

Genetic aspects of lifetime productivity in Merinos

A review commissioned by Australian Wool Innovation

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Summary

Industry concerns have been expressed on a range of issues related to lifetime productivity in Merinos, reinforced by a trend towards selecting animals at a very young age. Although the average age of recording has declined in recent years, selection of rams at 9-12 months with only six months of wool has been practiced since the mid-1970s. Research into the reliability of early records for predicting lifetime performance has been a feature of genetic research on Merinos for over half a century, with an increased emphasis since about 1987.

Bio-economic modelling indicates that with current prices for wool and meat, profitability in a self-replacing Merino flock is optimal with 5-6 age groups of breeding ewes. More age groups are optimal when prices for meat are high relative to wool, and fewer age groups are optimal when prices for wool are high relative to meat, or ewe mortality rates are high. Consequently, productivity up to 6-7 years of age is of direct interest.

Some of the earliest estimates of age effects on fleece weight published over 40 years ago are similar to those estimated recently, with fleece weights peaking at 3-4 years. Average FD¹ peaks at 5-6 years and CVFD peaks at 4-5 years. Preliminary information suggests that components of wool style deteriorate between two and four years of age; and that parturition and lactation cause most components of style to deteriorate. Net reproduction rate (NLW) peaks in Merinos at about 5-6 years of age – a consequence of litter size increasing till about 6-7 years, fertility peaking at about 4-5 years and NLB peaking at about 6 years of age.

In data derived from research and industry flocks, between-age genetic correlations for CFW and FD are high but imperfect. Yearling-adult correlations are lower than correlations between different adult expressions. Information currently contained in the Sheep Genetics database could be used to estimate parameters involving ages younger than a year. The increase in average FD after the first year (micron blow-out) is heritable but estimates of the genetic relationship between blow-out and mean FD are variable.

Research indicates that supplementing yearling fleece weight records with one adult record can lead to additional genetic gains across a range of micron premiums. Including an adult FD measure is only likely to be worthwhile when the objective is to reduce average diameter. Across-age correlations in other fleece characteristics have been less well researched. However, breeders concerned about changes in fleece attributes across ages should be encouraged to submit adult fleece records to help monitor and manage such changes. In the absence of (as well as in the presence of) adequate adult records, genomic selection offers the promise of increased gain in adult wool traits, provided the appropriate information is available for developing predictions. Good quality records of pedigree and lambing/rearing performance are needed to optimise genetic evaluation and particularly to make meaningful genetic progress in net reproduction rate. As only 18% of Merino flocks participating in Sheep Genetics provide reproduction records, this is a serious limitation.

¹ See page 6 for explanation of trait abbreviations.

Theoretical predictions, backed by observations with field data, indicate that no one experimental resource flock is likely to go anywhere near providing sufficient information to support precise estimates of between-age genetic correlations in reproduction rate, unless records are accumulated over 20 or 30 years. Even then, they are only likely to provide sufficient power for single estimates pooled across all genotypes; and would certainly be inadequate to detect differences in estimates between sub-sets of the flock (such as different sheep types or breeding philosophies). Consequently there is a paucity of reliable information in Merinos, but estimates of correlations involving two years and older in industry data from other breeds (principally meat-producing) appear to be high for litter size, NLB and NLW.

Relationships between wool production, reproduction, body weight and energy balance are complex and not fully understood. Phenotypic associations between fleece weight and lifetime reproductive performance suggest that the cumulative physiological load of reproduction can depress fleece production. However, the finding that lifetime reproductive success and early fleece measurements are not adversely associated supports the proposition that at the genetic level, the relationship between reproduction and wool production is not intrinsically unfavourable. Rather, both activities compete for energy resources and over a number of reproductive cycles this can become manifest as a small but negative genetic correlation – importantly, not large enough to preclude simultaneous genetic gains in both traits. However it is important that this adverse correlation is accommodated in genetic evaluation and that the full cost of reproduction (in terms of feed intake and other productivity foregone) is recognised.

Irrespective of the state of knowledge regarding physiological mechanisms, traits can be accommodated appropriately in a genetic improvement program if: a) all traits of importance and their associated costs are identified and included correctly in the breeding objective; b) genetic predictions are underpinned by sufficiently precise estimates of genetic associations among traits of importance; and c) appropriate phenotypic information is recorded.

Estimates of the effects of ewe age on progeny body weights appear to be relatively consistent across breeds and over time, being most pronounced for birth weight and declining in importance through to hogget age. Six-year old ewes tend to have the heaviest lambs at birth and five-year old ewes tend to have heaviest progeny at subsequent ages. Ignoring maternal genetic effects in genetic evaluation will lead to sub-optimal gains, but if an unfavourable correlated response in maternal effects on body weight occurs at all, data suggest that it is not likely to be large enough to be of concern. Conversely, including maternal genetic effects in genetic evaluation when there is inadequate data to estimate them properly, can lead to erroneous conclusions.

Research to date indicates that in the context of lifetime performance, selection for reduced WEC is best practiced in young sheep, but the most effective age between weaning and yearling is the subject of current research by Sheep Genetics. The genetics of age effects on susceptibility to other parasites and diseases in Merinos is not well-researched, though observations in breech strike selection lines suggest that weaners tend to be the most susceptible, followed by breeding ewes then yearlings. Until recently, little work has been done to pursue research done over 30 years ago that identified adverse associations between skin wrinkle and many components of lifetime reproduction.

Any attempts to establish additional research or demonstration flocks to specifically examine lifetime fleece weight / reproduction rate relationships at the genetic level, should be made with the awareness that estimating reliable genetic parameters involving reproduction requires very large amounts of phenotypic data. This means either an extremely large commitment for several years or a more modest commitment over a number of generations. The alternative of using existing information supplemented with well-recorded information from industry flocks is likely to be more cost-effective. Industry data has the added advantage of being unambiguously current and relevant; but obviously data quality is a consideration.

Recommendations (Suggested priorities: M – medium ; H – high)

- 1) With the approval and co-operation of the various institutions, all relevant historical research data should be included in the Sheep Genetics database as soon as possible, where it is likely to be far more accessible, useful and secure (H).
- 2) The Sheep Genetics database, when fully supplemented with data from research and demonstration flocks, should be used as a resource for further research into the genetic and phenotypic associations between lifetime reproduction and other traits (H).
- 3) The consolidated database should be used to test a number of hypotheses, including whether:
 - a) age effects differ between lines of sheep. Such analyses may provide some insight into whether or not certain strains of sheep are more predisposed to early declines in productivity (M)
 - b) fleece measurements recorded earlier than the current threshold used by Sheep Genetics (contemporary groups with a mean age of less than 232 days) are sufficiently reliable (H)
 - c) age-age correlations for NLW and its components are as high as currently assumed (M-H)
 - d) genetic associations between yearling and hogget fleece characteristics and lifetime reproductive performance can be estimated with better accuracy (M-H)
 - e) genetic associations involving lifetime reproduction rate differ in low fleece weight and high fleece weight animals (M-H).
 - f) the proposition can be substantiated that Merino strains with high wool production have lower lifetime reproduction rates (M).
- 4) Strategies to exploit the repeatable nature of reproductive performance and the possibility of tailoring management of different flock segments (based on their reproductive performance) warrant further investigation (M).
- 5) The current practice in Sheep Genetics of predicting EBVs for fleece weight and reproduction in separate analyses warrants re-examination, as the two are inter-related, albeit not strongly at the genetic level (H).
- 6) The potential for also including wrinkle score in genetic evaluation of lifetime reproductive performance should be monitored as more data are accumulated from research and industry flocks (M-H).
- 7) The sensitivity of MERINOSELECT rankings to changes in assumed genetic associations and economic weights should be considered. In particular, it is not

clear whether or not the full costs of increasing fleece weight and body weight are adequately accommodated in MERINOSELECT (H).

- 8) There is a strong case for devoting resources to documenting and publishing the methodology and assumptions behind MERINOSELECT. Documentation facilitates proper peer review and can be used in extension to help build confidence in the indexes (H).
- 9) Breeders should be encouraged to submit more records from adult sheep for the purposes of genetic evaluation. Predicted outcomes at various ages for different measurement strategies, especially multiple-stage selection, should be included in extension material to provide encouragement. This would have the added advantage of enabling better estimates of the relevant genetic parameters (H).

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Abbreviations

Trait abbreviations use in this report:

BWt	birth weight
WWt	weaning weight
YWt	yearling weight
HWt	hogget weight
AWt	adult weight
CFW	clean fleece weight
CURV	fibre curvature
CVFD	coefficient of variation of fibre diameter
FD	average fibre diameter
GFW	greasy fleece weight
SDFD	standard deviation of fibre diameter
SS	staple strength
YLD	clean scored yield
EL/EJ	ewes lambing per ewe joined (fertility)
LB/EL	lambs born per ewe lambing (litter size)
LB/EJ	lambs born per ewe joined (number of lambs born or NLB)
LW/EJ	lambs weaned per ewe joined (net reproduction rate or NLW)
LW/LB	lambs weaned per lamb born (lamb survival)
WEC	worm egg count

Prefixes used by Sheep Genetics:

Age name	Abbreviation	Range	Approximate age
Birth	B	birth to 24 hours	
Weaning	W	42 to 120 days	6 to 17 weeks
Early post weaning	E	120 to 210 days	4 up to 7 months
Post weaning	P	210 to 300 days	7 up to 10 months
Yearling	Y	300 to 400 days	10 up to 13 months
Hogget	H	400 to 540 days	13 up to 18 months
Adult	A	540 days or older	18 months or older

(<http://www.sheepgenetics.org.au/Getting-started/How-to-use-the-databases/Age-trait-abbreviations>)

Introduction

The issue of lifetime productivity in Merino genetic improvement programs has recently come under scrutiny by the Merino industry. According to G. Lindon (*pers. comm.*), this is being stimulated by a number of factors:

- A trend for ram breeders to assess rams at less than ten months of age and as young as 8-9 months, using early fleece weight and fibre diameter information to sell rams at 13-14 months rather than 15-16 months
- An increase in the practice of joining rams and ewes at seven months of age
- Recent focus on meat prices and reproduction rates
- Interest in plainer-bodied sheep which don't require mulesing
- The historically high proportion of ewes in the national flock
- The introduction of genomic selection, which facilitates selection at very young ages, well before adult performance becomes evident.

Concern has been expressed that a reduction in the average age of selection may have the unintended consequence of breeding animals that excel in their early years to the detriment of lifetime productivity.

The idea that selection for productivity might lead to unexpected and unwanted changes in other traits is not unique to the Merino industry. Rauw (*et al.* 1998) cited over 100 reports of undesirable (cor)related effects of selection for high production efficiency, with respect to metabolic, reproduction and health traits, in broilers, pigs and dairy cattle. Indeed, the effects of selection in farm animals on fitness was the subject of a relatively recent symposium in Armidale (van der Werf *et al.*, 2009). The consensus around correlated responses was perhaps best articulated by J.W. James² when summarising one of the sessions (box):

“What is important in animal breeding is the productivity and profitability of livestock, and therefore breeders need to consider how components of fitness such as reproductive rate and viability contribute to the economic value of a population. Provided this is done properly, all relevant aspects of fitness will be taken into account”. J.W. James (in van der Werf et al., 2009).

The above comments by J.W. James apply of course to lifetime productivity, which is closely aligned with fitness³ through its influence on reproductive success, either directly or indirectly through culling decisions⁴.

² Pages 53-55 of proceedings.

³ As pointed out by J.S.F. Barker (pages 3-14 of proceedings), there is no universally accepted definition of “fitness”, but for the purpose of this review, the dictionary definition is adequate, viz: “Ability to survive and reproduce in a particular environment”

⁴ M.E. Goddard (page 126 of proceedings) aptly noted that “...In domestic populations, selection is not for natural selection but for some combination of traits decided by the breeder”.

According to ABARES (2013), ewes currently comprise approximately 80% of the adult sheep flock – an increase from about 60% in the early 1990s. Consequently, the productivity of ewes is even more important now than in the recent past. It is thought that in most modern commercial production systems, the productive lifetime for breeding ewes generally ends when they are removed from the flock around 6 years of age, following 5 annual lambing opportunities. In other words, the typical flock today has a ewe age structure similar to the optimal identified by researchers almost fifty years ago (see Brown *et al.* 1968). Aged ewes may sometimes stay in an individual flock (or national flock), for one or two more lambing opportunities during periods of flock build-up, or for mating to non-Merino rams for prime lamb production. Given that most selection decisions are made when breeding stock are less than two years old, with a trend towards selecting in their first year, the question is whether the animals being chosen have the genes for high production through a typical lifespan.

This review is intended to examine whether we are in fact considering lifetime productivity adequately in Merino breeding programs, and to assess whether the current state of knowledge is sufficient to predict or manage any potentially unfavourable consequences arising from typical selection practices.

What is lifetime productivity?

In the commissioning of this review, lifetime productivity was defined as “the net productivity of sheep whilst they remain in the flock, with an emphasis on ewe productivity”. However, this definition is not entirely satisfactory because there is no standard duration over which sheep remain in a flock. Essentially ewes are no longer part of the flock when they die from natural causes or are removed as the result of a management decision. Thus the main determinants of productive lifespan are mortality rate and culling decisions, both of which will vary for numerous reasons, some of which have little to do with genetics.

In some circumstances there can be little ambiguity about the meaning of lifetime productivity. For example, Rose (1982) reported that in order to maintain flock numbers many producers in north-west Queensland did not cull or cast for age. Under such conditions, almost all sheep would either die of natural causes or predation. Their lifetime is determined almost entirely by their fitness and random misadventure.

However, when on-farm mortality rates are not the sole determinant of an animal's lifetime expectancy, it is reasonable to assume that flock-owners will structure their flock in a way that maximises their profitability. For ram breeders this might mean that they favour an age structure that optimises rate of genetic gain for a given investment in recording, in anticipation of ram buyers valuing genetic worth. Commercial producers, however, will logically favour a flock structure that maximises current flock profitability, perhaps also taking into account the effects of age structure on future flock productivity.

It is worth examining the impact of the age structure of a ewe flock on productivity, as this will give some guidance as to the maximum age at which we should be interested in performance. For example, if ewes have their first parturition as two-year olds and it

turns out that profitability is maximised with three ewe age groups, then ewe performance beyond five years of age will be inconsequential in an optimally-structured flock.

Turner *et al.* (1968) showed in some detail the calculations and assumptions required to determine the optimal age structure of a Merino breeding ewe flock, in the special situation where the total breeding flock size is maintained from year to year. They noted that changes in age structure can affect productivity in six different ways:

Selection differential - as the number of ewe age groups increases, fewer replacements are needed annually. This in turn allows greater selection pressure to be applied when choosing replacements which leads to increased lifetime production of the current flock as well as increased genetic gain in the next generations

Generation length - the greater the average age of breeding animals, the longer the generation interval, which can impact on annual rate of genetic improvement

Surplus animals - the age structure of a flock affects the number of young animals that are not needed as replacements and also the number that are cast for age

Lamb production - reproduction rate varies with age, which directly impacts on the number of lambs produced

Wool production - wool growth and quality change with age and so the flock average (in terms of wool cut and wool quality) will vary with age structure

Environmental influences - wool quantity and quality are typically influenced by pregnancy, lactation, type of birth and age of dam. The proportions of ewes with different lambing status and with different maternal handicaps will vary with age structure, which in turn influences flock productivity.

As can be seen from Turner *et al.* (1968), the calculations required to determine an optimal age structure under any particular set of assumptions are actually very detailed⁵. For the range of inputs that they examined however, the general conclusion was that for a self-replacing flock breeding its own rams, two ram age groups and five ewe age groups of breeding ewes⁶ gave maximal returns under most conditions. Furthermore, using prices prevailing at that time, total flock returns from wool only declined by 1-2% for each additional ewe age group retained up to nine, which was the maximum that they considered⁷. The decline was greater when peak reproduction rate was earlier and less when ewe death rates were high. Beyond this standard flock model, the possibilities were considered too numerous to assess individually, but they did go on to describe the additional considerations that need to be taken into account with other situations, including flocks in which:

- rams are retained on genetic merit rather than culled at a fixed age;
- rams are subject to a preliminary culling at weaning;
- rams are purchased rather than bred within the flock;
- selection is beginning; and

⁵ These calculations are also included in Chapter 16 of the book by Turner and Young (1969)

⁶ The five age groups being 1½-2½ years through to 5½-6½ years so that ewes were cast for age at 6½ years.

⁷ Data from the Yalanbee “Natural Selection” flock run in south-western WA indicated that no ewes contributed more than 12 annual fleece weight records and very few lambs had a dam that was more than 11 years old – see Appendix 1

- inbreeding effects are accounted for.

Turner *et al.* (1968) did not consider a situation where ewes are also culled on current flock performance rather than age, as is practiced by many breeders who cull progressively based on either annual classing, decision support aids such as TGRM™⁽⁸⁾ or observed reproductive performance (e.g. Lee *et al.* (2009a). Nor did they consider in any depth the consequences of large increases in the relative value of meat versus wool, which would logically favour age structures where net reproduction rate of the flock is at a maximum – in other words, when the value of sale stock per unit of feed consumed by the entire flock is at a maximum.

Jardine *et al.* (1975) used linear programming to compare profitability across a wide range of wool:meat prices and levels of fertility in a hypothetical self-replacing Corriedale ewe and wether flock in Western Victoria. Under most of the scenarios considered, the optimal age to cull ewes was at 5½ years and wethers as lambs. If the average level of fertility declined or the price of meat declined relative to wool, the optimum shifted to disposing of wethers at 3½ years and ewes at 4½ years. At high meat prices, it was more profitable to dispose of wethers as lambs. Jardine *et al.* did not allow for different feed requirements of different classes of stock (which is equivalent to assuming that feed is not limiting), nor did they allow for current flock improvement through selection.

Since these early studies, there have been significant changes in costs and prices. To examine the current situation, a number of Merino flock structures were evaluated using software described by Woolaston (1992a) with costs and prices updated to those published by NSW DPI in December 2011⁹. Results are summarised in Appendix 2 using both the parameters outlined by Turner *et al.* (1968) and where relevant, more recent age effects published by Safari *et al.* (2007a). They indicate that in a self-replacing Merino flock with typical levels of production, age effects on survival and productivity, maternal effects etc., 5-6 ewe age groups appears to optimise profitability under a wide range of price assumptions¹⁰. Although there was very little difference between five and six ewe age groups in any scenario, fewer groups were only optimal when the price of wool increased substantially relative to meat or if mortality rates in the ewe flock were higher than those assumed. Conclusions were similar whether the age effects modelled were taken from Turner *et al.* (2008) or more recent estimates from Merino resource flocks reported by Safari *et al.* (2007a). In all combinations considered, ewes were assumed to have their first lambing opportunity at two years. (Lambing earlier at one year of age is feasible in some production environments but the possibility was not considered here, because of the dearth of relevant parameters for ewes joined at seven months of age.)

⁸ http://www.xprime.com.au/products/tgrm/individual/sheep/australian_sheep.html

⁹ http://www.dpi.nsw.gov.au/_data/assets/pdf_file/0005/175856/merino-ewes-18-microns.pdf

¹⁰ Note that optimal flock structures for genetic gain, as opposed to current flock productivity, generally involve 4 ewe age groups, unless selection is made across age groups or reproduction rates are high.

At current prices for wool and meat, profitability in a self-replacing Merino flock is optimal with 5-6 ewe age groups. More age groups are optimal when prices for meat are high relative to wool, and fewer age groups are optimal when prices for wool are high relative to meat, or ewe mortality rates are high.

Superimposed upon what might seem to be an optimal age structure based on modelling flock parameters under a system in equilibrium, there are practical realities that might assume far greater importance in determining the number, class and age of stock to run at any particular time. For example, seasonal conditions (and therefore carrying capacity) can vary greatly from year to year, as can the relative value of wool and meat as well as other considerations such as infectious disease outbreaks and the availability of farm labour. Nevertheless, some pertinent questions to ask might include whether:

- there is sufficient knowledge of the genetics of across-age patterns of productivity in Merinos to allow the design of optimum breeding programs addressing comprehensive objectives;
- there is any evidence of changes in across-age patterns of productivity since the earlier studies of Turner, Mullaney and colleagues;
- there is any evidence that these patterns differ appreciably between different Merino strains, bloodlines or types; and
- current genetic selection practices are likely to impact significantly on these patterns.

Given that modelling indicates the optimal age structure of a Merino flock to involve around six ewe age groups and that this number is relatively robust to changes in the prices of wool and meat from current levels, it is relevant to examine productivity up to seven or eight years of age. In the absence of reliable data at the older ages, the pattern of change up to the maximum available should provide a useful guide to lifetime productivity.

Predicting the effects of genetic selection on lifetime productivity

Probably the first detailed investigation of the consequences on lifetime production of selection for increased fleece weight was published by Brown *et al.* (1966). After comparing age profiles for 10 fleece and body characteristics in two lines of Merino selected for increased fleece weight with an unselected line, Brown *et al.* (1966) concluded that “...*Changes in age were present in all characteristics and were similar in the three groups. The finding that selection on wool weight at an early age had no effect on subsequent age changes in any characteristic is of considerable importance*”. It is time to revisit this conclusion with the benefit of far more comprehensive data sets from both research and industry flocks.

There are essentially four main sources of recent information available for estimating age effects and relevant genetic parameters. These are:

(a) Resource flocks established for research purposes by CSIRO and the various State agriculture departments, which by design incorporated little within-flock selection and

were aimed at providing genetic information essential for designing breeding programs (the Trangie D Flock and C Flock in NSW, the Katanning Base Flocks in WA, the Turretfield Base Flock in SA and the CSIRO Finewool flocks at Armidale NSW).

(b) Demonstration flocks, which were also run (or overseen) by the same government agencies and which generally superseded resource flocks, being more focussed on demonstrating selection methodology and industry participation (the QPLU\$ flock run by NSW Agriculture, the “Towards 13 micron” or T13 flock at CSIRO Armidale, the Rylington project overseen by WADA and the Selection Demonstration flock in SA).

(c) Information Nucleus flocks established by the Sheep CRC and which have largely been designed to collect, from across a wide range of production environments and genotypes, information that is relevant to genomic selection and hard-to-measure traits, and which by design are closely linked with industry flocks.

(d) the Sheep Genetics database which contains performance information submitted by breeders but also includes some of the key data from demonstration flocks and Information Nucleus flocks.

Additional information relevant to lifetime productivity could also potentially come from industry-organised central progeny testing programs, run under the auspices of AMSEA¹¹. However, the progeny of sires are not typically recorded across their productive lifetime and any that are, generally contribute the information to the Sheep Genetics database.

Average age of recording

There is a general perception that the age of performance recording for selection purposes has declined significantly over recent years. Evidence from the Sheep Genetics database indicates that there has indeed been a gradual decline in average recording age of Merinos since the early 1990s (Figure 1). The average age for mean fibre diameter in records submitted to Sheep Genetics (excluding adults) reached its maximum in males born in 1993 at around 14.5 months of age, and in females born in 1994 at 14.6 months. Distributions were very similar for greasy fleece weight, except average age peaked at 14.6 months in 1993-born males and at 14.5 months in 1994-born females (not shown).

¹¹ Australian Merino Sire Evaluation Association

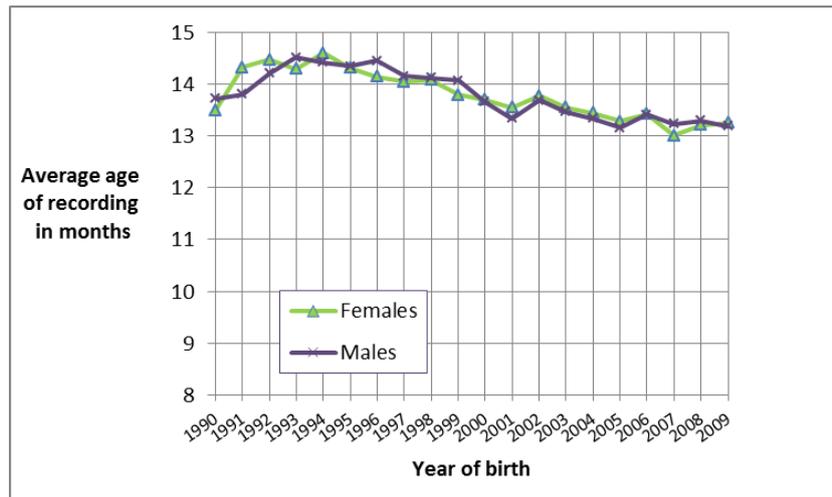


Figure 1. Average age of Merino records for mean fibre diameter in the Sheep Genetics database among animals classified as post-weaning, yearling and hogget. (source: D.J. Brown, pers. comm).¹²

Although the average ages in each year were similar for males and females, the total numbers of records differed, with the proportion of fibre diameter records derived from male hoggets being relatively constant at 15-20% of all records received (including adults), with those derived from female hoggets showing a marked decline from 30-35% in the early 1990s to less than 15% in the most recent years (Figure 2). The rate of increase in the proportion of yearling fibre diameter records submitted has been much steeper in males than in females¹³.

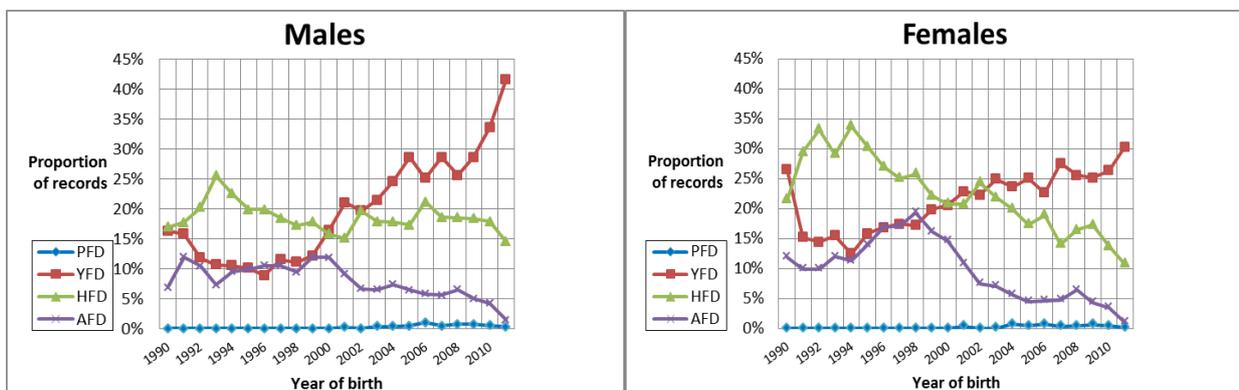


Figure 2. Proportions of fibre diameter records in the MERINOSELECT database, classified by sex, age class and year of birth (source: D.J. Brown, pers. comm)¹⁴

¹² Averages were computed assuming mid-point values for each class, namely 8.5 months for ‘Post-weaning’ records, 11.7 months for ‘Yearling’, 15.7 months for ‘Hogget’. These will differ slightly from actual averages as the distributions were not uniform within each class – see Appendix 5. Post-weaning records are currently in the database and comprise 0.4% of all records, but are not included in routine analyses.

¹³ Care should be taken in interpreting Figure 2 because only records on young animals are possible in the most recent birth years.

¹⁴ P denotes Post-weaning, Y is yearling, H is hogget and A is adult. Post-weaning records are in the database but are not currently included in routine MERINOSELECT analyses.

The results shown in Figure 1 provide an interesting comparison with those published by Kearins and Rogan (1987), who summarised the annual statistics since formation of the Trangie fleece measurement service in 1976. During that period, the average age of measured rams was actually only 10.8 months, with 6.7 months of wool growth (Figure 3). This suggests that there may have been an increase in the average age of rams being tested between the 1980s and 1990s.

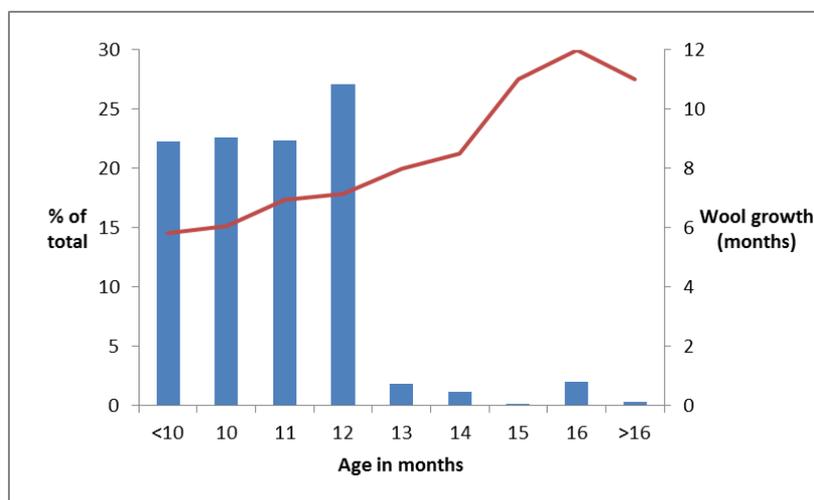


Figure 3. Age distribution of rams contributing samples to the Trangie Fleece Measurement Service 1976-85, with the average wool growth period (from Kearins and Rogan 1987).

Performance data maintained by the Trangie service is unlikely to have contained much fleece weight information recorded by breeders in other states, nor would it include on-farm fleece weight records that in the current era would generally be submitted to the Sheep Genetics database (which encourages submission of all available data). Nevertheless, it does illustrate that the use of records from rams aged 9-12 months with only about six months of wool growth, is not a practice that breeders have recently initiated.

Although the average age of recording has declined in recent years, selection of rams at 9-12 months with only six months of wool has been practiced since the mid-1970s.

Notwithstanding the earlier conclusion of Brown *et al.* (1966) that early selection had not affected lifetime performance in experimental lines, Atkins (1987) expressed concern over reliance of Merino breeders on early fleece measurement, noting that the heritability of fleece traits at such young ages was probably lower, due to inflation of error variance with maternal and early environmental effects. Furthermore, genetic correlations with later ages were likely to be imperfect, particularly for fleece weight. He showed that expected responses in adult fleece weight were greatly affected (by more than 25%) by relatively small changes in juvenile-mature correlations and predicted the likely efficiency of a two-stage selection strategy. Defining age effects on genetic parameters for fleece weight, in order to facilitate more effective selection for lifetime performance, was seen by Atkins (1987) as an urgent priority.

The issue of across-age correlations for fleece traits and litter size was addressed in more detail by Atkins (1990), who showed that in theory, obtaining reliable estimates for fleece weight and fibre diameter should be possible with several hundred sire families of a size typically found in research and industry flocks. Drawing on data from the Trangie D Flock, this study was the first to provide reliable genetic correlations for Australian Merinos covering annual fleece weights and fibre diameters from 1-6 years, to examine the heritability of changes across ages and to discuss the implications for breeding programs. Coelli *et al.* (1998) followed up this work by testing more complex genetic correlation structures for across age-expressions of fleece weight and fibre diameter, which will be discussed in more detail later in this document.

Research into the reliability of early records for predicting lifetime performance has been a feature of genetic research on Merinos for over half a century, with an increased emphasis since 1987.

Over the years, various studies have reported estimates of age effects on fleece characteristics in Merinos (e.g. Doney 1957, 1958; Brown *et al.* 1966, Atkins 1990; Woolaston 1992b; Coelli *et al.* 1999; Murray *et al.* 2001; Safari *et al.* 2007a). Most studies designed to estimate genetic parameters from mixed-age flocks include terms in models of analysis that account for the environmental effects of birth year, age of animal and year of measurement. Each of these factors can potentially (and usually do) influence production, but in many instances they are simply removed as “noise” and not reported¹⁵.

It is of some interest to see whether there have been any perceivable changes in published aged effects over time, by comparing some of the earliest estimates published for Merinos, with more recent and precise estimates from a large sample of lines designed to be representative of the Merino industry.

Age effects on wool characteristics

A detailed examination of age effects on wool traits was carried out in experimental CSIRO lines run at Cunnamulla, with effects in ewes reported by Brown *et al.* (1966) and in rams by Brown *et al.* (1968). The study involved 10,139 ewe records collected on animals born between 1947 and 1959, with 1,675 animals measured at 1½ years, declining to 1,111 at 5½ years and 281 at 10½ years. Three lines were involved - two lines selected for fleece weight and a third random control line. Rams from the same flock were analysed separately, comprising only animals in the control line (366 at 1½ years declining to 270 at 5½ years) and including five drops measured over nine years.

¹⁵ As pointed out by Turner and Young (1969, Ch4), birth year, age and year of measurement are not independent – specifying any two of the three factors automatically determines the third. Furthermore in flocks under selection, year of birth effects cannot be considered as random and estimates can be influenced by genetic trends. This emphasizes the need for caution when fitting multiple age-related factors and interactions, which can be readily done with modern analysis packages such as ASReml, without a great deal of thought.

More current information is available from the study by Safari *et al.* (2007a), which involved analyses of data pooled across seven resource and demonstration flocks established in recent decades, *viz.*:

- Trangie D flock (1975-89);
- Trangie C Flock (1984-95);
- QPLU\$ flock (1993-2003);
- WA Base Flocks (1984-2004);
- SA Base flocks (1989-97);
- CSIRO finewool flock (1990-2001); and
- SA Selection Demonstration Flocks (1997-2004)

In studies of the individual resource flocks that constitute the data set compiled by Safari *et al.* (2007a), age effects on production have usually been accounted for, but have not always been reported. In any case, comparisons of age effects in the different resource flocks are unlikely to be informative with respect to genetic differences, as resource flocks were not run together. Furthermore, comparisons of age effects among lines constituting each resource flock have not been reported. Consequently the few estimates that are available from pooling lines across individual resource flocks will not be investigated in detail here. Rather, the main focus will be on the results of Safari *et al.* (2007a), obtained from combining the various data sets and comprising over 100,000 records for the main fleece traits. Approximately 2300 sires were represented, from 67 bloodlines. Significant age effects were found between 2yrs and \geq 7yrs for CFW, GFW, FD, YLD, CVFD and SDFD, as well as the effects of dam age on these traits. Relative effects of age on CFW are shown graphically in Figure 4, with the mean at four years arbitrarily set to 100%. In this data set, 78% of records were from ewes with approximately 4 records per ewe, whereas rams generally had only 1 or 2 records. In the same figure, effects are shown separately for rams and ewes in the early CSIRO study by Brown *et al.* (1966, 1968).

In the CSIRO study, reproductive status of ewes was accounted for, whereas in study of resource flocks it was not. After allowing for the effects of reproduction in the early CSIRO lines (the combined effects of pregnancy and lactation on clean wool weight were estimated at 25%), age effects on fleece weight were more pronounced in rams than ewes. Lee and Atkins (1995) reported larger effects on fleece weight of 7-14% for pregnancy and 23-30% for lactation using a data from the Trangie D Flock, which was a subset of the combined resource flock data¹⁶. In the combined resource flock data, the greater decline at six years and beyond may at least partially reflect the impact of reproduction and changes in gender composition over time, which were not reported. Despite these differences between studies, Figure 4 indicates that the trends were broadly similar in the three groups. The CSIRO lines appeared to reach maxima at three years compared with four years in the resource flocks, but the former were actually reported as having been measure at 3½ years.

¹⁶ Most estimates of the effects of pregnancy and lactation on other traits may possibly contain a small bias arising from the fact that ewes are not randomly allocated to the different reproductive categories.

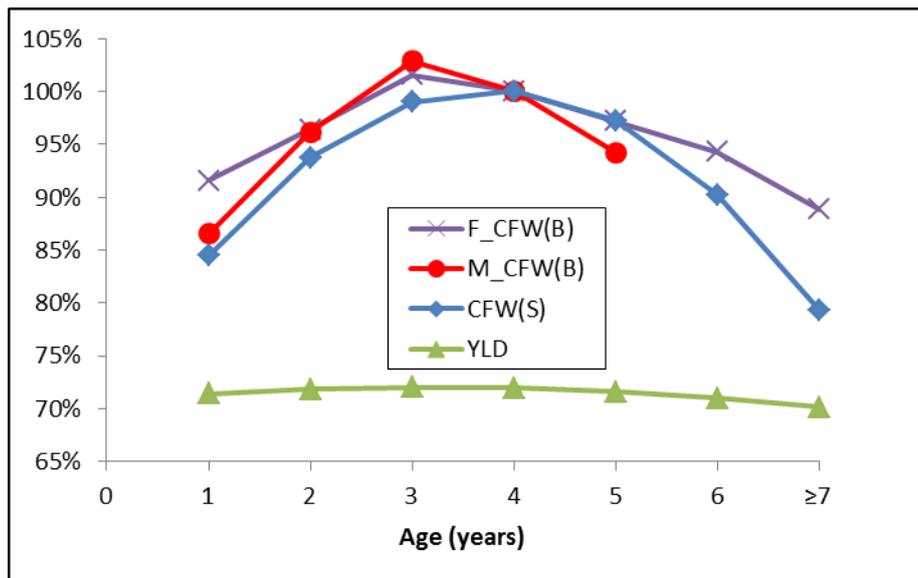


Figure 4. Relationship between age and clean fleece weight estimated separately in ewes (F_CFW) and rams (M_CFW) by Brown *et al.* (1966 and 1968, respectively), and comparable effects reported by Safari *et al.* (2007a) (CDW(S)) in mixed sexes. CFW at 4 years was set to 100%. Effects of age on YLD as reported by Safari *et al.* (2007a) are also depicted.

Equivalent age trends for GFW from the three reports have not been plotted together here but were slightly more pronounced. This can be seen in Appendix 3 for the early CSIRO lines and inferred from age effects on YLD in the study by Safari *et al.* (2007a), included in Figure 4. Yields increased slightly from one year to three years and declined slightly to seven years. Brown *et al.* (1968) also reported maximum yields between 3½ and 6½ years in ewes, while in rams, yields declined by over 10% between 1½ and 6½ years (Appendix 3).

Safari *et al.* (2007a) reported that almost all differences in average fleece weights between adjoining age groups were statistically significant, even in mature ewes, and suggested that when enough records are available to estimate differences, then age-specific adjustments are preferable to applying the same adjustments across all mature age groups. Notter *et al.* (2005) drew a similar conclusion regarding ewe age effects on lamb weaning weights in Polypay sheep in the US. Despite these significant differences due to age, Mortimer *et al.* (2001) found that adjustments for environmental effects had a much smaller impact on improving selection accuracy than including pedigree information or including fleece measurements at a second stage of selection.

Estimates of age effects on fleece weight published over 40 years ago are similar to recent estimates, with fleece weights peaking at 3-4 years.

Although not mentioned explicitly in their report, Safari *et al.* (2007a) did not appear to test for the importance of the bloodline x age interaction on wool traits. Provided it was not simply caused by scale effects, any evidence of an interaction might provide some insight into whether or not different types of sheep raised in the same environments have different lifetime patterns of wool growth. The same investigation could of course

be carried out in any of the individual resource flocks, which all comprise multiple bloodlines.

Equivalent results for average fibre diameter in the same data sets are shown in Figure 5. This indicates that mean FD of rams in the early CSIRO study increased until their sixth year, when measurements stopped. In ewes, measurements continued until 10½ years of age, with mean FD peaking at 6½ years; though the rate of increase was much slower than in rams. Rose (1982) reported that in a flock of breeding ewes run at Julia Creek averaging 19 microns, FD also reached a maximum at 6½ years, about 0.7 microns greater than at 3½ years and 10½ years. Coelli *et al.* (1999) reported a significant increase in mean FD across ages up to 5 years in wether trial data.

In the mixed-sex data set of Safari *et al.* (2007a), the increase between the first and second shearing was similar to the CSIRO ewes, then from the second to the fifth shearing, was similar to the CSIRO rams, and thereafter similar to the CSIRO ewes.

A number of studies have identified a strong negative association between CVFD and SS at both the genetic and phenotypic level (see review by Safari *et al.* 2005 and also Matebesi *et al.* 2009), but to the author's knowledge, no published reports have discussed age effects on SS in breeding ewes. Safari *et al.* (2007a) did however report that the standard deviation of fibre diameter varied significantly with age, resulting in a curvilinear pattern for the coefficient of variation as shown in Figure 5 - a consequence of SDFD decreasing when mean FD was increasing, and *vice versa*. In contrast, Rose (1982) found that CVFD was at a minimum at 2½ and a maximum at 7½ years. This inconsistent pattern may have been a consequence of the variable seasonal conditions noted by the author.

Estimates of age effects on average fibre diameter published over 40 years ago are similar to recent estimates, peaking at 5-6 years. The coefficient of variation of fibre diameter is at a minimum at 4-5 years. Industry perceptions of important bloodline differences in age effects could be readily tested in data from multiple-bloodline research flocks, but there is very little information reported in the published literature.

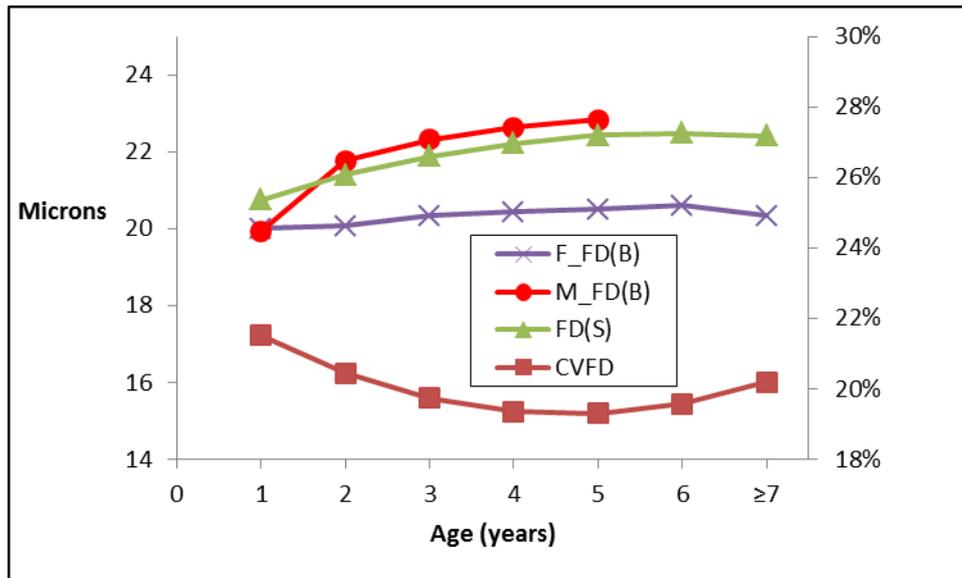


Figure 5. Relationship between age and average fibre diameter estimated separately in ewes (F_FD) and rams (M_FD) by Brown *et al.* (1966 and 1968, respectively), and comparable effects reported by Safari *et al.* (2007a) in mixed sexes. Changes in coefficient of variation of fibre diameter with age as reported by Safari *et al.* (2007a) are also depicted.

There has been little appear in the scientific literature related to age effects on other wool traits since the early report of Brown *et al.* (1998), with the relevant figures from that report reproduced in Appendix 3. Murray *et al.* (2001) did report changes on staple length and visually assessed traits in the QPLU\$ flock up to 4 years of age. They found that after accounting for reproductive performance, wool colour and tip were not affected by ewe age, but staple length and other components of wool style (crimp definition and staple definition) deteriorated between 2 and 4 years of age (see Figure 6).

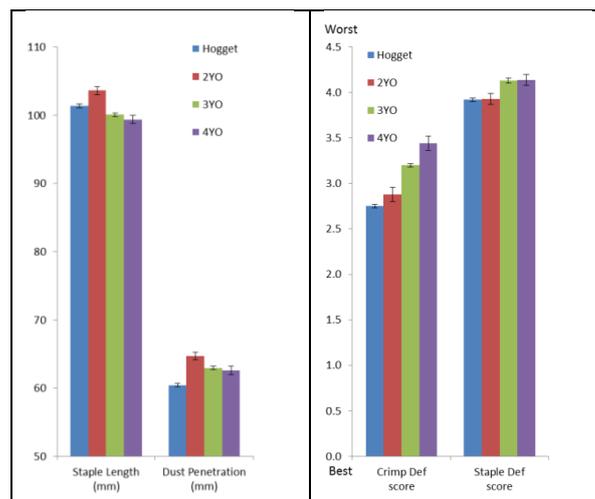


Figure 6. Relationship between age and wool traits in the QPLU\$ flock (from Murray *et al.* 2001).

They also noted that as reproductive burden increased, wool style tended to deteriorate. The analyses were indicated as preliminary, which was to be repeated as further data were collected.

Preliminary information suggests that components of wool style deteriorate between two and four years of age; and that parturition and lactation cause most components of style to deteriorate.

Genetic parameters for age effects on wool traits

Most reports of genetic parameters for wool traits (as summarised by Safari *et al.* 2005) involve either measurements at just one age or have simply classified records according to whether they have come from yearlings or adults. When adult records are treated as repeated records of the same trait, the weighted average age of adult records can be relatively low, as there are typically more pedigreed records available from young adults than aged adults. This point can be readily illustrated using research flock data. According to the survey by F.D. Brien *et al.* (2013), fleece records were available from ewes up to nine years of age in the SA Selection Demonstration Flocks, but the weighted average age of adult measurements (> 18 months old) was only 3.6 years. The comparable average in the CSIRO Finewool flock was 3.4 years and in the Trangie D Flock was 3.9 years. For the important traits of fleece weight and average fibre diameter, however, changes in genetic variation across individual ages have been analysed in some detail.

Estimates from research flocks

Coelli *et al.* (1998) compared different covariance structures for modelling changes with age and concluded that in the Trangie multiple bloodline flock (D Flock), clean fleece weight was best modelled by separating among-age adult correlations from hogget-adult correlations. For fibre diameter however, a different model of correlations was more appropriate, with a banded correlation structure being statistically the best fit. This is a structure where the correlations are graded, becoming progressively smaller as the age interval increases. Despite this patterned correlation being the best fit statistically, they concluded that correlations between ages were sufficiently high that given a hogget measurement at 15-16 months, repeat measures of FD were unlikely to greatly improve selection accuracy.

Asadi Fozi (2005) extended the work of Coelli *et al.* (1998) in some detail using a wider range of models and more stringent model selection criteria, comparing covariance structures for FD expressions across ages in the CSIRO Finewool flock (born 1990-1997) with those in the medium wool Trangie D flock (1975-1981). Data from the finewool flock were recorded in both sexes but only ewes in the Trangie flock¹⁷. Reproductive status was accounted for in both data sets. Asadi Fozi compared the fit of

¹⁷ Asadi Fozi did not report the ratio of wether and ewe records in the finewool data, but it is known that wether records were much more highly represented in the earlier ages than later ages. According to A.A. Swan (*pers comm*) it is reasonable to assume that the fine wool results were largely driven by ewe data.

a repeatability model across five different expressions with eight different correlation structures varying in complexity from homogeneous to completely unstructured. Random regression models for direct additive genetic effects were also evaluated, by fitting legendre polynomials of order 2 to 5. In both data sets, a repeatability model was a poorer fit than multivariate models, supporting the hypothesis that expressions at different ages are genetically different, with the first being the most different from the remainder.

In the finewool flock, mean fibre diameter increased sharply from the first to the second expression, then remained relatively stable. The most parsimonious model involved a pre-structured multivariate arrangement, whereby genetic variances for the 2nd-5th expressions were constrained to equality and correlations between the 1st and 2nd, as well as the 2nd and 3rd expressions were unconstrained. Patterns of expression were somewhat different in the medium wool flock, with a steady increase in the mean FD across all five expressions. The most parsimonious model again involved a pre-structured multivariate structure, whereby genetic variances for the 3rd-5th expressions were constrained to equality and the correlation between the 1st and 2nd expressions was unconstrained. Differences between the two optimal structures can be seen more clearly in Table 1.

Table 1. Estimates of genetic parameters for FD taken at first, second, third, fourth and fifth shearing using the most parsimonious models in both fine wool and medium wool data sets (Asadi Fozi 2005). Heritabilities are on diagonal and genetic correlations below diagonal. Within each flock, genetic variances shown in the same colour were constrained to equality and correlations within the same border were also constrained to be equal.

Expression in finewool data					Expression in medium wool data						
	1	2	3	4	5		1	2	3	4	5
1	0.65					1	0.63				
2	0.89	0.67				2	0.93	0.62			
3	0.76	0.94	0.66			3	0.89	0.96	0.69		
4	0.76	0.91	0.97	0.61		4	0.89	0.96	0.99	0.62	
5	0.76	0.91	0.97	0.97	0.55	5	0.89	0.96	0.99	0.99	0.56

Asadi Fozi concluded that FD changed genetically up to 3 years of age and could be statistically separated into 3 different traits: yearling /hogget, 2 years and adults of 3, 4 and 5 years of age. Thus prediction of lifetime performance for FD will be somewhat inaccurate when based on first shearing alone, especially in fine/superfine wool Merinos. In these data sets, pattern differences cannot necessarily be ascribed to the type of sheep, because age at first shearing differed between the two data sets (10-12 months in fine wools and 15-16 months in medium wools¹⁸), they had different sex compositions and they were of course run in different environments. A potentially important difference is that in the finewool data set, the first expression contained a large proportion of wethers, which became much smaller in subsequent drops. This was not quantified but is known to be the case and be inferred from the histograms in

¹⁸ Medium wool animals also received a lamb shearing at about 3 months, which were not reported here.

from Appendix 4. Thus it cannot be ruled out that imperfect between-sex correlations may also have contributed to the greater disparity between first and subsequent FD expressions shown for fine wools in Table 1. Finally, it appears that comparable analyses have not been conducted with fleece weight in finewool flock data (A.A. Swan, *pers comm*). Given industry concerns about the reliability of early fleece measurements particularly in finer-woolled sheep, this would be a study worth undertaking.

Estimates from industry data

Brown *et al.* (2013) used records from approximately 200,000 mixed-sex animals in the MERINOSELECT database to estimate between-age correlations for GFW and FD for each annual expression from yearling through to the sixth adult shearing, as well as at hogget age¹⁹. The distribution of records was heavily skewed towards younger ages, such that almost 90% of the records were from animals aged 2 years or less, and only about 2.5% were from animals 5 years or older. As shown in Figure 7, the pattern of heritabilities for FD was similar to that reported by Asadi Fozi (Table 1) with the heritability of fleece weight increasing up to 2yo then decreasing after 5yo (although the final estimate was imprecise due to low numbers).

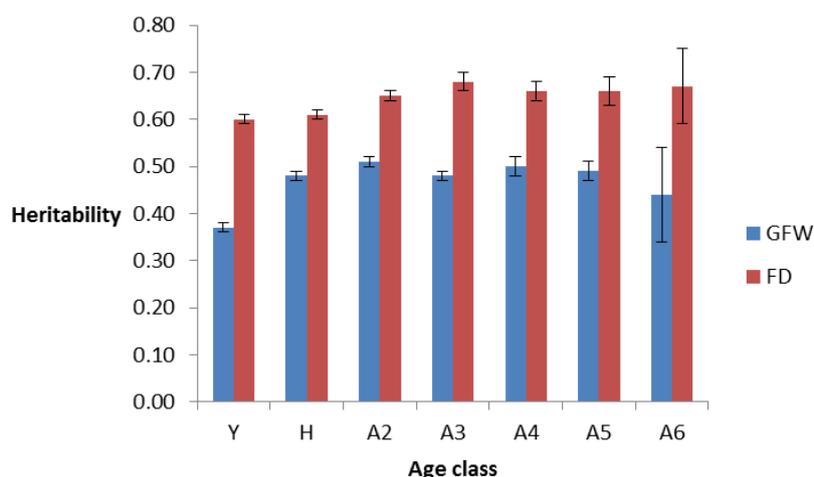


Figure 7. Estimated heritabilities of greasy fleece weight (GFW) and average fibre diameter (FD) in MERINOSELECT records as yearlings (Y), hoggets (H) and adult ages 2 to 6 yo (A2-A6). Bars depict standard errors. (From Brown *et al.* 2013).

Consistent with results from research flocks, estimated genetic correlations between ages were all high, more so for FD than fleece weight (Figure 8). These were estimated using an unstructured covariance matrix, so that no equality constraints were imposed. Alternative structures such as those described by Coelli *et al.* (1998) and Asadi Fozi (2005) were not explored, although for both traits, the differences in correlations between yearling and adult expressions were greater than between different adult expressions. As expected, correlations involving hogget measurements were intermediate.

¹⁹ Some resource flock data were included in this study but generally not repeated adult records (D.J. Brown, *pers. comm.*).

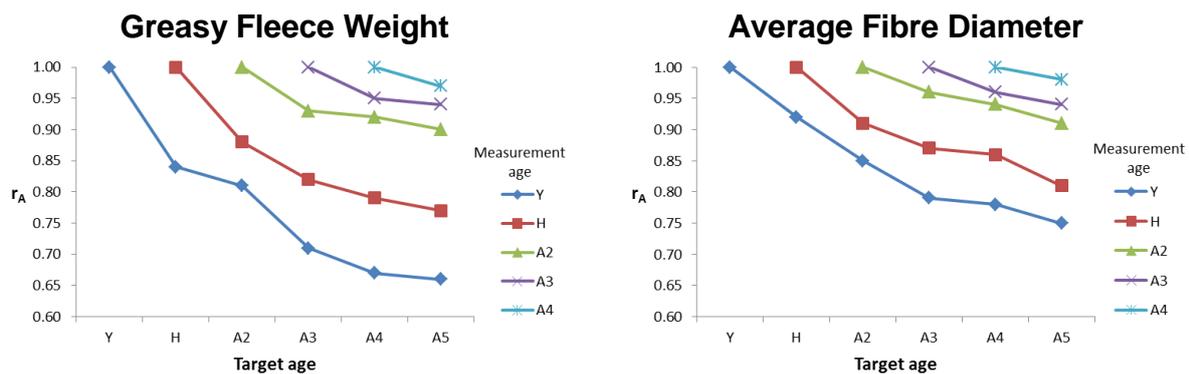


Figure 8. Estimated between-age genetic correlations for greasy fleece weight and average fibre diameter in MERINOSELECT records as yearlings (Y), hoggets (H) and adult ages 2 to 5 yo (A2-A5)²⁰. (From Brown *et al.* 2013).

Apart from being based on industry data, these analyses differ from those in research flocks as the models did not include additional random effects and no adjustments were made for ewe reproductive status. More detailed analyses to accommodate these additional complexities are planned (D.J. Brown, *pers comm.*). Nevertheless, the high degree of similarity of results from industry and research data are encouraging.

The obvious research gap is the heritability of fleece measurements taken prior to yearling age. D.J. Brown (*pers comm.*) has proposed an alternative set of age thresholds that would make sufficient data available at young ages for reliable parameter estimates – see Appendix 5.

In data derived from research flocks and industry flocks, between-age genetic correlations for fleece weight and average fibre diameter are imperfect. Yearling-adult correlations are lower than correlations between different adult expressions. Information currently contained in the Sheep Genetics database could be used to estimate parameters involving younger ages.

Micron blowout

Genetic variation has been found in the pattern of FD changes with age, or “micron blowout”, with studies reported by Atkins (1990), Hickson *et al.* (1994), Cottle *et al.* (1995) and Hill *et al.* (1999). After examining genetic parameters related to FD change with age in the CSIRO Finewool flock and Trangie D flock²¹, Asadi Fozi (2005) went on to predict the consequences of different selection strategies for FD in both flocks, and in a comprehensive multi-trait breeding objective²² in the finewool flock only. He found that in the finewool flock, micron blowout between 1 and 2 years was moderately

²⁰ Correlations involving 6yo animals (A6) were reported in the paper but were excluded from this figure because of the small number of records involved.

²¹ Note that studies of micron blow-out by Hickson (1995) and Cottle *et al.* (1995) used subsets of these data.

²² The objective was a standard RAMPOWER objective including CFW, SS, CVFD, YW and NLW with a 30% micron premium.

heritable (0.29)²³, as was blowout between 2 years and subsequent ages (0.19). In the medium wools, blowout was less heritable (0.16 and 0.14, respectively). These results are not dissimilar to those found by Hill *et al.* (1999) in the medium-strong woolled Turretfield flocks, where estimates were in the range 0.10-0.29, depending on sex of the animal and ages involved.

Asodi Fozi (2005) found that the genetic correlation of the first FD measure with blowout between 2 years and adult age was unfavourable in the fine wool data set (-0.37) but slightly favourable in the medium wool data (0.17). Estimates by Hill *et al.* (1999) in the Turretfield flock were essentially neutral between early ram FD measures and micron change in ewes from 16-40 months, provided variances were appropriately scaled. Taken together, these results indicate that the relationship between mean FD and changes in FD with age following an initial measurement, may not be consistent across bloodlines or environments.

Whilst it is possible that including other traits such as weaning weight helps predict lifetime performance for FD (Asodi Fozi estimated the genetic correlation with micron blowout to be -0.28), logic suggests that it is likely to be a less effective predictor than an actual adult FD measure, albeit cheaper. The relative effectiveness could be quantified readily using selection index methodology.

Asodi Fozi (2005) concluded that for fine wool sheep with a multi-trait objective, additional FD measurements did not provide any extra information where selection was based on FD, CFW, CVFD, YWt and EL/EJ, all recorded at yearling age. He also concluded that in medium wools (as did Coelli *et al.* 1998), adding more fibre diameter measurements after hogget age is not likely to improve selection accuracy for lifetime FD expression. Thus, using additional FD measurements after first shearing was not seen as beneficial for either inference population (fine or medium wool) and micron blowout was not considered an important issue in either case. Asadi Fozi further concluded that in both flocks, the economic value of the first shearing was such that reducing micron blowout at the expense of genetic change at the first shearing was “not economically attractive”.

The increase in average FD after the first year (micron blow-out) is heritable but estimates of the genetic relationship between blow-out and mean FD are variable.

Mortimer *et al.* (2001) showed by selective use of records retrospectively in the QPLU\$ flock, that including fleece measurements from a second shearing at 16 months (following a 10 month shearing), would improve selection accuracy in rams by 11-34%; and that prediction of genetic merit of Merino ewes across age groups could be greatly improved by including adult records on female relatives and two-stage shearing records on male relatives.

Subsequent work by Brown *et al.* (2013) and Swan and Brown (2013), based on data in the Sheep Genetics database, led them to the conclusion that although yearling fleece

²³ Standard errors not reported; but record numbers in the finewool flock were 9233, 4414 and 3340-2272 for ages 1, 2 and 3-5 years, respectively; and in the medium wool flock were 3800, 2487 and 2398-2037, respectively.

measures are strongly correlated with adult expressions, worthwhile additional gain in both fleece weight and fibre diameter can be achieved by supplementing hogget records with a single adult record. Increased gain in fleece weight worth up to \$1.1 per ewe per year was predicted over 10 years of selection. The increase in gain for FD was lower, to a maximum of \$0.7 per ewe per year when the micron premium was high. However, there was little benefit in multiple adult measurements of these traits. Genomic selection of young rams resulted in further increases in gain when combined with adult measurements, particularly for fleece weight. Notably, MERINOSELECT analyses already accommodate one adult measurement, so most of the gains possible can be realised by breeders with the existing evaluation system.

Research indicates that supplementing yearling fleece weight records with one adult record can lead to worthwhile genetic gains across a range of micron premiums. Including an adult fibre diameter is only likely to be worthwhile when the objective is to reduce average diameter. Breeders concerned about changes in fleece attributes across ages should be encouraged to submit adult fleece records. Genomic selection offers the promise of increased gain in adult wool traits, provided the appropriate information is available for developing predictions.

Age effects on reproductive traits

Average age effects on reproduction in resource flocks²⁴, taken from the least-squares means tabulated in Safari *et al.* (2007a), are shown in Figure 9. These estimates were based on over 69,000 reproduction records, with each ewe providing an average of 2.2 records. As was the case with wool traits, significant age effects were detected for the four traits reported, viz, FER, LS, LB/EJ and LW/EJ. Age patterns were again curvilinear with adjacent age categories almost always differing statistically ($P < 0.05$).

Patterns in the resource flocks differ slightly from the earlier study of Turner and Dolling (1965), who reported that:

- LW/EJ peaked when ewes were 6 years old then declined (compared with 5 years in resource flocks);
- litter size (LW/EL) increased to a maximum at around six years then plateaued (6-7 years in resource flocks);
- fertility (EL/EJ) increased to five years, plateaued until seven years then declined (4-5 years in resource flocks); and
- LB/EJ peaked later than LW/EJ at six to eight years (5-6 years in resource flocks).

²⁴ Strictly speaking, data analysed by Safari *et al.* (2007a) were derived from both resource and demonstration flocks, but for convenience they will simply be referred to as “resource flocks” hereafter.

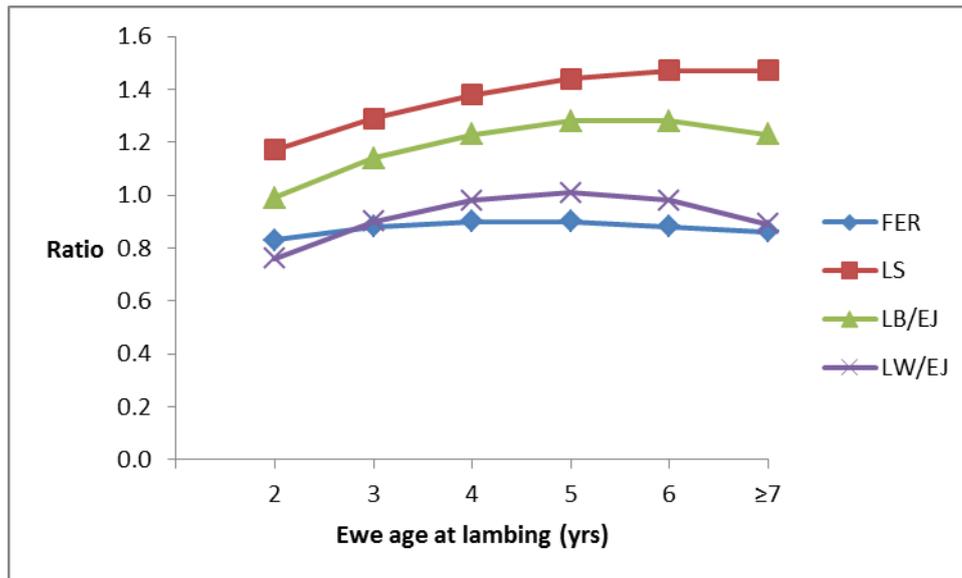


Figure 9. Relationship between age and ewe reproductive traits estimated in resource flocks by Safari *et al.* (2007).

Consistent with the early report by Turner and Dolling (1968) and the more recent report by Safari *et al.* (2007a), Brien *et al.* (2009) found that lamb survival was lowest when the dam was either young (2 years) or old (7+ years), with dams of intermediate age providing the highest lamb survival in both singles and twins. That this is consistent with Safari *et al.* (2007a) is hardly surprising however, given that much of the data from the SA resource flocks that were analysed by Brien *et al.* (2009), also formed part of the Safari data set.

In evaluating age structures in Merino flocks, Turner *et al.* (1968) modelled four different patterns for EL/EJ across ewe ages – three based on experimental evidence from different CSIRO flocks (Peppin-based) at Cunnamulla, Armidale and Denilquin,²⁵ and the fourth from a survey of commercial Merino flocks in eastern Australia²⁵. A contemporary study of fine-wool Merinos was carried out in four commercial flocks in western Victoria by Mullaney and Brown (1969). Age effects in NLW from the two early studies are plotted in Figure 10, together with more recent results from the resource flocks (Safari *et al.* 2007a).

²⁵ These correspond to patterns 1, 2, 3 and 4 respectively in Figure 7. Pattern 2 is from the same flock as reported by Turner and Dolling (1965) referred to in the preceding paragraphs.

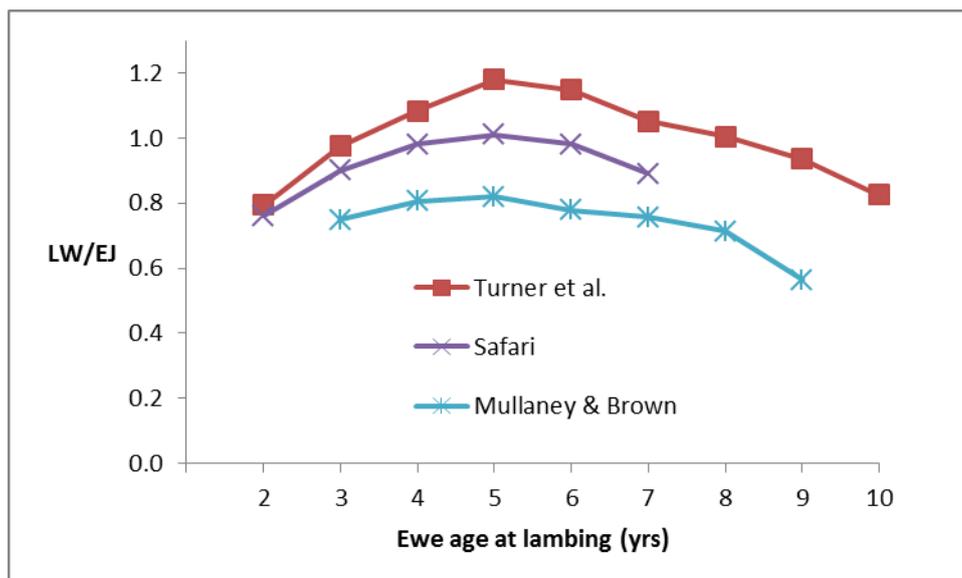


Figure 10. Relationship between age and LW/EJ reported in early experimental and commercial Merino flocks (average of four patterns from Turner et al. 1968), in four commercial flocks (Mullaney and Brown 1969) and in pooled resource flock data by Safari et al. (2007a).

The number of lambs weaned per ewe joined peaks in Merinos at about 5 years of age.

Although the Victorian study did not report NLW (also called LW/EJ) at two years, the general pattern was similar to that in the other two studies – peaking at five years and then declining at 6-7% per year of age. At two years of age, ewes in the resource flocks had a mean NLW similar to the average of the earlier CSIRO flocks, but at six years of age, resource flock ewes had similar reproductive performance to nine and ten year old ewes in the earlier flocks. In other words, the rate of increase in NLW in the first four parities was lower in the resource flocks than in the average of the early CSIRO reports. It should be stressed that this is by no means proof of a genetic decline in lifetime NLW performance between the 1950s and later years, as there were undoubtedly also differences in management and environment. However, differences between the early and more recent studies in the patterns from two to five years, as indicated in Figure 10, do appear to be more pronounced than the differences portrayed in Figures 4 and 5 for fleece weight and average fibre diameter.

It is therefore relevant to examine genetic parameters to assess whether there is evidence of imperfect genetic correlations between different age expressions of reproduction.

Between-age genetic correlations for reproduction

Atkins (1990) calculated that, in contrast with the data requirements for fleece and body parameters, many hundreds of large sire group families would be needed to obtain

acceptable precision for between-age correlations involving a trait with a heritability of around 0.1, such as litter size. In fact between-age correlations for litter size would need to be less than 0.5 before any published experimental data set could claim significant departures from unity. Even large research flocks were not typically structured to provide such information for reproduction rate.²⁶

Reproduction parameters in research flocks

The predictions of Atkins (1990) were validated by Dominik and Swan (2006), who found that over 17000 reproductive records from 5850 ewes in the CSIRO Finewool flock provided insufficient information for reliable estimates of between-age correlations for either pregnancy rate, fecundity, lambs weaned or lamb survival. Furthermore, Kelly *et al.* (2005) found by simulating seven years of data based on the structure of the 2000-ewe Finewool flock and replicated 50 times, that even correlations estimated between one measure of average fibre diameter and the mean of approximately 2.8 reproduction records were not only likely to be imprecise, but also may be biased. Potential explanations given for the bias were:

- a) Inadequate power of the experimental design (i.e. sampling variation)
- b) An artefact of the small genetic variance of fecundity; or
- c) Constraints on variance estimates to be positive.

Whatever the reason, it is clear that in order to obtain precise estimates of genetic correlations involving reproduction traits, a lot of data are needed. As further evidence of this, Ingham (2004) attempted to estimate genetic correlations between yearly expressions of reproductive traits using repeated records from almost 2100 ewes aged 2-5 years in the Turretfield Resource Flock. Unfortunately (and as further validation of Atkins' predictions), the data set was too small to support reliable estimates, which varied in magnitude from 0.90 ± 0.71 to 1.39 ± 0.37 for NLW, 0.79 ± 0.33 to 1.65 ± 0.59 for fertility, 0.45 ± 0.27 to 0.88 ± 0.16 for litter size and 0.69 ± 0.30 to 1.44 ± 0.45 for rearing ability.

Although they did not attempt to estimate genetic correlations between ages, Lee *et al.* (2009b) analysed lifetime (2-6yo) reproductive records from over 7000 ewes across the D Flock, C Flock and QPLU\$ flocks run by NSW DPI, estimating heritabilities for EL/EJ, LB/EL, LW/LB and LW/EJ. Their results were consistent with a repeatability model (i.e. assuming repeated measures of the same trait) and they concluded that it was better to target net reproductive success (LW/EJ) than its components. In a further study of the same data, Lee *et al.* (2009a) investigated the distributions of lifetime EL/EJ and identified potential opportunities to strategically target segments of the flock to improve flock reproductive performance. The authors did not report the number of sires (of ewes) represented in the data and these were only detailed for the D Flock by Mortimer and Atkins (1989) but not for the C Flock (described by Mortimer *et al.* 1994) or the QPLU\$ flock (described by Taylor and Atkins 1997). However, in the D Flock, there

²⁶ Calculations using a modification of the method outlined by James (1979) and summarised in Appendix 6, indicate that an experimental design with 75% statistical power would require records on about 7,000 ewes to demonstrate that an age-age correlation less than 0.8 was significantly less than unity at the 5% level when the heritability is 0.1. This assumes a sire model with very large half-sib families of 50 ewes, which could only be achieved with AI. If the half-sib family size is only 10 ewes, over 30,000 records are required at each age.

appeared to be approximately 7.4 ewes per sire – too few for precise estimates of between-age genetic correlations in a data set of this size²⁷.

The clear message from this work is that no one experimental resource flock is likely to go anywhere near providing sufficient information to support precise estimates of between-age genetic correlations in reproduction rate, unless records are accumulated over 20 or 30 years. Even then, they are only likely to provide sufficient power for single estimates pooled across all genotypes; and would certainly be inadequate to detect differences in estimates between sub-sets of the flock.

Reproduction parameters in industry data

In the US, Lee *et al.* (2000) published a genetic correlation of unity between number of lambs born to ewes at 2-3 yrs of age and >3 yrs of age, using records from 1100 Rambouillet ewes. However they did not publish a standard error. Experiences with research data discussed earlier suggest that it is probably so high as to render the estimate totally meaningless, particularly as heritabilities were very low (0.02±0.03 and 0.04±0.03, respectively).

Using large data sets from Swiss industry flocks²⁸, Hagger (2002) found that between-age correlations for litter size were mostly in excess of 0.90, at least for the first three parturitions. The standard errors were acceptably low at around 0.02 and smaller. Hagger's data sets were each 4-5 times the size of that examined by Dominik and Swan (2006) and 7-13 times the size of that used by Ingham (2004), ranging from approximately 15000 to 26000 ewes, each with an average of 2.09-2.31 records.

Based on selection index calculations, Brien *et al.* (2011) illustrated the importance of good quality records for pedigree and lambing/rearing performance to making meaningful genetic progress in net reproduction rate. Given that only 18% of Merino flocks participating in Sheep Genetics supply reproduction records (which probably overstates the true situation as some flocks have incomplete recording) this is a serious limitation, Researchers at AGBU are currently undertaking research to examine the merit of including the components of reproduction (fertility, litter size and lamb survival) in genetic evaluation rather than simply NLW. The aims are to improve the quality of on-farm data, gain a better understanding of the relevant genetic relationships and develop improved and more flexible genetic evaluation. Using component traits should also allow to improve modelling of economic values (which can change, for example, with mean litter size). The emphasis is on considering reproduction at all ages, particularly lambing during the first year of age, which is being increasingly practised with maternal breeds, with some interest also being shown by Merino breeders (K.L. Bunter, *pers comm*). Using 19335 records²⁹ from the Sheep Genetics database (19

²⁷ The report by Safari *et al.* (2007b) indicates that across the resource flock data that they compiled, there were 69388 NLW records with an average of 2.2 records per animal, with 2312 sires represented. This suggests an average half-sib family size for the ewes of 13.6.

²⁸ Breeds studied by Hagger (2002) were White Alpine, Brown-Headed Meat, Black-Brown Mountain and Valais Black-Nose. Respective numbers of ewes with records were 26274, 25165, 18913, 14953 and 21726.

²⁹ Record numbers declined considerably with age, with only 24% of all NLW records coming from ewes > 2 years old.

flocks and five maternal breeds), Bunter and Brown (2013) found that the relative contributions of component traits varied with ewe age. Differences between yearling and older ewes were particularly pronounced for fertility, where age differences were found in heritabilities and phenotypic variances. They concluded that relatively low genetic correlations supported treatment of reproductive traits in yearling and older ewes as genetically different traits. The only exception was litter size, where genetic correlations were statistically no different from unity. As shown in Figure 11, estimates were imprecise as a consequence of relatively low record numbers. Litter size appeared to be less heritable in yearlings than older ewes (not shown), but correlations across age were high. For NLB and NLW, expression in two-year old ewes was more akin to expression in older ewes than was expression in one-year old ewes.

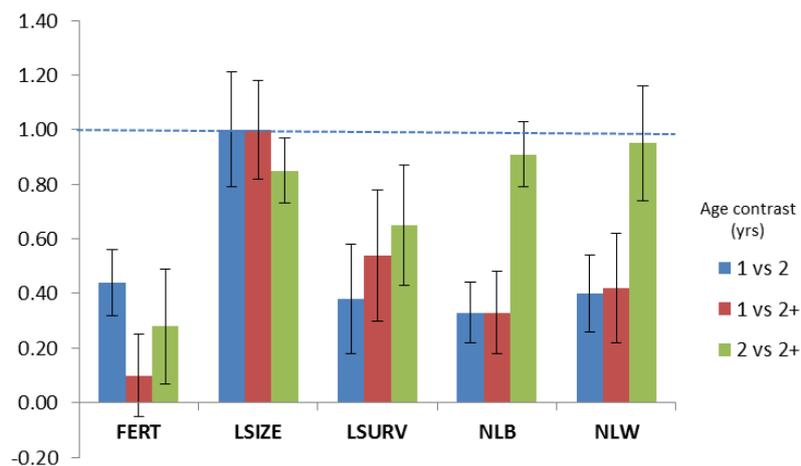


Figure 11. Estimated across-age genetic correlations for components of reproduction using data from maternal sheep breeds in industry flocks
 Source: Bunter and Brown (2013).

These estimates should be regarded as preliminary because of the standard errors, but they are sufficient to demonstrate the low accuracy implicit in using records from yearling ewes to predict lifetime reproductive performance, for all component traits except litter size.

Very large data sets are required to estimate between-age genetic correlations for reproduction rate with any precision. There is a paucity of reliable information in Merinos but estimates of correlations involving two years and older in other breeds appear to be high for litter size, NLB and NLW.

Association between reproduction and wool production

Studies reporting genetic associations between reproduction and other traits should be interpreted with some caution, because reproduction places a physiological load on a ewe, which can directly impact on other traits. In some studies this is taken into account during parameter estimation (e.g. Brown *et al.* 1966, Coelli *et al.* 1998), whereas in other it is not (Safari *et al.* 2007 a,b,c). Whether or not fleece traits have been adjusted for reproductive performance affects interpretation of genetic parameters and also how

costs of increased production are handled when deriving economic weights for a selection index.

Using all the relevant information from resource flocks that was available at the time, Safari *et al.* (2007c) estimated the genetic correlation between CFW and LW/EJ to be negative but small (-0.26 ± 0.05), consistent with the average found in an earlier literature review of -0.12 (Safari *et al.* 2005). Correlations of this magnitude are obviously not large enough to preclude simultaneous improvement in both traits and indeed, unfavourable correlated responses have not been found in experimental lines selected for increased fleece weight. For example, Piper *et al.* (2007) found that in CSIRO fleece weight selection lines there was no adverse response in lifetime reproduction rate, similar to the Trangie fleece weight selection lines (Barlow 1974)³⁰ and selection lines in Western White-face ewes in the US (Saboulard *et al.* 1995). Adams *et al.* (2006) argued that reproductive performance may be adversely affected in animals with increased capacity for wool production, especially if feed supplies are reduced. Support for this proposition can be found in the study of ewes in the Trangie QPLU\$ flocks by Hatcher and Atkins (2007), who reported that progeny of ewes with high hogget CFW had poorer survival than lambs with low CFW dams. This impacted adversely on the lifetime NLW of high CFW ewes. At the phenotypic level, high hogget bodyweight was positively associated with subsequent NLW, while FD showed no association.

A novel insight into the relationship between reproduction and other production was provided by Lee *et al.* (2009a), using data from over 7000 ewes in the Trangie C, D and QPLU\$ flocks. They found that ewes in the top quartile for lifetime reproduction rate (LW/EJ), adjusted for the effects of birth year and bloodline (or selection line), produced the same or slightly more clean wool as hoggets than ewes in the bottom quartile, suggesting that there is no intrinsic antagonism between reproductive potential and wool production when ewes are not reproducing³¹. This is consistent with the results of Piper *et al.* (2011) who looked at lifetime reproductive rate in classified ewes on their performance at 18 months in random-mating flocks at Cunnamulla. Ewes identified as superior for fleece weight, fibre diameter or two selection indexes at Cunnamulla had similar lifetime reproduction to others in their cohort, while there was a positive association between hogget liveweight and lifetime reproduction. In this environment, feed supplies are regularly compromised, and their analyses showed that these associations were statistically consistent across good and bad years (Piper *et al.* 2011). In a larger study of random-mating ewes at Armidale, results were similar except that there was also a positive association between wool traits and reproduction (Piper *et al.* 2013).

Lee *et al.* (2009a) went further and looked at the association between lifetime reproductive quartile and lifetime wool and body characteristics. They found that ewes in the top (best) quartile for lifetime NLW produced 6-8% less clean wool during their lifetime than ewes in the bottom quartile, illustrating the cumulative effects of reproduction. The differences between the top and the bottom reproduction quartiles

³⁰ Barlow (1974) did report a significant NLW difference in 2yo ewes in favour of the Fleece-minus lines but the Fleece-plus lines produced more multiple births so that lifetime NLW was similar in both lines.

³¹ Differences between the top and bottom quartiles in terms of net reproduction rate were large and highly significant ($P < 0.001$), equivalent to about one lamb per ewe per year or over 100% of the mean, and were expressed in all components – fertility (about 50% of the mean), fecundity (25%) and lamb survival (60%).

were much smaller in average pre-mating liveweights (0-1%) than for wool weight; whereas as hoggets, the top quartile ewes averaged 3-6% greater body weight than the bottom quartile ewes.

Together, these observations indicate that ewes that were heavier as hoggets tended to have a greater net reproduction rate during their lifetime. However, as shown by Lee *et al.* (2009a), over the course of the ewes' productive life this increased reproductive load eliminated any liveweight advantage and was associated with a decline in wool weight. Effects on average fibre diameter tended to operate in the same direction but were very small i.e. ewes in the top quartile for lifetime reproduction tended to have average fibre diameters about 0.1 microns greater than bottom quartile ewes as hoggets, but over their lifetimes, the micron differential was reversed. The authors cited evidence from other species suggesting that females with a high lifetime reproductive performance have greater longevity and lower reproductive costs than their less productive contemporaries. They also hypothesized that the great variability found in lifetime reproductive performance could be exploited to advantage by applying targeted management/supplementation strategies to different flock segments. Similar analyses could usefully be carried out with data from other resource flocks.

At the level of Merino strains, Greeff (2005) concluded that: "*Merino strains with high wool production have lower lifetime reproduction rates*". However, the paper's title was arguably misleading because this conclusion was based on defining lifetime reproduction rate as the weight of lambs weaned over at least three lambing opportunities (not lifetime and not NLW), defining wool production as wool produced per kg of body weight (not CFW) and deeming one of the six data points (fine wool) to be an outlier but not another that also had quite anomalous lambing rates (medium wool). If average NLW is plotted against fleece weight, the trend is actually the opposite (Appendix 7), but could be (non-significantly) in the claimed direction if the two "foreign" flocks are ignored. This is of course not to say that Merino strains that produce more wool don't produce fewer lambs, but the data presented by Greeff (2005) do not convincingly support this claim. It would be a relatively straightforward exercise to examine this proposition more stringently across the entire resource flock data base.

Despite inconsistent phenotypic associations being found within flocks and published across-strain evidence being questionable, it is reasonable to expect that fitness traits may decline when finite resources are diverted to production traits, as predicted by resource-allocation modelling (van der Waaij 2004). This point was acknowledged by Swan *et al.* (2007), who in their discussion of breeding objectives for Australian Merino sheep, stressed the importance of including important fitness traits in the breeding objectives and as selection criteria. Ostensibly, the most important aspects of fitness are net reproductive performance and disease resistance; and the current genetic evaluation system will already accommodate these traits, in combination with the main production traits (including adult performance), if the relevant information is supplied. Whether or not an additional fitness trait should be introduced such as longevity, which is used in the Australian dairy industry (Pryce *et al.* 2010) warrants some debate. However if sheep breeders cannot (or are reluctant to) provide reproductive records for genetic evaluation, it is difficult to imagine that they would enthusiastically embrace the idea of providing longevity records, complete with details of why animals exited a flock prematurely. If there was support, there is no technical reason why such a trait could not

be included, but its utility above and what exists already would need to be carefully assessed.

Quite apart from questions around the extent to which reproduction and fleece production are likely to compete for resources, it should be recognised that the actual value of reproduction rate relative to wool production is highly dependent on the assumptions made about feed intake³². Atkins (1987) calculated that if stocking rate was reduced in proportion to expected feed intake, the value of NLW fell by over 70% relative to a situation where feed intake was ignored, the value of adult body weight changed from positive to negative, while the value of fleece weight and average fibre diameter were both unaffected. It can be shown that the direct economic value of increasing reproduction is very small indeed in a situation where feed is fully utilised, the impact of reproduction on fleece value is fully costed and wool prices are high relative to meat prices.

Finally, it is clear that the physiological relationships between liveweight maintenance, wool production, reproduction and energy balance are complex and not fully understood, as discussed recently in a review by Ferguson *et al.* (2013). The key to accommodating these relationships in a breeding program, particularly in light of the comments by James (2009³³) and Swan *et al.* (2007³⁴), is to ensure that all traits of importance and their associated costs are included in the breeding objective. Furthermore, selection programs need to be underpinned by sufficiently precise estimates of genetic associations among traits of importance. With this framework in place, rational decisions can then be made about which combination of trait measurements (or genotyping strategies) will be the most cost-effective in securing optimal genetic gain.

More research is needed to better understand the genetic and phenotypic associations between lifetime reproduction and wool production as well as the impact of any trade-offs on design of breeding objectives. Strategies to exploit the repeatable nature of reproductive performance and the possibility of tailoring management of different flock segments (based on their reproductive performance) warrant further investigation.

Age effects on progeny body weights

Age of dam effects on progeny weights at four different ages in pooled resource flock data are shown in Figure 12. In estimating these age effects, Safari *et al.* (2007a) accounted for differences in birth-rearing status, gender and birth date. In relative terms, dam age effects were greatest at birth and declined up to hogget age. Birth weights reach a maximum when ewes were six years old, but subsequent weights were greatest in progeny of five year old ewes.

³² Whether feed is costed only when likely to be limiting or costed all year round is in fact one of the reasons why results from wether trials and MERINOSELECT may appear to differ (Brown *et al.*, 2012).

³³ Cited on page 8

³⁴ Cited on page 34

Many individual studies simply accounted for dam age in terms of whether dams were maiden or mature, including early studies of CSIRO lines (Young *et al.* 1965); but as noted by Safari *et al.* (2007a) the patterns evident in Figure 9 are consistent with those reported in South African Mutton Merinos (Cloete *et al.* 2002), Rambouillet (Lewis *et al.* 1989), Baluchi sheep (Yazdi *et al.* 1998) and US breeds (Notter *et al.* 2005). They are also within the range of dam age effects on weaning weights found in six Merino ram studs in Victoria in 1970-71 (Ransom and Mullaney 1976).

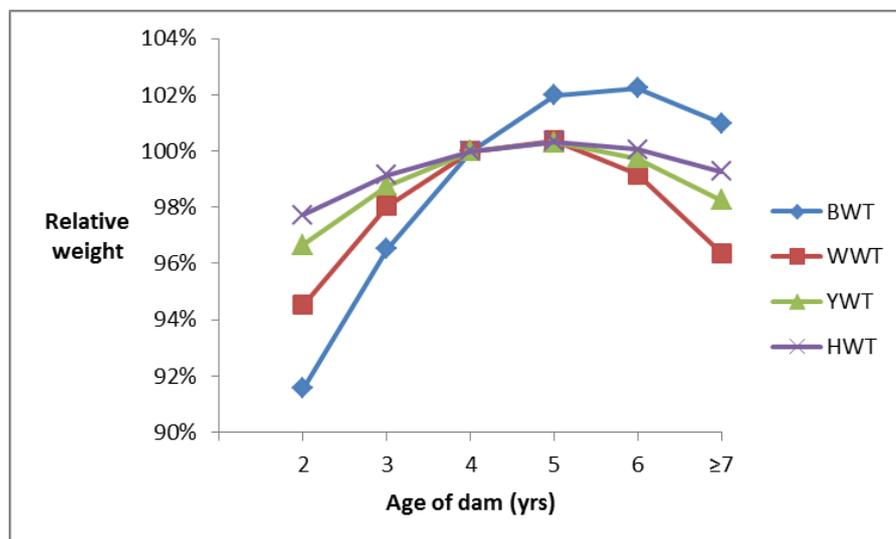


Figure 12. Relationship between ewe age and live weights progeny at birth (BWT), weaning (WWt), yearling (YWt) and hogget (HWt), relative to four-year-old ewes. Source: Pooled resource flock data, Safari *et al.* (2007a).

Collectively, evidence suggests that the effects of dam age on body weights up to hogget age have been consistent across breeds and time, and the circumstantial evidence is that the pattern of influence of a ewe on the growth rates of its progeny is relatively invariant to genetic changes in other traits.

Estimates of ewe age effects on progeny body weights appear to be relatively consistent across breeds and over time, being most pronounced for birth weight and declining in importance through to hogget age. Six-year old ewes tend to have the heaviest lambs at birth and five-year old ewes tend to have heaviest progeny at subsequent ages.

Genetic aspects of body weight at different ages

Changes in the relative contributions of direct and maternal genetic effects on body weights, and maternal environmental effects up to about 17 months of age were examined in some detail by Safari *et al.* (2007a), using the pooled resource flock data set. Essentially as lambs became older, direct genetic effects on body weight increased (heritabilities increased from 0.18 at birth to 0.38 as hoggets), maternal genetic effects

decreased (0.19 at birth to 0.03 as hoggets³⁵), maternal permanent environmental effects decreased (0.07 to zero), litter effects decreased (0.33 to 0.06) and the direct-maternal correlation changed from negative to positive (-0.15 to 0.25). This information has little to do with lifetime productivity but it does provide some guidance as to what is likely to change when selection is focused on any of these early stages of growth; and they are generally consistent with temporal patterns in dam age effects on lamb growth.

Additive genetic effects assumed for body weight in MERINOSELECT analyses are shown in Table 2. According to A.A. Swan (*pers comm.*), ‘Adult weight’ refers to mature weight and can be recorded from 2 years and up. The average age of adult weights in the MERINOSELECT database is relatively low, at 780 days, or a little over two years. The author is unaware of estimates of between-age genetic correlations among different mature weights of Merino sheep having been published, which is somewhat surprising given that ewe weights are typically recorded at least annually in resource flocks.

Table 2. Additive (direct) genetic correlations and heritabilities assumed in MERINOSELECT. Heritabilities are on the diagonal and genetic correlations below the diagonal. (source: A.A. Swan, *pers. comm.*)

	WWt	PWt	YWt	HWt	AWt
WWt	0.25				
PWt	0.79	0.30			
YWt	0.70	0.84	0.35		
HWt	0.66	0.80	0.90	0.40	
AWt	0.60	0.70	0.80	0.89	0.40

Any index with a positive weighting for one or more of the early weights will almost certainly lead to a positive correlated response in adult weights, because of the strength of the correlations. However, the magnitude of such a correlated response expressed towards the end of a ewe’s productive lifetime cannot be deduced from the available literature. In any case, given that mature weight has a low economic weighting in Merino breeding objectives (and can actually be negative³⁶ e.g. Atkins 1987), changes in body weights that might occur unexpectedly at six or seven years as a correlated response are unlikely to be of major economic consequence in itself. It is only if there are associated changes in wool or reproduction that this would assume some importance.

The level of body fat in mature ewes is a component of mature ewe weight and is of some relevance to their reproductive performance (e.g. Oldham and Thompson 2004) and their ability to survive a period of under-nutrition. Although fat depth can be included as selection criterion in some common Merino indices (e.g. the DP+ index of MERINOSELECT, A.A. Swan, unpublished), fat is not assigned an economic value *per se* in any standard breeding objectives. Rather, it is used as an indirect indicator for other traits of importance such as eye muscle depth and NLW.

In a study of factors affecting Merino ewe weight and fat over time, using lifetime body weights of animals in the Trangie D flock, Walkom *et al.* (in press) found the genetic component of weight and body condition remained relatively constant across a ewe’s

³⁵ Expressed as a proportion of phenotypic variance

³⁶ This is because of its association with the nutritional cost of maintenance

production cycle and age. The overall additive genetic effect accounted for 92% of the genetic variation in weight of Merino ewes bred across five production cycles. They concluded that to improve weight and condition of ewes during periods of under-nutrition, selection should be directed at improving weight and condition at all times. Given that body condition is only one aspect of maternal performance, the focus in a genetic improvement program should be on the traits of direct economic value, which is perhaps the main message from this work and from other studies involving body weight.

Maternal genetic effects on production

Following reports of maternal genetic effects having significant influences on fleece and body weights in Merinos (e.g. Swan and Hickson 1994, Mortimer and Atkins 1994, Hickson *et al.* 1995 and review by Safari *et al.* 2005), an investigation was undertaken by Asadi Fozi *et al.* (2005), using information from the CSIRO Finewool flock to examine in some detail the consequences of accounting for maternal genetic effects. Significant maternal genetic effects were found for wool and body weight traits (GFW, CFW, BWT, WW and YW) and heritabilities were over-estimated if maternal effects were ignored. However, maternal effects were not important for traits related to fibre diameter and NLW. Direct-maternal genetic correlations for the wool and body weight traits were moderately negative, suggesting that if maternal effects were ignored in a breeding program, they may deteriorate over time, depending of course on the breeding objective and correlations with other traits. Asadi Fozi *et al.* (2005) explored the potential consequences of accounting for maternal genetic effects in both the selection criteria and breeding objectives across a range of micron premiums. Essentially, ignoring these effects altogether led to over-estimation of total responses by 3-36% compared with including them in the genetic covariance matrix, with the magnitude dependent on micron premium (greater at low premium). Taking the additional step of assigning a value to maternal effects in the breeding objective increased the predicted response by up to 14%. After modelling a wider range of traits, Huisman *et al.* (2008) concluded that fitting maternal genetic effects (and covariance between direct and maternal genetic effects) was warranted for most of the bodyweight traits, greasy and clean fleece weight, fibre diameter and coefficient of variation of fibre diameter.

Examining maternal genetic trends in industry data is problematic because of incomplete recording of maternal genetic linkages in the MERINOSELECT database. According to D.J. Brown (*pers. comm.*) Sheep Genetics research has found that inadequate data quality can lead to incorrect partitioning or (co)variance components. Notwithstanding this caveat, A.A. Swan (*pers. comm.*) observed that overall, the maternal genetic trend for body weight since 2001 in MERINOSELECT flocks has been negative but extremely small - equivalent to about 1kg loss per 50 years. For fleece weight, there was also a very small negative trend of 0.15kg per 50 years. In two fully-pedigreed Merino flocks, maternal genetic trends varied from very small negative to moderately positive. This, together with evidence of a relatively strong maternal genetic trend for body weight in terminal sire breeds (where maternal effects are not included in the objectives, A.A. Swan, *pers. comm.*), suggests that ignoring maternal genetic effects will certainly lead to sub-optimal gains, but if an unfavourable correlated response occurs at all, it is not likely to be large enough to be of concern.

Pedigree information is required to adequately account for maternal effects. Ignoring maternal genetic effects in genetic evaluation will lead to sub-optimal gains, but if an unfavourable correlated response occurs at all, data suggest that it is not likely to be large enough to be of concern.

Age effects on worm egg counts

Selection for low worm egg counts (WEC) is typically carried out using measurements on weaners, which is when they are most susceptible to worm infection. As noted by Woolaston and Eady (2004), the natural immunity of Merinos gradually increases to about 12 months of age, after which susceptibility is usually only a problem in the peri-parturient period - from the final one or two weeks of pregnancy through to mid-lactation. It is important to know whether selecting at weaning age will confer relative resistance at later periods during an animals' first year and during the peri-parturient period. Evidence from experimental flocks indicates that if sheep are selected after weaning, this confers degree of resistance as early as 9 weeks old (Ward *et al.* 1999), which is also evident later in life whether ewes are in a peri-parturient state or dry. Although he only examined data from one year, Woolaston (1992c) found no statistical differences in worm egg counts across the five ewe age groups during infection. In a larger study involving Uruguayan Merinos, Goldberg *et al.* (2012) estimated the genetic correlation between WEC in post-weaning lambs and peri-parturient ewes to be 0.81 ± 0.11 , with no detectable age effects in peri-parturient ewes. Furthermore, selection was far more efficient when sheep were measured as weaners, whether the objective was to reduce WEC at that age or in the peri-parturient ewe.

Work is currently in progress by L. Li and colleagues to examine between-age correlations in over 20000 WEC records collected in nine Sheep CRC Information Nucleus flocks during 2007-2011. The four ages categories considered are weaning, early-post-weaning, yearling and hogget, with 42% of the records coming from progeny with a Merino sire (D.J. Brown, *pers. comm.*).

Research to date indicates that in the context of lifetime performance, selection for reduced WEC is best practiced in young sheep, but the most effective age between weaning and yearling is the subject of current research by Sheep Genetics.

Age effects on other diseases

Following a footrot outbreak in the mixed-age CSIRO *Haemonchus* selection lines, Woolaston (1993) found a progressive and statistically significant increase in severity score between 2yo and 7yo ewes, which also translated into a higher severity score among lambs with mature dams than those with maiden dams. Little quantitative information was available on other diseases on the extent to which susceptibility is affected by adult age. It is known that wrinkle score tends to increase with age in both ewes and rams (Brown *et al.* 1968), as shown in Appendix 3. Fleece rot and flystrike incidence are both recorded on adult ewes in the Armidale breech strike genetics flock, but age effects have not been published to date. J.L. Smith (*pers comm.*) observed that

in general, weaners tend to be the most susceptible, followed by breeding ewes then yearlings. In the equivalent WA flock at Mt Barker, flystrike incidence is not recorded among adult ewes.

Skin wrinkle and reproduction

The degree of skin wrinkle in Merinos has been associated at the phenotypic and genetic level with poorer performance in most aspects of reproduction (Young *et al.* 1963, Fels 1963, Dun 1964, Dun and Hamilton 1964, Drinan and Dun 1965, McGuirk 1969, Donnelly 1978, Rose 1978). Although many breeders have undoubtedly been cognisant of these findings when implementing their selection decisions, little work has been done since these early studies to see whether this could be exploited more systematically in selection programs. Mortimer *et al.* (2009) used records pooled across four research flocks to confirm that neck and body wrinkle scores are highly correlated genetically, have high heritability and are phenotypically variable. Furthermore, wrinkle was positively correlated genetically with GFW, CFW, CVFD and CURV, while negatively correlated with YLD, SL and HWT (or YWT). Using records in the Sheep Genetics database, Brown (2012) estimated a negative genetic correlation (about -0.2) between body wrinkle and NLW, consistent with earlier research. This suggests that wrinkle score may have the potential for a greater role in predicting lifetime reproductive performance, as it is not currently included in analysis of reproduction in Sheep Genetics analyses. Any additional benefit for predicting NLW will need to be weighed against the increased computational demands of including additional traits but perhaps more importantly, the consequences of using imprecise genetic parameters or tenuous assumptions about genetic group covariances. In particular, it is important to recognise that across-flock associations may differ from between-flock associations.

Standard breeding objectives for Merinos

The QPLU\$ flocks at Trangie were established to demonstrate the consequences of selection using different breeding objectives. Although lifetime productivity has not been reported in detail³⁷, bulletins released during the course of the program indicate that selection generally achieved the desired effects, with very few unexpected, undesirable trait changes (Appendix 8).

Standard MERINOSELECT breeding objectives have been developed for three main production systems: Dual Purpose (meat focused), Merino Production (wool and meat) and Fibre Production (wool focused). Table 3 indicates the profit traits included in each.

³⁷ The QPLU\$ flocks did contribute data to the study of lifetime reproduction performance by Lee *et al.* (2009a,b) (described on page 27), which also examined average lifetime performance for fleece traits and body weight.

Table 3: Traits which affect commercial flock profitability for each production system (A.A. Swan, pers comm.)

Trait group	Trait	Dual Purpose	Merino Production	Fibre Production
Wool	Yearling clean fleece weight (%)	✓	✓	✓
	Adult clean fleece weight (%)	✓	✓	✓
	Yearling fibre diameter (micron)	✓	✓	✓
	Adult fibre diameter (micron)	✓	✓	✓
	Yearling staple strength (Nkt)	✓	✓	✓
	Adult staple strength (Nkt)	✓	✓	✓
	Yearling curvature (degrees)			✓
	Adult curvature (degrees)			✓
Growth and carcass	Yearling body weight (kg)	✓		
	Hogget body weight (kg)		✓	✓
	Adult body weight (kg)	✓	✓	✓
	Maternal body weight (kg)	✓	✓	✓
	Dressing percent (%)	✓	✓	✓
	Saleable meat yield (%)	✓	✓	✓
	Carcass eye muscle depth (mm)	✓		
Worm resistance	Worm egg count (%)			✓
Reproduction	Number of lambs weaned (%)	✓	✓	✓

Adult expression has been differentiated from yearling or hogget expression for fleece weight, fibre diameter, staple strength, fibre curvature (Fibre Production objective only) and body weight, but not for reproduction. This implies that for any particular set of recorded measurements, some emphasis is directed towards improving adult expression in these traits, quite apart from improvements at younger ages. The distribution of genetic gains in the various objective traits depends on the index chosen but also on exactly which traits are measured, as well as the assumed and actual genetic parameters.

A.A. Swan (unpublished) used stochastic simulation to predict trait gains in the various objectives over a 10 year period, assuming that phenotypic data were only collected at weaning (weight), post-weaning (WEC) and yearling age (weight, carcass and fleece traits), with selection criteria varying between objectives. Contributions to total gains from adult animals in the form of fleece traits, reproduction, adult weight and maternal effects accounted for:

- 37-39% in Dual Purpose indexes
- 33-37% in Merino Production indexes and
- 55-62% in Fibre Production indexes

The rest of the gain came from young animals, with contributions coming from meat, wool or worm resistance, depending on the index. These computations therefore indicate that 38-67% of the gains from a Merino breeding program are likely to come from traits that are expressed close to measurement age, but that 33-62% come from gains expressed at later ages, beyond the age of measurement. As logic would suggest, the greatest disparity between the age of measurement and the age of economic impact occurs with indexes that have the most emphasis on fibre production.

Accordingly, assumptions about age effects *per se* or about juvenile-mature genetic correlations are more important when fibre production is the main focus.

Errors due to incorrect assumptions can be mitigated if breeders submit at least some phenotypic records collected at these later ages. This would have the benefits of:

- a) providing more accurate predictions because of the inclusion of extra information;
- b) redirecting some of the gains to traits expressed later in life simply because of the correlations between index and objective traits; and
- c) placing less reliance on juvenile-mature correlations (about which our knowledge is imperfect).

Consequences from applying incorrect assumptions about juvenile-mature correlations during genetic evaluation can also be quantified using existing methodology (e.g. see Sales and Hill 1967a, 1967b; Safari *et al.* 2006). It seems logical to test the impact of using incorrect parameters for associations where knowledge is least robust. This might include age-specific expressions of reproduction rate and associations of other traits with lifetime reproductive performance.

Aside from reproduction, feed intake is an important trait about which our knowledge of genetic parameters is even more limited. However, intake is not currently included directly as a trait in the breeding objective (as suggested by van der Werf 2004), but rather its cost is included as a function of production. As alluded to earlier, Atkins (1987) showed that varying the assumptions about the importance of feed intake can affect the economic value of NLW by over three-fold, and can change the value of adult body weight from positive to negative. If the assumption is made that no feed is wasted (e.g. so that stocking rate is determined entirely by intake), then the value of reproductive rate was greatly reduced. He identified feed costs as a priority for further research – a priority that still remains to this day, awaiting the development of technology that can accurately and reliably measure the intake of grazing animals.

Conclusions and observations

1. Modelling indicates that with current costs and prices and with typical productivity profiles, the optimum age structure in a self-replacing Merino flock involves 5-6 ewe age groups. This compares with five age groups when first examined by Turner and colleagues in the 1960s; although the optimum can vary depending on reproduction rates, death rates and the relative prices of wool vs meat. High meat prices favour retaining ewes longer than high wool prices. Nevertheless, differences in profitability between four and seven ewe age groups are generally small.
2. Age effects on the main production traits have been well studied using data sets combined across flocks, but very little has been published on whether age “trajectories” differ between bloodlines or different sheep types run under the same conditions. There is quite a lot of information available from resource flocks and the Sheep Genetics database to test whether age effects differ between lines of sheep. Such analyses may provide some insight into whether or not certain types of sheep are more predisposed to early declines in productivity.
3. The genetic control of fleece weight and average fibre diameter up to at least six years of age has been well characterised in Merino populations, as it has with the associated traits of yield, CVFD and SDFD. However, further investigation into between-age correlations for fleece weight in existing fine-superfine data is warranted.
4. As is the case for resource flocks, the distribution of adult records in the Sheep Genetics database is very much skewed towards younger ages. In most research flocks, ewes have been culled after four or five lambing opportunities, so there is generally insufficient information from older animals for satisfactory estimates of genetic parameters at the upper extreme. This is particularly the case for NLW, where very large numbers of records are required to estimate between-age correlations. In addition, the number of cohorts with cast-for-age measurements available is typically 4 or 5 less than the total number of years that records are collected. This is because foundation ewes are generally not included (or if they are they are unpedigreed with limited knowledge of prior management), so there can be a lag until experimental animals reach their final age.
5. An obvious knowledge deficiency is in the predictability of very early fleece measurements. Sheep Genetics researchers are aware of this and are currently examining the feasibility of using records in the Sheep Genetics database to help fill knowledge gaps; and perhaps changing the current age thresholds. Using existing data to further examine the predictability of early fleece measurements is warranted. Although early fleece records are not currently used in genetic evaluation (contemporary groups with a mean age of less than 232 days), they are still maintained in the MERINOSELECT database if submitted and could be used for research purposes.
6. Because fleece records from young animals are not included in routine analyses, there is an incentive for breeders with such data to furnish incorrect age information. The extent to which this is occurring is not fully known, but the incentive could be negated if parameters were available for young ages so that they could be included in routine evaluation.

7. Phenotypic associations between fleece weight and lifetime reproductive performance suggest that the cumulative physiological load of reproduction can depress fleece production. However, the finding that lifetime reproductive success and early fleece measurements are not adversely associated supports the proposition that at the genetic level, the relationship is not fundamentally unfavourable. In other words, the propensity for an animal to grow wool is not at odds with an animal's propensity to produce lambs. This suggests that it is only when an animal is asked to do both, that a small negative genetic correlation becomes apparent – probably as a consequence of both activities competing for available energy.
8. No adverse consequences on reproduction were found in long-term selection experiments directed at improving fleece weight, even in a challenging environment when resources were frequently limiting. In the Trangie QPLU\$ lines, ewes identified with high hogget fleece weights had lower subsequent lamb survival (and consequently lower NLW) than ewes with low hogget fleece weight. This contrasts with the CSIRO random-bred line where ewes with high hogget fleece weight had higher lifetime NLW than ewes with low hogget fleece weight.
9. These results can be interpreted in two ways. The first is that selection for fleece weight whilst ignoring reproduction rate may lead to a small decline in the latter across generations (though the literature is far from unambiguous on this point). An alternative perspective is that reproduction has a significant physiological cost, which must be adequately accounted for when assessing the economic value of reproduction.
10. This illustrates that the relationships between wool production, reproduction, body weight and energy balance are complex and not fully understood. These relationships can be accommodated appropriately in a genetic improvement program if: a) all traits of importance and their associated costs are identified and included correctly in the breeding objective; b) genetic predictions are underpinned by sufficiently precise estimates of genetic associations among traits of importance; and c) appropriate phenotypic information is recorded. The consequences of varying the key assumptions can readily be determined and this is a useful way of identifying the critical knowledge gaps.
11. Although it is the genetic relationships assumed in genetic evaluation that are most important, it is worth examining the claim that Merino strains producing the most wool have lower lifetime reproduction rates, using data from all contemporary comparisons of bloodlines in resource flocks.
12. The economic value of reproduction is heavily dependent on feed costs. Imperfect knowledge of feed intake in grazing animals as well as its genetic variation and covariation with production, remains a limitation to properly assigning economic values, particularly to reproductive performance and to a lesser extent, body weight.
13. Performance information collected in the various resource and demonstration flocks, particularly when combined, represent an extremely valuable research asset that has not been fully exploited. Although there is an initiative presently under way to rectify the situation, good information on exactly what records exist in the various resource flock databases is still lacking at the time of writing. There appears to be quite a lot of variability between the different institutions in the quality of record keeping and archiving (probably due to budgetary/resourcing

constraints). Copies of some of these data have been added to the Sheep Genetics database but it is far from complete. With the approval and co-operation of the relevant institutions, all relevant historical research data should be included in the Sheep Genetics database, where it is likely to be far more accessible, useful and secure.

14. Although genetic correlations between other production traits and NLW have been estimated with relatively high precision using resource flock data by Safari *et al.* (2007c) the average number of reproduction records for each ewe in that study was only 2.2. This indicates that reproduction data were mainly provided by young ewes; and consequently the co-heritabilities of production traits such as hogget liveweight, fleece weight and fibre diameter with later reproductive performance are less well characterised.
15. Advanced analytical methods such as random regression can help aid interpretation of genetic changes with age, but data inadequacies at the ends of the distributions (such as in very young and very old animals) remain a constraint no matter which analytical method is used.
16. Evidence from other breeds suggests that between-age correlations for NLW are very high, but this still needs to be established in Australian Merinos. Attempts to estimate these correlations from individual resource flocks have been predictably unsuccessful. However, adding all available data from the publicly-funded resource and demonstration flocks to the Sheep Genetics database should allow more robust investigations of the relationships between lifetime reproduction rate and lifetime wool production than is possible from individual flocks. Priorities include estimates of age-age correlations for NLW and its components, and genetic associations between yearling and hogget fleece characteristics and lifetime reproductive performance. If the data permit, comparing the associations in low fleece weight and high fleece weight animals would be informative.
17. Any attempts to establish additional research or demonstration flocks to specifically examine lifetime fleece weight–reproduction rate relationships at the genetic level, should be made with the understanding that that estimating reliable genetic parameters involving reproduction requires very large amounts of phenotypic data. This means either an extremely large commitment for several years or a more modest commitment over a number of generations. The alternative of using existing information supplemented with good quality information from industry flocks may well be more cost-effective. Industry data has the added advantage of being unambiguously current and relevant.
18. Further enhancements to Sheep Genetics methods to better account for lifetime productivity appears to be warranted. In particular, the practice of predicting EBVs for fleece weight and reproduction in separate analyses warrants closer scrutiny, as the two are inter-related. Combining EBVs in selection indexes without recognising the inter-relationship, as is currently the case, can lead to sub-optimal outcomes.
19. Investigations into the potential for including wrinkle score in evaluation of lifetime reproduction should continue as more data become available.
20. Current MERINOSELECT objectives take account of adult performance and any deviations from assumed parameters as animals approach their final age in the flock are not likely to be the source of major errors or inefficiencies. This could be

usefully tested by modelling a number of “what-if” scenarios using conventional methodology. However, it is not clear whether or not the full costs of increasing fleece weight (and perhaps body weight) are adequately accommodated in MERINOSELECT. This warrants investigation.

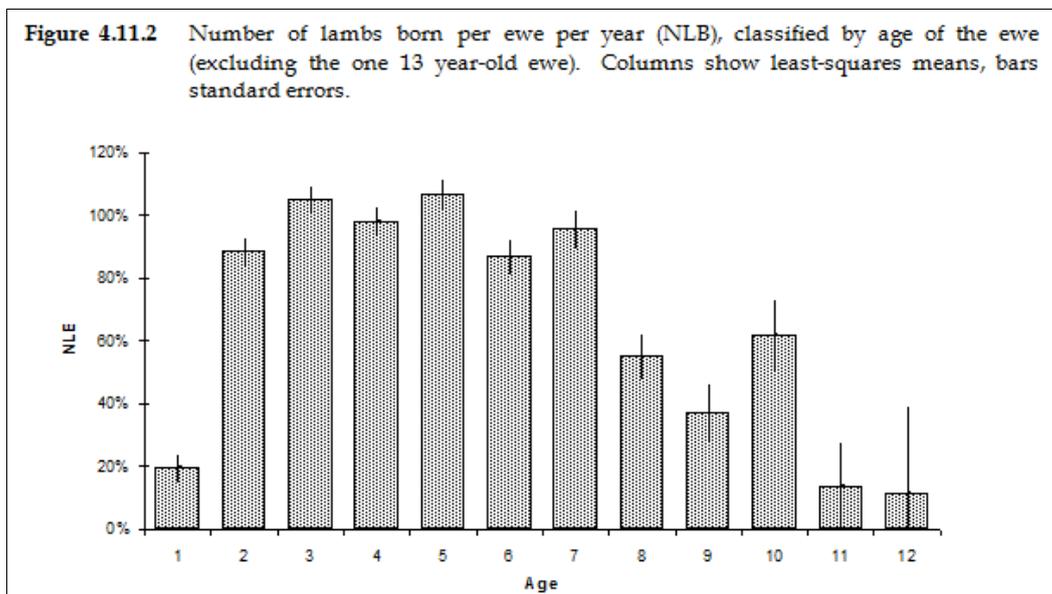
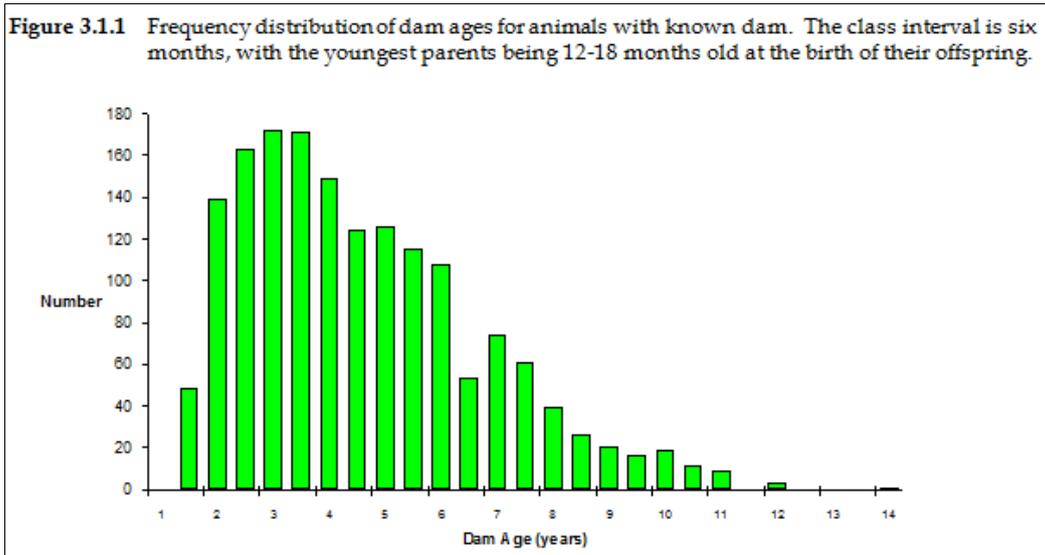
21. There appears to be a case for devoting resources to documenting and publishing the methodology and assumptions behind MERINOSELECT, in a manner analogous to the description of the Australian Profit Ranking in dairy cattle (Pryce *et al.* 2010). Documentation facilitates robust peer review and can be used in extension to help build confidence in the indexes. It also allows others to examine the consequences of varying some of the critical assumptions.
22. If the assumptions and computations behind the MERINOSELECT indexes are correct, then no matter what information is provided by breeders, the indexes will allow ranking of animals on the best prediction of their lifetime productivity given that information. This relies on details supplied by breeders being correct. The relative gains in the traits that contribute to lifetime performance will vary according to the selection criteria, but the aggregate value of these gains will be optimised for any particular combination.
23. Consequently, if breeders are concerned about being able to more accurately identify animals that will perform well at advanced ages, this can be readily accommodated by the current system if they supply records on at least some of their animals at the appropriate ages. This will improve the accuracy of prediction for those ages and change the relative gains accordingly. Whether or not there is sufficient awareness of this fact is not clear. As reinforcement, outcomes at various ages for different measurement strategies, especially multiple-stage selection, could be readily predicted, costed and included in extension material.
24. Some debate about the merits (or otherwise) of introducing another measure of fitness such as longevity is warranted, taking account of points 22 and 23 (above).
25. Researchers working on BREEDPLAN have done much work examining data quality and its impact for genetic improvement of beef cattle. Some of this is equally applicable to sheep breeding.
26. Encouraging breeders to submit records from older animals would have the added advantage of enabling better estimates of the relevant genetic parameters.
27. As noted by both Falconer (1967 Ch. 19) and Turner and Young (1969 Ch 9), correlations can be expected to change under selection, although as found by Sheridan and Barker (1974), the change is not always in the expected direction. Consequently, estimates do need to be reassessed over time.
28. Limitations in predictability that exist with conventional BLUP-based evaluation due to data inadequacies will also be a limitation using genomic selection. Adequate good-quality phenotypic information is equally a requirement for the estimation of reliable genetic parameters as it is for developing genomic predictions.
29. The ewe lifetime productivity trial being planned will have scientific value more so if its data can be added to the existing R&D and industry data. However, it should be assessed on a cost-benefit basis against alternative options and other priorities for breeding research, including the need to adequately fund reference populations for the development and application of genomic selection.

30. In summary, some research gaps and opportunities identified in this review which would expand our understanding of lifetime productivity and help build confidence in index rankings [with approximate page numbers in parentheses, where relevant] are:
- (a) Ensure that all available resource flock data are held in the Sheep Genetic database and adequately documented, so that many of the following research questions can be addressed.
 - (b) Investigate whether contemporary lines of sheep in the various resource flocks differ in lifetime productivity profiles [19], including a more robust test of the proposition that Merino strains with high wool production have lower lifetime reproduction rates [34].
 - (c) A detailed examination of lifetime wool production in fine and superfine animals using data from the CSIRO finewool flocks (FD has already been adequately characterised) [24].
 - (d) Characterise age effects on components of wool style, including an updated study using QPLU\$ data [22].
 - (e) Determine fleece measurements recorded earlier than the current threshold used by Sheep Genetics (contemporary groups with a mean age of less than 232 days) are sufficiently reliable [25].
 - (f) Determine whether there are sufficient data to estimate between-age correlations for NLW, its components and co-heritabilities with other traits [30], by pooling information across resource flocks and possibly combining ages.
 - (g) Assess the feasibility of developing more comprehensive (multi-trait) genetic evaluation models for lifetime reproduction [42] and determine the sensitivity of prediction to sampling errors in parameter estimates.
 - (h) Data permitting, examine the genetics of staple strength in breeding ewes [20] and interactions with fleece weight and reproduction.
 - (i) Extend the studies by Lee *et al.* (2009a) on relationships between wool production and lifetime reproduction to other resource flock data [33].
 - (j) Examine strategies to exploit the repeatable nature of reproductive performance and the practicalities of tailoring management of different flock segments based on their reproductive performance [35].
 - (k) Assess the potential for also including wrinkle score in genetic evaluation of lifetime reproductive performance [40].
 - (l) Determine the sensitivity of MERINOSELECT index rankings to changes in assumed genetic associations and economic weights. In particular, a re-examination of whether the full costs of increasing fleece weight and body weight are adequately accommodated in standard breeding objectives [46].
 - (m) Full documentation of the methodology and assumptions behind MERINOSELECT. This facilitates proper peer review and can be used in extension to help build confidence in the indexes [46].
 - (n) Examine incentives to that encourage breeders to submit more records from adult sheep for genetic evaluation.
 - (o) Assist breeders understand the cost effectiveness of alternative measurement strategies, especially multiple-stage selection [26].
 - (p) Examine whether the development of a longevity trait is warranted [34].
 - (q) Continue to monitor developments that might permit better measurement of feed intake at pasture and improved understanding of the genetics of feed efficiency [42].

Appendix 1. Age-specific statistics in a flock subjected largely to natural selection with random culling. Figures are taken from a report of the Yalanbee natural selection Merino flock (Woolaston 1992b). A summary of the flock's management can be found in Woolaston et al. (1995).

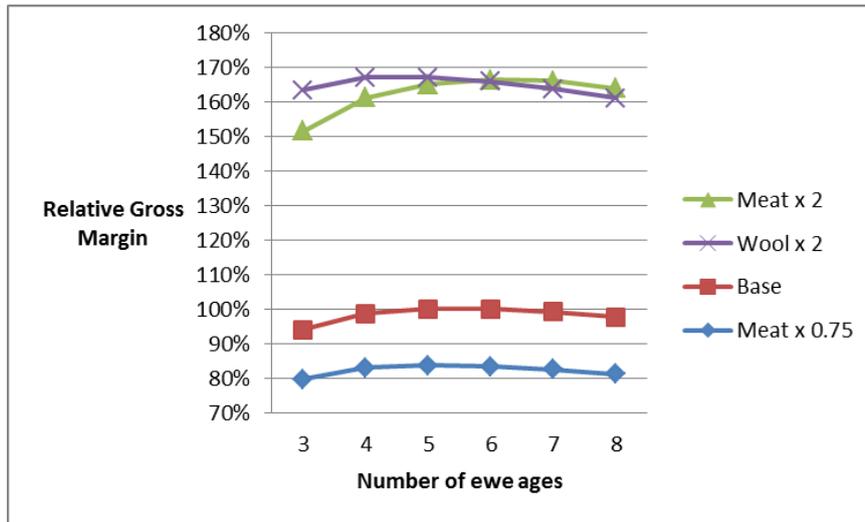
Table 4.2.1 Distribution of greasy fleece weights according to the number of records for each animal.

No of records	1	2	3	4	5	6	7	8	9	10	11	12	Total
No of Animals	258	111	97	91	64	46	54	28	20	13	7	1	790
Total	258	222	291	364	320	276	378	224	180	130	77	12	2732

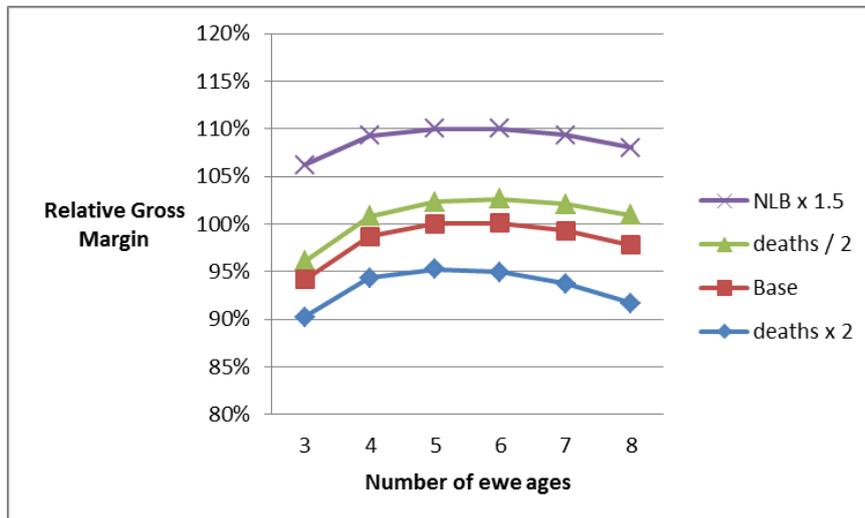


Appendix 2. Effect of ewe age groups on profitability for a range of assumptions. Gross margin with five age groups was set to 100% for the base case in all graphs³⁸. Results were derived using the method described by Woolaston (1992a), using the assumptions detailed in Table A2³⁹.

1. Impact of product prices, using economic parameters from DPI (2011) for an 18 micron ewe flock. Age effects and many other assumptions based on Turner and Young (1969) and other literature values, summarised in Table A2.



2. Impact of changes to base with increased reproduction rate and changes in ewe mortality rate, where the base is the same as in (1) above.



³⁸ Gross margins differ from those in DPI (2011), in that they included pasture maintenance as a variable cost, whereas in these calculations it was treated as a fixed cost, assumed to be the same across all scenarios. Including pasture maintenance increased variable costs by 18% and reduced gross margins by 9%. This would affect the scale of the vertical axes but not the shape of the curves.

³⁹ Similar software for examining flock structures is described on the Sheep CRC web-site but has not been investigated. See: <http://www.sheepcrc.org.au/resources/software--smart-merino.php>

3. *Impact of product prices and mortality rates, where the base was determined using economic parameters from DPI (2011) for an 18 micron ewe flock with age effects on wool and reproduction derived from resource flocks (Safari et al., 2005) as in assumptions #27, #29 and #30 below.*

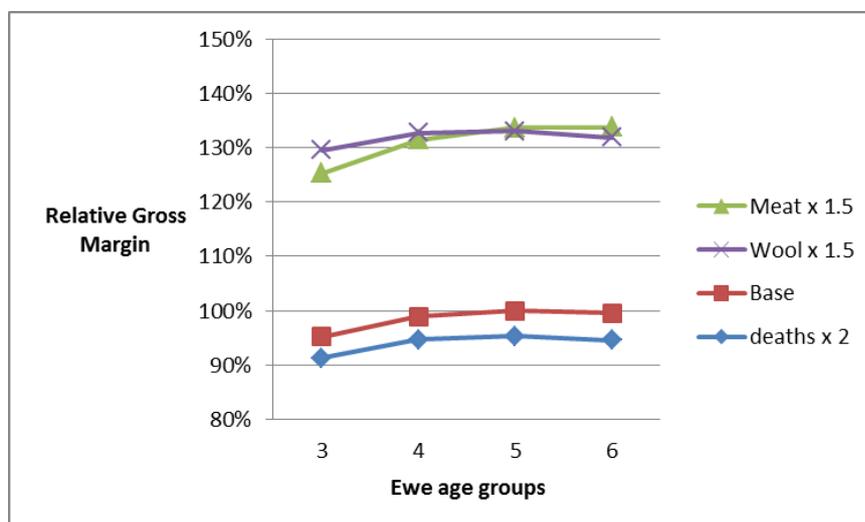
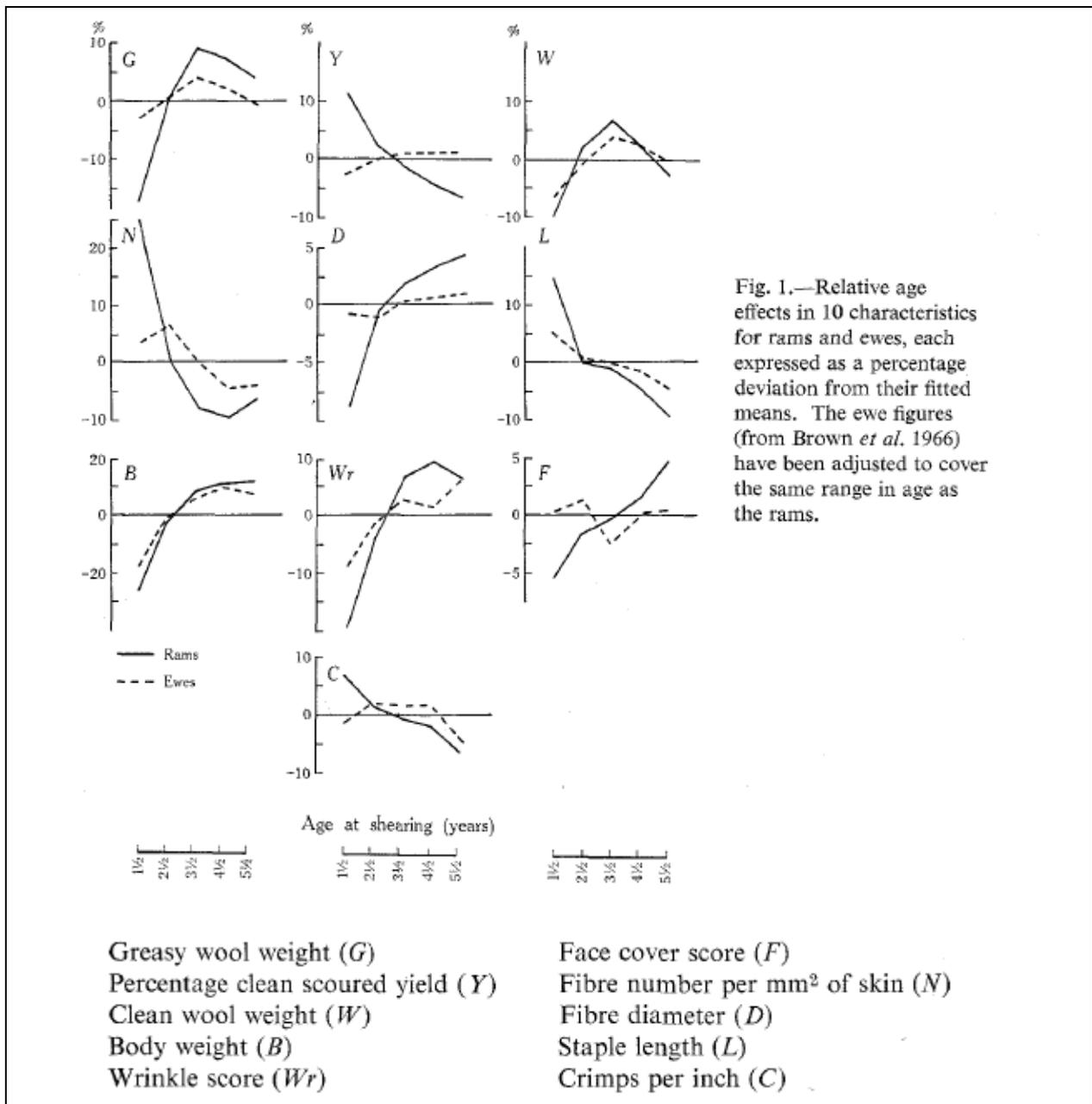


Table A2. Summary of parameters assumed

1. Ram percentage	2%
2. Number of ram age groups	2
3. Number of ewe age groups	Variable
4. Number of wether age groups	0 (sold as lambs)
5. Mortality- pre-marking in twins and singles	30%, 15%
6. Mortality- between marking and weaning	1%
7. Mortality- weaners and adults	2.2%
8. Drenches for ewes, weaners, hoggets and wethers	2,2,2,na
9. Vaccinations for ewes, weaners, hoggets and wethers	1,2,1,na
10. Jettings for ewes, weaners, hoggets and wethers	1,1,1,na
11. Unit costs of- shearing, crutching, wool packs, dipping, marking, mulesing, drenching, vaccinating, jetting, stock cartage, wool cartage and rams	As per DPI (2011)
12. Lambing percentage	NLB = 121% in 3yo ewes
13. Relative GFW due to reproduction	0/0-100%; 1/0-93%; 1/1-87%;2/1-86%;2/2-82%
14. Relative FD due to reproduction	Same across all classes
15. Relative GFW due to BR status	1/1-100%; 2/1-95%;2/2-90%
16. Relative GFW due to BR status	1/1-100%; 2/1-97.5%;2/2-95%
17. Relative GFW due to BR status	1/1-100%; 2/1-99%;2/2-99%
18. Base prices received for for weaners, surplus ewe hoggets, four tooth wethers, cfa ewes and cfa rams	As per DPI (2011)
19. Fibre diameter of wool from ewes, wethers and lambs	18 microns in 3½ yo ewes
20. Prices received for wool from ewes, wethers and lambs (c/kg greasy)	906; na;598
21. Interest rate applicable to the livestock inventory	0%

22. Base wool cuts for dry ewes, hoggets and weaners (kg greasy)	6.2; 6,2; 1.5
23. Proportion of young ewes culled on other than fleece weight	5%
24. Clean scoured yield	72%
25. Age effects on mortalities (ages 1.5 to 9.5yrs)	3%, 4%, 4%, 5%, 6%, 8%, 13%, 20%, 25%
26. Age effects on NLW (ages 1.5 to 9.5yrs)	-18%, 0, 11%, 21%, 18%, 8%, 3%, -4%, -15%
27. Age effects on NLW (resource flocks, ages 1.5 to 6.5yrs)	-16%, 0%, 9%, 12%, 9%, -1%
28. Age effects on GFW (ages 1.5 to 9.5yrs)	5%, 10%, 18%, 10%, 0%, -5%, -15%, -25%, -35%
29. Age effects on GFW (resource flocks, ages 1.5 to 6.5yrs)	2%, 2%, 0%, -5%, -12%, -22%
30. Age effects on MFD (resource flocks, ages 1.5 to 6.5yrs)	-5%, -2%, 0%, 2%, 3%, 2%
31. Micron premium	10%
32. Age effects on cfa value	x 1.6, 1.6, 1.5, 1.4, 1.2, 1.0, 0.8, 0.6, 0.4
33. Relative feed intakes - ewe reproduction class	0/0:1.2, 2/0&1/0:1.25,1/1:1.35,2/1:1.4,2/2: 1.5
34. Relative feed intakes – others	Lambs 0.1, ewe replacements 1.09, rams 2.0
35. Repeatability and standard deviation of wool weight	0.65, 0.5kg
36. Proportion of barren, single- and twin-bearing ewes as 3yo	0.02, 0.74, 0.24
37. Age effects on wether prices	na
38. Fibre diameter price schedule	na

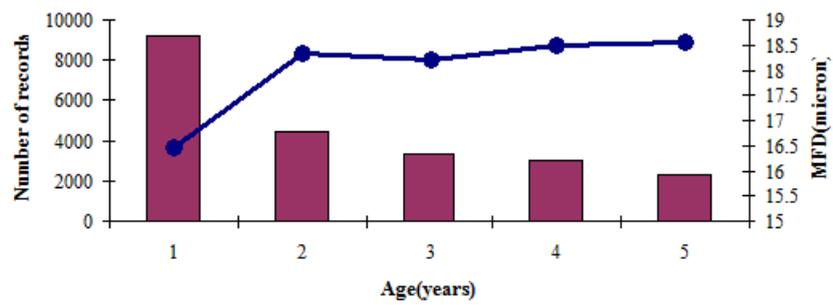
Appendix 3. Age effects on various wool and body traits, taken from Brown *et al* (1968) (dotted line represents ewes, unbroken line is rams).



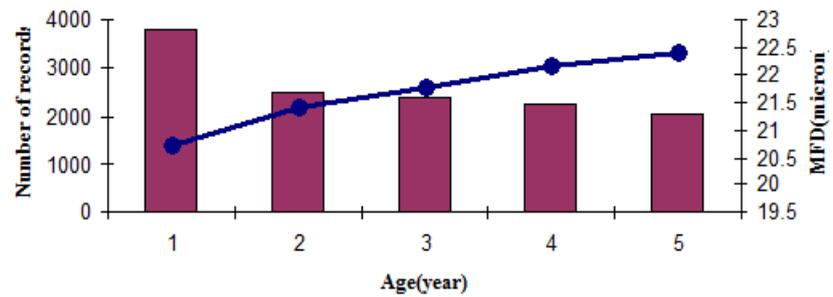
[This figure is reproduced with the kind permission of CSIRO Publishing. The original paper can be accessed at <http://www.publish.csiro.au/nid/40/paper/AR9680825.htm>.]

Appendix 4. Numbers of records and mean FD at different years for fine wool data (top chart) and medium wool (bottom chart) in study by Asadi Fozi (2005).

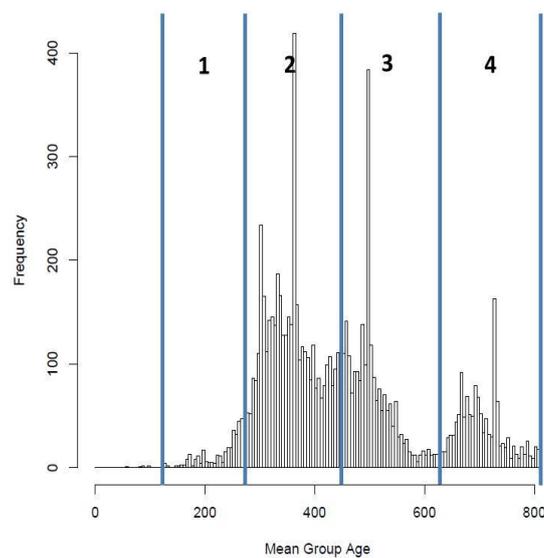
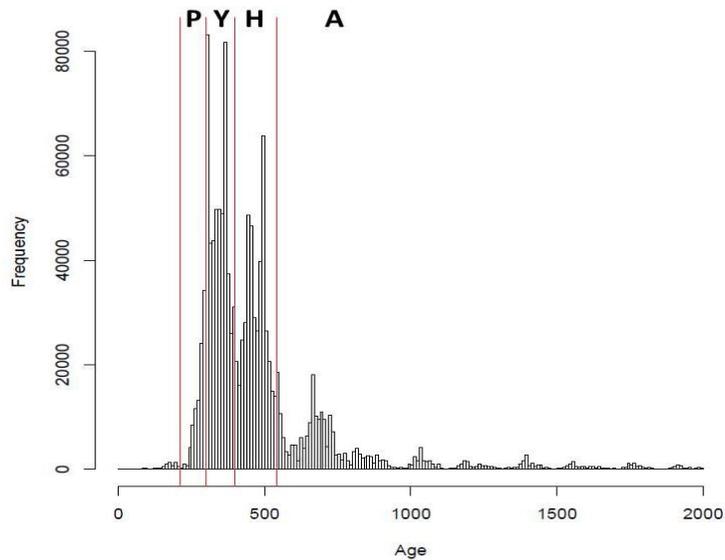
Fine wool



Medium wool



Appendix 5. Distribution of fibre diameter records in the MERINOSELECT database showing standard thresholds for Post-weaning (P), Yearling (Y), Hogget (H) and Adult (A) age classes in routine analyses. Wool data for P are received by the database but not included in analyses. The bottom figure shows an alternative method of classification (D.J. Brown, pers. comm.) which would allow parameters to be estimated from data on younger animals.



	1	2	3	4
Count	42,835	744,172	363,493	130,043
Groups	388	4,322	2,286	1,357
Mean Age	237.7	358.7	505.2	706.6
Min Age	127.0	275.5	450.0	630.2
Max Age	275.0	450.0	630.0	810.0

Figures kindly supplied by D.J. Brown, 14 May 2013.

Appendix 6. Minimum values of a between-age genetic correlation that are significantly ($P < 0.05$) different from unity for 75% and 90% power, with a trait having heritability of 0.1 or 0.6, and with different numbers of sires and progeny group sizes (after James 1979). See footnotes for further information.

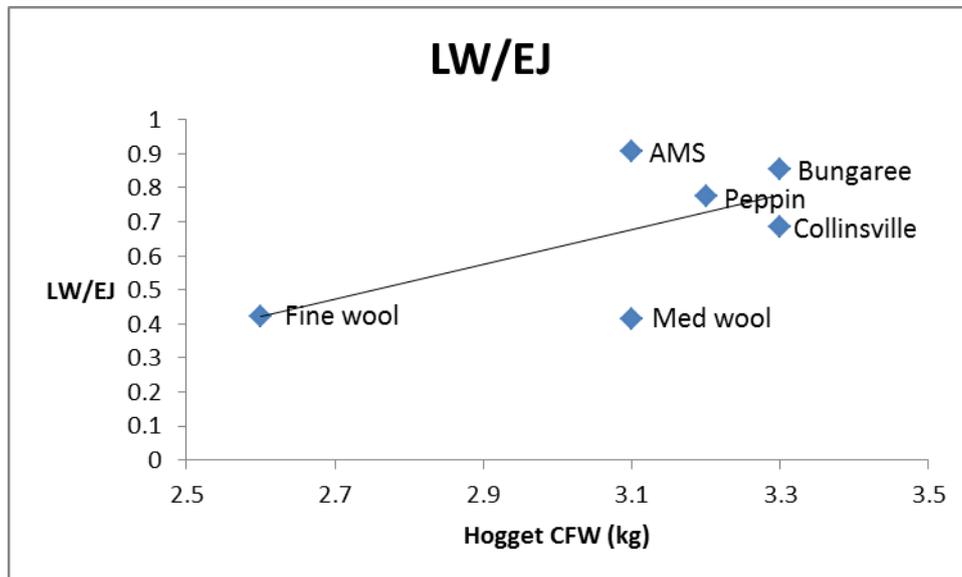
Sires	Power	Progeny per sire, $h^2=0.1$				Progeny per sire, $h^2=0.6$			
		10	45	70	100	10	45	70	100
50	75%	0.29	0.67	0.76	0.82	0.74	0.93	0.96	0.97
	90%	0.23	0.59	0.69	0.76	0.68	0.91	0.94	0.96
100	75%	0.39	0.75	0.83	0.87	0.81	0.95	0.97	0.98
	90%	0.32	0.69	0.78	0.83	0.77	0.94	0.96	0.97
200	75%	0.49	0.82	0.87	0.91	0.87	0.97	0.98	0.99
	90%	0.42	0.77	0.84	0.88	0.83	0.96	0.97	0.98
3100	75%	0.80	0.95	0.97	0.98	0.97	0.99	1.00	1.00
	90%	0.76	0.94	0.96	0.97	0.96	0.99	0.99	1.00

1. The above numbers are based on a sire model for a trait such as NLW with a heritability of 0.1 (left side) or a trait such as FD with a heritability of 0.6 (right side). In deriving the methodology for these calculations, James (1979) was investigating the power of different designs to test for a significant sire x environment interaction, analogous to a sire x age interaction, when expression at each age is measured in different progeny (which has a slightly different expectation of the error variance). It made no assumptions about approximating the standard errors of genetic correlation estimates. The paper went on to express the critical values of interaction variance in terms of genetic correlations, analogous to the table above. For these computations, a correction was made to a formula on page 21 of James (1979).
2. Using a full animal model instead of a sire model to estimate parameters provides additional information through all known relationships, but extra terms may need to be fitted to accommodate the changed expectations of variance components (see Becker 1984, Konstantinov *et al.* 2002). To the author's knowledge, little has been published on the power of experimental designs using animal models, except by simulating data structures and estimating parameters (e.g. Kelly and Swan 2005). See Arnold *et al.* (2011) for methods of using simulation to estimate the statistical power of mixed model designs.
3. Values in bold represent genetic correlations of 0.8 or greater. For example, in an experiment with a statistical power of 75%, a genetic correlation of 0.8 for NLW would be statistically different from unity with 3100 sire families each with 10 ewe progeny (having one record at each age), 200 sire families each with 45 progeny, 100 sire families each with 70 progeny, or 50 sire families each with 100 ewe progeny. These represent ewe progeny numbers of 31000, 9000, 7000 and 5000, respectively.
4. For a statistical power of 90%, the ewe numbers in (2) above for NLW should be multiplied by about 1.6.
5. If the aim is to test the genetic correlation between the average of the first two NLW records (e.g. as 2yo and 3yo) and the average of the last two NLW records (e.g.

5yo and 6yo), then the number of ewe progeny would be reduced to about 35-40% of those shown in (2) above, assuming a repeatability of 0.15. That is, for a power of 75%, about 1100 sire groups would be required if each sire had 10 ewe progeny with records, or about 280 sire groups if each sire had 20 ewe progeny.

6. If the heritability of NLW is less than 0.1, more observations would be required.

Appendix 7. Plot of average number of lambs weaned versus hogget clean weight taken from the paper by Greeff (2005). LW/EJ was calculated as the product $EL/EJ \times LB/EL \times LW/LB$.



Appendix 8. *Realised responses in lines subjected to balanced selection*

The following quotes were taken from progress reports of the QPLU\$ selection lines⁴⁰, described in more detail in Pope (2006)⁴¹

Issue 6 – July 2006

As a consequence of the selection imposed on fleece weight and fibre diameter within the QPLU\$ lines:

- *there were variable responses in staple strength, with the only significant change a 4.8 N/ktex increase in the fine selected line.*
- *staple length generally increased in the selected lines*
- *yield increased significantly in the fine and broad 8% lines*
- *clean price increases ranged from 11 to 168 cents/kg based on wool prices 2003-2005*
- *fleece value increases ranged from \$5.91 to \$11.32 per head*
- *fleece values increased from 14% – 35% per head.*

These estimates are based on a market period of relatively low wool prices and historically low premiums for fine wool. The fleeces also suffered the effects of drought conditions for much of the wool growing period (high dust content, low yield and low staple strength). Over the next 12 months we will undertake more comprehensive economic analyses covering a broader range of wool market and micron premium scenarios.

Issue 7- December 2006

- *Generally small and variable but sometimes significant changes in carcass characteristics.*
- *Any negative change found, can be easily accounted for using a selection index which includes those traits*
- *Other than for carcass weight, the changes observed are of minor commercial significance to the current slaughter value of surplus animals.*

Issue 8 – August 2007

- *Large permanent improvements in lifetime fleece weight and/or fibre diameter in all selected lines*
- *No change or improvements in most fibre characteristics in both age groups (hoggets and adults)*
- *No change or improvements in most fleece characteristics and classer grade*
- *No change or increases in adult ewe body weight*
- *No change or reductions in lamb survival and weaning percentage in three selected lines*

⁴⁰ <http://www.dpi.nsw.gov.au/aboutus/resources/periodicals/newsletters/a-few-selected-lines>

⁴¹ C E Pope (Editor), Trangie QPLU\$ Merinos – Open Day 2006

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