighter, white more photostable wool. However, while an objective test method of brightness and whiteness was developed in the mid 1980s (International Wool Textile Organisation, 2003), it was necessary to develop a test method to accurately measure the photostability of large numbers of small fleece samples. The solution was to develop an apparatus capable of irradiating up to 48 scoured wool samples that had been packed into PMMA cuvettes with a UVB (280 – 320nm) light source which ensured that all samples regardless of initial yellowness were following exposure and avoided photobleaching (Millington and King, 2010). Measuring the brightness and whiteness of the scoured sample before and after 4 hours of UVB irradiation allowed the photostability of brightness (i.e. ΔY) and whiteness (i.e. Δ(Y-Z)) to be quantified.

Measurement of the Sheep CRC IN Merino progeny for brightness, whiteness and photostability and analysis of that data found that brightness (Y) is a low to moderately heritable trait (0.20 and 0.36 for yearling and adult animals respectively), clean colour (Y-Z) is highly heritable, (0.58 and 0.80) and the photostability of both brightness (ΔY) and clean colour (Δ(Y-Z)) are lowly heritable (less than 0.03 and 0.17 respectively, Hatcher and Preston, unpublished). Therefore while each of the traits will respond to selection, the predicted genetic responses to selection in Y, (Y-Z), ΔY and Δ(Y-Z) from using common Merino selection indexes over a 10-year period were significantly lower than that required to replace the routine use of oxidative bleaching during wool processing (Hatcher *et al.*, 2013). Nevertheless, as innovations in product development and processing technology further increase the penetration of wool into the casual trans-seasonal markets which require bright, white photostable wool, premiums for such wool may arise which will increase the relative economic value of these traits and their importance in selection indexes thus increasing the genetic response. Until then the EverWhite Wool process provides the means for wool to effectively compete with cotton and synthetic fibres in the trans-seasonal knitwear, sports and leisurewear markets.

Conclusion

New research products can help Merino breeders to deal with the challenges associated with the increasing number of traits of importance in breeding the 'modern Merino' able to capitalise on opportunities in markets for wool, and sheepmeat as well as being easier to manager through being resistant to parasites and well adapted to the environment.

Acknowledgements

The Sheep CRC was supported by the Australian Government's CRC program, Australian Wool Innovation Ltd and Meat & Livestock Australia. Considerable staff and resources were also provided by the partner organisations at each IN site: NSW Department of Primary Industries, University of New England, Department of Primary Industries Victoria, SA Research and Development Institute and the Department of Agriculture and Food WA. We acknowledge the large and dedicated team of scientists and technical staff at each of the Sheep CRC IN sites who were responsible for the management of the animals at each site and the collection of the vast amount of data on all aspects of sheep production.

References

ABARES (2014).Agricultural Commodities: March Quarter 2014 Vol. 4 No. 1: Department of Agriculture, Australian Government.

Alexander, G., Stevens, D. & Mottershead, B. (1983). Problems in the accurate recording of lambing data. *Australian Journal of Experimental Agriculture* 23(123): 361-368.

Australian Wool Innovation & Meat and Livestock Australia (2013). *Visual Sheep Scores - Researcher Version.* Australian Wool Innovation and Meat & Livestock Australia.

Bell, A. M., Henshall, J. M., Gill, S., Gore, K. P. & Kijas, J. W. (2013). Success rates of commercial SNP based parentage assignment in sheep. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 20: 278 - 281.

Brien, F. D., Rutley, D. L., Mortimer, S. I. & Hocking-Edwards, J. E. (2013). Genetic relaitonships between lamb survival and meat traits. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 20: 237 - 240.

Brown, D. J. & Swan, A. A. (2014). Genetic importance of fat and eye muscle depth in modern Merino breeding programs. *Unpublished data*.

Brown, D. J., Swan, A. A. & Gill, J. S. (2013). Genetic correlations across ages for greasy fleece weight and fibre diameter in Merino sheep. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 20: 110 - 113.

Brown, D. J., Swan, A. A. & Graser, H. U. (2010). Genetic relationships between indicator traits for fly strike resistance and production traits in Merino sheep. *Proceedings of the 9th World Congress on Genetics Applied to Livestock Produciton*: 0924.

Brown, D. J., Swan, A. A. & Mortimer, M. L. (2011). Pedigree MatchMaker: can it tell us more than just pedigree? *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 19: 231 - 234.

Calnan, H. B., Jacob, R. H., Pethick, D. W. & Gardner, G. E. (2014). Factors affecting the colour of lamb meat from the longissimus muscle during display: The influence of muscle weight and muscle oxidative capacity. *Meat Science* 96(2, Part B): 1049-1057.

Clark, S. A., Hickey, J. M., Daetwyler, H. D. & van der Werf, J. H. J. (2012). The importance of information on relatives for the prediction of genomic breeding values and the implications for the makeup of reference datasets in livestock breeding schemes. *Genetics Selection Evolution* 44: 4.

Curtis, K. (2009) Recent changes in the Australian sheep indusry (The disappearing flock). Department of Agriculture and Food, Western Australia.

Dominik, S., Henshall, J. M. & Hayes, B. J. (2012). A single nucleotide polymorphism on chromosome 10 is highly predictive for the polled phenotype in Australian Merino sheep. *Animal Genetics* 43(4): 468-470.

Fleet, M. R., Millington, K. R. & King, A. L. (2010). Sunlight exposure caused yellowing and increased mineral content in wool. *Animal Production Science* 50(4): 300-308.

Fogarty, N. M., Safari, E., Mortimer, S. I., Greeff, J. C. & Hatcher, S. (2009). Heritability of feed intake in grazing Merino ewes and the genetic relationships with production traits. *Animal Production Science* 49: 1080-1085.

Gardner, G. E., Kennedy, L., Milton, J. T. B. & Pethick, D. W. (1999). Glycogen metabolism and ultimate pH of muscle in Merino, first-cross, and second-cross wether lambs as affected by stress before slaughter. *Australian Journal of Agricultural Research* 50(2): 175-181.

Gardner, G. E., Williams, A., Ball, A. J., Jacob, R. H., Refshauge, G., Hocking Edwards, J. E., Behrendt, R. & Pethick, D. W. (2014). Carcase weight and dressing percentage are increased using Australian Sheep Breeding Values for increased weight, and musclinig and fat depth. *Meat Science* Submitted.

Hatcher, S. & Preston, J. M. V. (2013).Staple strength - What have we learnt from the Sheep CRC's Information Nucleus? In *Sheep Produciton Seminar*, 21 - 30 (Ed P. G. Refshauge). Cowra, New South Wales: Australian Society of Animal Production - Southern NSW Branch.

Hatcher, S., Preston, J. M. V. & Millington, K. R. (2013). Can selection for brighter, whiter more photostable wool replace oxidative bleaching during processing? *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 20: 53 - 56.

Horton, B. J., Banks, R. G. & van der Werf, J. H. J. (2014). Industry benefits from using genomic information in two- and three-tier sheep breeding systems. *Animal Production Science*: http://dx.doi.org/10.1071/AN13265

International Wool Textile Organisation (2003).Method of the measurement of colour of raw wool IWTO-56-03., 29 Ilkley, United Kinddom International Wool Textile Organisation.

Kelman, K. R., Alston, C. L., Pethick, D. W. & Gardner, G. E. (2014). Genetic and non-genetic factros impacting growth in lambs. *Animal* Submitted.

Kijas, J. W., Lenstra, J. A., Hayes, B. J., Boitard, S., Porto Neto, L. R., San Cristobal, M., Servin, B., McCulloch, R., Whan, V., Gietzem, K., Paiva, S., Barendse, W., Ciani, E., Raadsma, H. W., McEwan, J. C. & Dalrymple, B. (2012). Genome-wide analysis of the world's sheep breeds reveals high levels of historic mixture and strong recent selection. *PLoS Biology* 10(2): e1001258.

Kijas, J. W., Townley, D., Dalrymple, B., Heaton, M. P., Maddox, J. F., McGrath, A., Wilson, P., Ingersoll, R. G., McCulloch, R., McWilliam, S., Tang, D., McEwan, J. C., Cockett, N., Oddy, V. H., Nicholas, F. W. & Raadsma, H. W. (2009). A genome wide survey of SNP variation reveals the genetic structure of sheep breeds. *PLoS One* 4(3): e4668.

Millington, K. R. (2013). EverWhite Wool Technical Information. Sheep CRC and CSIRO Materials Science & Engineering.

Millington, K. R., Giudice, M. d., Hatcher, S. & King, A. L. (2012). The effects of bleaching on the photostability of white fleece wools. *The Journal of the Textile Institute* 104(6): 655-660.

Millington, K. R. & King, A. L. (2010). Measuring colour and photostability of small fleece wool samples. *Animal Production Science* 50: 589-592.

Moghaddar, N., Swan, A. A. & van der Werf, J. H. J. (2014). Genomic prediction of weight and wool traits in a multi-breed sheep population. *Animal Production Science* 54(5): 544-549.

Pannier, L., Gardner, G. E., Pearce, K. L., McDonagh, M., Ball, A. J., Jacob, R. H. & Pethick, D. W. (2014a). Associations of sire estimated breeding values and objective meat quality measurements with sensory scores in Australian lamb. *Meat Science* 96 (2, Part B): 1076-1087.

Pannier, L., Pethick, D. W., Geesink, G. H., Ball, A. J., Jacob, R. H. & Gardner, G. E. (2014b). Intramuscular fat in the longissimus muscle is reduced in lambs from sires selected for leanness. *Meat Science* 96 (2, Part B): 1068-1075.

Richards, J. S. & Atkins, K. D. (2004). Simultaneous assortment of animals for meat and wool production in Merino flocks. *International Journal of Sheep and Wool Science* 52(3): 193-201.

Richards, J. S. & Atkins, K. D. (2007). Determining pedigree by assocaition in Merino flocks. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 17: 403 - 406.

Richards, J. S., Atkins, K. D., Mortimer, M. & Semple, S. J. (2006).Pedigree assignment by electronic matching of lambs and dams. In *Australian Society of Animal Production*, Short Communication Australian Society of Animal Production.

Russell, A. J., Mortimer, S. I., Murray, W., Atkins, K. D. & Taylor, P. (2006).The costs and benefits of improving selection accuracy in Merino studs. In *Trangie QPLU$ Merinos - Open Day 2006*, 19 - 26 (Ed C. E. Pope). Trangie, NSW: NSW Department of Primary Industries.

Safari, A., Fogarty, N. M., Mortimer, S. I., Greeff, J. C., Hatcher, S., Lee, G. J. & Gilmour, A. R. (2007).Feed intake and its genetic relationship with growth traits in Merino sheep. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 17: 199-202.

Swan, A. A. & Brown, D. J. (2013). The impact of measuring adult fleece traits with genomic selection on economic gain in Merino selection indexes. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 20: 233 - 236.

Swan, A. A., Johnston, D. J., Brown, D. J., Tier, B. & Graser, H.-U. (2012). Integration of genomic information into beef cattle and sheep genetic evaluations in Australia. *Animal Production Science* 52(3): 126-132.

Turner, H. N. & Young, S. S. Y. (1969).Quantitative genetics in sheep breeding. Victoria: Macmillan of Australia.

van der Werf, J. H. J., Kinghorn, B. P. & Banks, R. G. (2010). Design and role of an information nucleus in sheep breeding programs. *Animal Production Science* 50(12): 998 - 1003.