Breeding Focus 2021 - Improving Reproduction

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Preface

"Breeding Focus 2021 – Improving reproduction" is the fourth workshop in the series. The Breeding Focus series was developed to provide an opportunity for exchange between industry and research across a number of agricultural industry sectors. With this goal in mind, workshops have included presentations across multiple agriculturally relevant animal species to take participants outside their area of expertise and encourage them to think outside the box. Reproduction is a main driver for profitability and genetic gain. We will discuss existing knowledge, identify gaps and explore genetic and management strategies to improve reproduction further in multiple species.

Successful reproduction is a complex characteristic comprising the formation of reproductive cells, successful mating and fertilisation, embryonic and fetal growth and eventually a successful birthing event. In livestock species, reproduction traits have mostly low heritabilities, which makes it challenging to improve reproduction as part of a multiple trait breeding objective. The complexity arises not just from the cascade of processes required to result in successful reproduction, but the relevant traits are different in males and females and they are influenced through health and fitness, nutrition, climate and other environmental and management factors.

Challenges to the improvement of reproduction can vary widely for different species. For less domesticated species such as abalone, the ability to produce and reproduce the animals in captivity presents a major challenge. In bees, reproduction has not been given great attention and little research has been undertaken to understand the underlying genetics of drone and queen reproduction. However, in all industries reproduction is recognised as the basis for genetic and economic gain. It directly influences the selection intensity that can be applied. It also determines how many animals are not required for replacement and can be sold. In all industries, irrespective of the challenge, cost-effective and easy to measure phenotypes of reasonable heritability are central. New technologies and approaches enable the development of novel phenotypes for genetic improvement which will be combined with a growing amount of genomic data in livestock species and together these developments provide new and exciting opportunities to improve reproduction further.

We would like to thank everyone who has contributed to this event for their time and effort: the authors for their contributions to the book and presentations, the reviewers who all readily agreed to critique the manuscripts. We would like to express a special thanks to Kathy Dobos for her contributions into the organisation of this workshop and the publication. Thank you!

Susanne Hermesch and Sonja Dominik

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Improving reproduction in ewes

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Abstract

Improving reproductive performance in sheep is important from both economic and welfare perspectives. To achieve successful change at an industry level, it is necessary to record phenotypes and pedigree and apply sophisticated analyses (single step best linear unbiased prediction, SSBLUP, using genomic data tied to reference phenotypes) to obtain accurate breeding values for selection candidates. Breeders are then able to incorporate this information into breeding decisions. This paper outlines practical issues affecting the ability of sheep breeders to obtain suitable phenotypes for genetic evaluation, ultimately influencing the choice of traits and models used for genetic evaluation. A new genetic evaluation system replaces breeding values for number of lambs weaned with the corresponding components of reproduction (conception, litter size and rearing ability) along with providing new breeding values for other ewe traits (maternal behaviour and condition scores). An illustration of genetic gains in reproductive traits made to date by industry, on average, versus a flock accurately recorded for reproductive outcomes, demonstrates that despite low trait heritabilities typical of reproductive traits, genetic gain can be achieved through sustained selection for reproductive performance, and this is more evident when recording of reproductive data is comprehensive.

Introduction

Reproduction accounts for between 10-35% of the breeding objective in Merinos and maternal sheep breeds contributing to first cross ewes (Anon: 2019a, 2019b). Consequently, reproduction is an important trait for sheep breeders to record. However, in typical Australian sheep production systems, ewe reproductive performance can be difficult to record. Ewes tend to be managed in large mobs under extensive grazing conditions. Further, there is a reluctance by breeders (particularly of Merinos) to potentially interfere with ewe-lamb bonding post-birth by initiating tagging and recording of lambs from birth. Consequently, recording of individual lambs to dams is frequently delayed until later ages, long after lamb losses occur. In addition, Merino breeding has historically focussed on highly heritable traits such as wool characteristics or growth, which respond well to phenotypic selection. As a consequence, obtaining pedigree for more accurate selection of these traits has often not been a priority for Merinos, whereas full pedigree along with reproductive data is essential to improve reproductive performance.

In contrast, breeders of maternal sheep breeds have recognised this requirement and structured their lambing systems and data recording to enable recording lambs to dams from birth.

From a producer's point of view, it is also important to match the genetic potential for reproductive performance with a suitable environment and management. In particular, the production environment influences both ewe and lamb mortality rates. The upper limit for reproductive output then depends on high conception rates and achieving the environment and management required to maximise expression of the genetic potential for litter size and the survival of lambs. Amongst other things, this includes appropriate nutrition and management pre- and post-joining, attention to ewe and lamb health, suitable timing of joining and lambing events and the provision of adequate shelter and protection from predators at lambing. Providing supervision during lambing is also a factor known to improve ewe and lamb survival rates, but producers vary widely in their perspectives on and capacity to monitor and intervene in lambing in extensive production systems.

From the breeding perspective, low trait heritability and sex-limited expression after the primary point of selection are characteristics of reproductive traits, which dictates that ewe reproduction needs to be accurately recorded in large, pedigreed populations to achieve reasonable accuracy of breeding values and therefore genetic change through selection. While large flocks are common, dam pedigree – connecting dam data to offspring, which are future selection candidates – and accurate data on reproductive traits are not universally common. This paper outlines the main considerations for improving reproductive performance in sheep. However, the paper is predominantly limited to typical flock scenarios for Australia. It does not cover in detail implications of less common activities, such as pharmaceutically assisted reproduction (AI, ET, synchronisation), accelerated lambing programs (eg more than one lambing per year, out-of-season breeding), artificial lamb rearing (eg dairy sheep) or high input lamb rearing programs associated with very large litter size, which are specialist activities to achieve specific goals. Further, aspects of male reproductive performance are not discussed in detail.

The species challenge

Each livestock species creates specific challenges for recording and improving reproductive performance. Unlike predominantly single-bearing species like cattle, sheep can have more than one offspring per pregnancy, hereafter termed a multiple pregnancy. Further, the incidence of multiple pregnancies is influenced by breed, age and environmental conditions. A multiple pregnancy increases the risk of ewe death (leading to censoring of these ewes from reproductive data). For multiple-bearing ewes that successfully lamb, there are also increased opportunities for failing to assign all offspring to the correct dam even close to birth, predominantly due to mis-mothering (lambs deserted, temporarily stolen or reared by other ewes) and predation of smaller, weaker lambs. Ewes lambing at night also have delayed or missed observation relative to ewes lambing in daylight hours. These sources of error are only eliminated completely by individual penning of ewes for lambing indoors, which is a management strategy not routinely practised in Australia. The extent of predation in literature is very variable, but can be high

in some environments (Hinch and Brien 2014), resulting in unobserved lambs. To exacerbate these issues, many breeders do not practice regular lambing rounds, or tag individual lambs at birth, allowing further opportunities for mis-mothering post-lambing and lamb loss to remain unidentified in the paddock-lambing scenario.

Pregnancy scanning is used as an alternative data source to establish conception or litter size for ewes, providing the scan is for fetal count and ewes are scanned at an appropriate fetal age (Bunter *et al*. 2016). Scanning for multiples is replacing scanning for conception as the preferred option, because it provides the information required to optimise management of single versus multiple-bearing ewes. Scanning is generally most accurate for assigning conception and/or litter size for single-bearing ewes, and is generally less accurate for distinguishing litter sizes of a multiple pregnancy. In addition, while fetal loss (post-scanning to lambing) at the flock level generally affects less than 2% of ewes (Anon. 2012), repeated scans demonstrate that fetal loss is more likely to occur in apparently healthy ewes with multiple pregnancies relative to single-bearing ewes (Dixon *et al*. 2007). Ewes with a single pregnancy typically lose their pregnancy before scanning and would therefore be observed as a dry ewe or late pregnancy (resulting from re-mating) instead. Despite possible sources of error at scanning, scanning data may provide a more accurate data source for the number of lambs born in environments where lambs are not observed regularly at birth and/or there is high predation.

Litter size has direct implications for the survival of lambs because it affects the risk of complications before or during parturition, and also has a direct effect on lamb birth weight and vitality. Therefore, it is highly desirable to know litter size accurately when comparing ewes for the number of lambs weaned, because the ability to rear all lambs born is preferable to weaning fewer lambs than were born. All lambs lost represent both a waste of resources and a welfare concern. In any given environment, mortality rates of twins are typically 2-2.5 times that of single born lambs (Hinch and Brien, 2014). Lamb survival (%) generally decreases exponentially with any further increase in litter size, but is greatly affected by the prevailing environment and management of multiple-bearing ewes. The number of lambs weaned is also the predominant driver of total weight weaned, which has also been recommended as a selection criterion by some authors (Cloete *et al*. 2003; Fogarty *et al*. 1984). However, total weight weaned combines several trait groups in addition to reproduction (eg maternal birth weight, lambing ease, milk and rearing ability plus the lambs genetic merit for birth weight, lambing ease, survival and growth) and is not, strictly speaking, a trait which represents only reproductive performance.

As an additional complication, litters with more than one offspring also introduce the potential for litter mates to have different sires. For example, sire parentage may differ between maternal full-sibs with syndicate mating. This complication is revealed only through DNA testing of lambs to confirm parentage. Similarly, DNA parentage verification may also be used to correct dam pedigree for mis-mothered lambs. However, in this situation, strategies to retain the nurse rather than biological dam as the ewe responsible for the lamb reared, along with litter size details, could become complicated for assigning rearing ability phenotypes. The extent of mixed litter parentage and natural cross-fostering are not well quantified. However, a recent analysis has identified that 589 out of 1095 multiple-born lambs (representing about 50% of 546 multi-

ple litters) were heteropaternal within litter, from syndicate mating of Merino ewes (Clarke *et al*. 2021). Correct parentage of individually identified lambs is required for any genetic evaluation of the direct genetic effects on lamb survival, whereas sire parentage and identification are not essential when the survival of lambs is considered as a trait of the ewe. Thus, rearing ability of the ewe can be recorded and analysed from both single sire and syndicate mating scenarios, whereas lamb survival analyses would require full discrimination of lamb pedigree. In both cases identification of biological dam-lamb pairs is, of course, required for lambs to receive breeding values for ewe reproductive traits, benefitting in accuracy of selection from the recording of their dam for reproductive performance.

The problem of terminology versus trait definitions

In sheep enterprises, overall reproductive performance is typically described using mob-based parameters: eg. the count of lambs or the count of ewes joined at any specific time period, expressed as percentages (eg scanning, marking, lambing or weaning percentages). Consequently, there has been a history of expressing reproductive phenotypes for individual ewes in a similar form (eg number of lambs born or weaned for joined ewes) for genetic evaluation (Brown *et al.* 2007). Sheep Genetics currently analyses the traits number of lambs born (NLB) and weaned (NLW), expressed annually by joined ewes. While breeders perceive these trait definitions as desirable and familiar, this terminology can be problematical, particularly as litter size increases.

Firstly, phenotypes such as the number of lambs born (NLB) or weaned (NLW) per ewe joined do not distinguish between underlying reasons for differences between ewes in outcomes, or enable different models and parameters to be accommodated for traits with different biology. For example, a ewe may fail to rear any lamb(s) because she was not joined (eg service sire failure), or she failed: a) to cycle and/or conceive; b) to retain her pregnancy; c) to lamb successfully, d) to rear her lambs, or e) she died – potentially as a result of pregnancy related complications. Consequently, ewes can have identical phenotypes for NLW due to multiple reasons. Eg NLW = 0 for both ewes which fail to conceive and ewes which lost all lambs(s), or NLW=1 for ewes with litter size of one or greater than one. Therefore, using NLW, the breeder is no clearer as to the genetic potential for ewe fertility (ie a ewe's ability to conceive), litter size (essentially ovulation rates and/or fetal survival) or other maternal attributes (eg lambing process, lamb weight and vitality, milk production, maternal behaviours) which assisted in the successful rearing of the lamb(s) that were born. In addition, there is no capacity to alter selection for any specific component based on their relative economic importance in the production environment or welfare emphasis. For example, lamb losses are poorly established if ewe phenotypes do not distinguish between lambs never born versus lambs lost. Lamb losses are a major welfare problem, and also have different economic implications depending on their timing. Lamb survival will also be economically more important if lamb losses are high.

Secondly, the phenotypes and resulting breeding values are not true percentages. A one unit change in the ASBV for NLW does not represent a 1% change in performance relative to the

mean. The more appropriate interpretation of these breeding values is outcome per 100 ewes. Breeders still perceive these values to be percentages and wish them to be described as such, even for traits (eg NLW) whose phenotypes are essentially a function of several component traits. This is partly an historical artefact of largely single-bearing flocks and the discussion of reproductive performance as mob based percentages, described above. For example, if sheep only had single pregnancies, then counts by ewe OR lamb are equivalent and a unique percentage can be easily obtained: eg. 95% ewes conceived + 5% ewe mortality + 10% lamb mortality = 95% scanning rate and 80% marking rate, with mean number of lambs scanned = 0.95/ewe joined and mean NLW = 0.80/ewe joined. However, where litters involving multiples are involved, the translation to a percentage relative to ewes or to litter size is not perfect because both ewe and lamb mortality are litter size dependent. Therefore, the average phenotypes are a function of proportions of ewes in each litter size group, and percentages do not simply reflect the percentage of ewes affected.

As an example, assume conception rate = 95% and the proportion of singles, twins and multiple bearing ewes are 55%, 35% and 5%. Ewe mortality is 2% for single or 3% for multiple litters (total 5%), and lamb mortalities are 10% single lambs, 15% twin lambs, 40% triplets, with 10% of ewes affected by lamb loss. In this scenario, 100 ewes will be scanned to be pregnant with 95 litters, with lambs distributed across ewes as 55 singles, 70 twins and 15 triplets (N=140 lambs, mean litter size =1.4/pregnant ewe, mean number of lambs scanned =1.33/joined ewe). However, only 53 singles, 68 twins and 9 triplets are born due to ewe losses (N=130 lambs born: 10 instead of 7 lambs lost due to ewe death). This reflects the expected 5% reduction (relative to ewes joined) in ewes lambing, but a 7.1% reduction (relative to lambs expected) in lambs born. Of the remaining litters, the numbers of lambs weaned are close to 48 from single litters, 58 from twin litters and 5 from triplet litters (N=111 lambs: 19 instead of 10 lambs lost). This reflects an overall reduction of 10% ewes weaning lambs, but -12.8% lambs weaned relative to lambs born or -20.7% lambs weaned relative to lambs initially scanned. The accompanying mean NLW=1.11/ewe joined is a larger reduction (-16.5%) relative to ewes joined than was expected (-15%) from 5% ewe mortality and 10% ewes with lamb(s) lost. Clearly mob-based parameters versus individual traits should be considered as different, although related, descriptors of performance.

Finally, composite traits such as NLW require that breeders record whether all ewes joined conceived or were dry, when traditionally ewes have only been recorded as dams (ie for pedigree purposes) if they lambed and/or if they weaned lambs. Therefore, lamb based data frequently exhibits 100% conception rate and/or 100% lambs reared, even though such outcomes would rarely be seen at the mob level. This also creates no variation amongst contemporary ewes for these traits. Moreover, identifying individual lambs only at the point of marking or weaning, instead of at birth, occurs after most of the lamb mortalities have taken place. Therefore, the extent of recorded lamb losses can be biased downwards and the extent of lamb loss is essentially unknown. In both cases, these data should be eliminated from the genetic evaluation process because ewes are not compared with valid phenotypes for their reproductive performance. Therefore, the number of records which can be analysed is reduced unless recording starts at

joining, to identify all joined ewes, including those that remained dry or lambed and lost all lambs. Similarly, recording lamb losses requires close monitoring from birth.

A new paradigm for genetic evaluation

To overcome limitations such as the above, particularly associated with these composite trait definitions (eg NLB and NLW), genetic evaluations for ewe reproductive performance have recently been re-developed to evaluate maternal (ewe) component traits as separate traits: namely conception, litter size and rearing ability (Bunter *et al*.: 2019 and 2021). Turner (1969) previously described these components as fertility, fecundity and lamb survival. However, the trait definitions are modified for genetic evaluation and therefore the trait names are also changed, for clarity. The breeding values thus represent the probability of conception in a timely manner, the resulting litter size (via lambs or scan), and the proportion of lambs that are weaned relative to litter size born, termed ewe rearing ability. In particular, rearing ability captures lamb losses for ewes and is an alternative to a lamb mortality trait, considered at the lamb level. Breeding values from these component traits can also be reverse engineered to obtain the more familiar breeding values for NLW, but based on considerably more data more closely scrutinised for quality, and with better models to derive breeding values for each of the component traits.

This new system accommodates trait specific detection of errors, enabling breeders who record only a single component well (eg litter size) to receive breeding values for that trait, when they would have previously failed to receive any breeding values for NLW. Yearling and adult performances of ewes are treated as genetically different traits (Bunter and Brown 2013), as the performance of ewes joined to lamb as yearlings is affected by their ability to attain puberty before joining commences. Two-year old ewes are also placed in different contemporary groups depending on whether they are maiden ewes or have previously lambed (where known). Breeding values for each of these component traits are then derived from trait specific models and correlations between each component trait with other indirect traits that may influence reproductive outcomes are more accurately established and used in the improved genetic evaluation procedures. This strategy provides better use of the available data (eg lambs versus scan data), even when some data are not recorded by breeders, for example dry ewes are not recorded.

In summary, the new genetic evaluation system for reproductive traits:

- uses phenotypes from resulting lambs and/or pregnancy scan records to develop phenotypes (conception, litter size and rearing ability) for ewes, evaluated separately for yearling and adult ewes, replacing analysis of NLB and NLW phenotypes

- scrutinises data at the component trait level for errors (eg eliminating contemporary comparisons, such as 100% or 0% conception within contemporary group, 100% singles, 100% twin survival, , service sire failure for CON etc.)

- enables separate contemporary groups for pre-joining (affecting conception, litter size) and pre-lambing management (affecting rearing ability)

- accounts for all known major systematic effects for all ewes (eg contemporary group) as well as specific effects for particular classes of ewes (eg month of birth, stage of dam for yearling ewes; previous outcome for 2-year old ewes) fitted within flock. The ewe age effect is fitted across flocks. All systematic effects are fitted directly to the data, replacing pre-analysis corrections

- Includes additional phenotypes for maternal behaviour and ewe pre-joining condition score

- Includes indirect traits relating to body or reproductive development, such as scrotal circumference of male relatives, weights, scanned fat and eye muscle depth

- Uses single-step best linear unbiased prediction (SSBLUP) procedures and multiple trait analyses to produce breeding values for conception, litter size, rearing ability, maternal behaviour and condition score from phenotypes and genomic data

Population specific differences in genetic parameters

A common question by breeders is how different are genetic parameters between breeds? This is an interesting question, as trait groups typically have very similar parameters across species for comparable traits, let alone across breeds. In addition, there are many conserved biological pathways common to different breeds and species. It is often assumed by breeders that breeds will have different genetic parameters describing trait heritabilities and the relationships between traits. However, differences between breeds in genetic parameters do not necessarily solely reflect true biological differences in the underlying relationships between traits. They can also reflect differences in data structures and recording practices.

Breeders of different sheep breeds tend to have very different data recording strategies. For example, maternal breeds (eg. Border Leicester, Corriedale, Coopworth) are typically characterised as tagging and mothering up at lambing (i.e. lambs identified to dams). Mothering up at lambing is facilitated by relatively smaller flock size and short joining periods. This strategy generally maximises opportunities to correctly assign all lambs to dams, facilitates recording of additional maternal data, but is not infallible in the context of a low frequency of daily observation (once versus twice daily?), the potentially unrecognised impact of predators, and the close presence of other ewes which might mis-mother offspring soon after lambing due to strong maternal behaviours. Being present in the lambing paddock close to the lambing event is also obviously a pre-requisite to score lambing ease, record birthweight data, or maternal behaviour score. Even in this scenario, ewes lambing at night will still have several hours unobserved after lambing, and increased predator loss can also be expected for these ewes. Smith *et al*. (1988) concluded that twice-daily mothering up under-estimated lamb numbers by up to 10%, largely due to a substantial difference in accuracy (lambs scanned versus observed) for ewes that lambed during the day (94.2%) versus ewes that lambed overnight (80.4%), resulting in unobserved lambs at times when predators are more active.

In contrast, the majority of Merino lambs are frequently only individually identified at marking or weaning, mothering up of live lambs may be absent, partial or complete, typically well after the lambing event, and parentage will frequently be unrecorded, particularly for dead lambs. Breeders of Merinos instead prefer to rely on pregnancy scan data to obtain data for conception and litter size of a ewe, but also have no accompanying strategy to check accuracy of scanning relative to lambing outcomes. Reluctance to perform regular lambing rounds for Merinos is generally due to relatively larger flock sizes, a perception that there are insufficient benefits to performing lambing rounds (eg due to assumed low litter size, or low importance of litter size, in this breed) and/or that lambing rounds themselves will interfere with the ewe-lamb bonding and result in higher lamb mortality. Further, extended joining periods are common for Merino flocks, increasing the amount of time over which observations for lambing events would be required. In this situation, it will not be possible to definitively establish phenotypes for rearing ability, nor lamb survival, lambing ease, maternal behaviour etc, because lambs are not initially observed at birth. The difference between lambs scanned and lambs reported at birth is generally affected by random errors and is not heritable (Brown *et al*. 2021). This makes scan count suitable for assigning litter size phenotypes, but potentially less suitable as a starting point for calculating rearing ability, particularly since both more and fewer lambs can be born than were identified during scanning. Fetal loss post-scanning to lambing is expected to be low in healthy ewes (Anon, 2012), whereas embryonic or fetal loss between ovulation and scanning is well established (Kleeman and Walker, 2005).

A similar limitation to the completeness of data occurs if parentage is only from assignment based on DNA of live lambs, combined with litter size solely established from scanning. That is, parentage of surviving lambs may be known, but the accuracy and timing of inferred lamb losses is not. Thus, it is possible to have a fully pedigreed flock, but with biased data regarding reproductive performance. This data is also eliminated from genetic evaluation (Bunter *et al*. 2021). Failing to update lamb losses after lamb tagging is also a common data problem, as is the failure to identify lamb losses that are the result of ewe deaths. However, there are some technological advances with promise. Attributing lambs to dams soon after birth using Pedigree matchmaker is one option with demonstrated utility to obtain pedigree (Richards and Atkins 2007). Alternative strategies to connect dams to lambs through proximity measures are under development, but all potential methods currently are limited with respect to confirming lamb numbers at birth.

As a result of the above, it can be hypothesised that the number of lambs observed will typically be below that suggested by pregnancy scanning results, on average. Triplets are typically under-reported from scanning, further exacerbating sources of bias in populations with scanned high mean litter size. Concurrently, heritabilities of the reproductive traits are relatively lower for Merino populations (or populations with similar recording strategies) because of increased error rates for reproductive phenotypes. For data to be included in the new genetic evaluation system for reproductive traits, more than 70% of lambs must have dams known (within flock-year) and the consistency of birth type with lambs recorded per litter must be over 80%. These filters are an attempt to reduce bias introduced by errors in assignment of lambs to dams and unreported lamb losses. There is ultimately a trade off at an industry level: very well recorded

flocks tend to have higher heritabilities for reproductive traits, but fewer animals and flocks would ultimately receive breeding values if filters became too stringent and therefore fewer flocks were represented in the genetic evaluation.

In a similar vein, it can be hypothesised that differential management of industry versus research or maternal versus Merino breed flocks (due to improved environments or nutrition provided) could also alter trait heritabilities and potentially genetic and/or phenotypic correlations between body development (weight, fat-depth, muscle-depth, condition score, scrotal circumference of males) and female reproductive traits (conception, litter size and rearing ability). Poorer environments may also increase the importance of ewe condition for reproduction. Variability in the relationships between reproductive and body development traits by flock was illustrated extensively by Walkom (2014). Merino flocks are often located in less favourable, more extensive environments, relative to maternal breeds or crossbreds, so breed and environmental effects could be partially confounded. However, using standardised data processing and analytical models has resulted in very similar estimates of genetic parameters, and correlations between all traits for both maternal and Merino breed datasets (unpublished data). The exceptions were slightly stronger favourable relationships between body development traits and reproduction on Merinos relative to maternal breeds (Bunter *et al*. 2021), and a detrimental correlation between muscle depth and litter size for maternal breeds (Bunter *et al*. 2019), not evident for Merinos. The general relationships between trait groups are illustrated schematically in Figure 1.
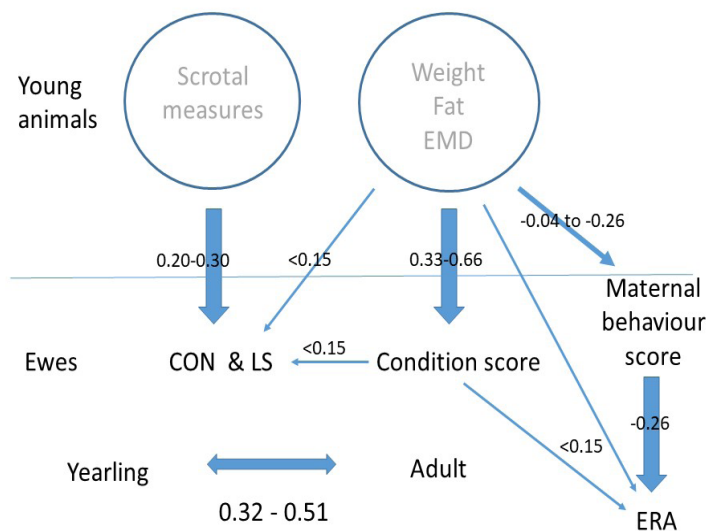

Figure 1. Schematic illustrating the magnitude of genetic correlations between trait sets (adapted from Bunter et al. 2021); CON: conception, LS: litter size, ERA: rearing ability, EMD: eye muscle depth

Other important traits

Adequate development of young ewes and nutritional a management are important for yearling reproduction of crossbreds (eg Fogarty *et al.*, 2007) and Merinos (Thompson *et al*., 2019). Similarly, pre-joining nutrition affects reproductive levels of mature ewes. Because of these characteristics, sheep breeders have developed some reliance on using several indirect traits (eg weight, body condition, fat or muscle depth) as a means to improve reproductive performance. However, since these traits are related to ewe age and also highly correlated with mature weights and relatively lowly correlated genetically with reproduction (Figure 1), improving reproductive performance in this way is relatively less efficient than selection based on reproductive data, and will be accompanied by the undesirable consequence of increased mature ewe size.

In contrast to cattle, ewes are not required to conceive while lactating, so lactational anoestrus is not an issue. However, rearing multiple lambs can have a very large impact on ewe body condition, and therefore recovery prior to the next breeding event becomes important, particularly if re-breeding typically occurs at or after times of poor pasture availability. The new genetic evaluation system for sheep produces breeding values for pre-joining condition score of ewes, which is moderately to highly correlated with weight, fat and eye muscle depths recorded at earlier ages. Parameter estimates for non-genetic (permanent environmental) effects quite clearly demonstrate that individual ewes with high reproductive performance lose more body weight and wool production annually than ewes with lower reproductive levels. Therefore, it is also important not to compare ewes phenotypically for these traits without knowledge of their reproductive level each year.

Yearling reproductive performance is also affected by the attainment of adequate body development and puberty by the time joining commences. However, adequate body weights and composition do not guarantee that puberty has been reached. Therefore, these indirect measures are not reliable predictors of reproductive outcomes for individual young ewes. The attainment of puberty can be hard to measure directly, although progesterone is known to be higher in post-pubertal ewes, reflecting the presence of a *corpus-luteum*. Using progesterone levels as an indicator, it can be demonstrated that mean progesterone levels and conception rates for yearling ewes were positively correlated (Bunter and Newton, 2014). Therefore, breeders wishing to increase yearling reproductive performance could benefit from recording progesterone levels. An alternative is to use serial scanning to identify the age at which ewes have their first ovulation, as currently used for beef cattle (Johnston *et al*. 2009). However, logistically such data would be challenging to obtain and, so far, has no traction as a routine data source for sheep breeders.

Breeders have also expressed interest in improving maternal behaviour at lambing, because maternal behaviour affects lamb survival outcomes (Dwyer 2014). Maternal behaviour must be scored temporally close to the completion of lambing, so is typically recorded only by breeders that mother up at lambing. In addition, there are a variety of scoring systems, some where the high score is favourable, others where low values are favourable, leading to confusion in literature. The Australian genetic evaluation system is based on a five score system (lowest score

is favourable) representing the ewes response to the breeder handling her lambs for processing (ie tagging, weighing etc) (Brown *et al*. 2016). The resulting maternal behaviour score has favourable (negative) genetic correlations with both rearing ability and also ewe condition score (Bunter *et al*. 2021).

Genomic data

Reproductive performance traits have low heritability, are sex-limited with late in life (post-selection) expression. Therefore, these are traits that can benefit relatively more from using best linear unbiased prediction (BLUP) and genomic data to improve the accuracy of selection and reduce generation intervals, enabling more genetic gain. Genomic reference populations for reproductive traits have only recently been generated through the Sheep CRC and Merino Lifetime Productivity (Australian Wool Innovation) projects, with ongoing collection of genomic data in industry flocks. These are now combined with pedigree using single-step procedures (Legarra *et al*. 2014). Improvements in the accuracy of component trait breeding values for young sires due to genomic data are of the order of 6% for Merinos. As a consequence of significant volumes of genomic data and multi-trait analyses, it is necessary to have very efficient analysis systems to obtain breeding values routinely, as described by Boerner and Johnston (2019).

Other genetic evaluation systems

While reproductive performance in Sheep Genetics is based on ewe (maternal) traits, some reproductive traits in other genetic evaluation systems are not always analysed as maternal traits. For example, Sheep Improvement Limited (NZ) estimates genetic merit for litter size using NLB, and lamb survival with direct (lamb-level) and maternal (ewe-level) components. Maternal behaviour score, condition score and birth weights are not recorded. We propose maternal trait emphasis is the most efficient approach for the majority of the Australian sheep industry because:

- conception and litter size are not lamb-level traits, they are characteristics of the ewe

- in normal circumstances, lambs are completely dependent on the expression of maternal care to survive past birth (Dwyer, 2014)

- ewes have repeated records, enabling increased accuracy of breeding values for both ewes and their offspring for traits expressed at the ewe level

- lamb pedigree is not required to evaluate any of the traits conception, litter size and rearing ability. However, full pedigree of both dead and alive lambs are required for lamb survival analyses correctly accommodating maternal effects

- maternal effects for lamb survival are typically proportionally higher than direct effects (eg Burfening 1993; Hatcher *et al*. 2010), such that rearing ability (a maternal trait) should be more informative than lamb survival (a lamb trait), where dead lambs (non-selection candidates) will generally have the lowest breeding values, and

- maternal traits for reproduction align well with other phenotypes for ewes (eg. condition score, maternal behaviour), facilitating multi-trait models. The new maternal component trait analyses for Sheep Genetics contain 19 traits for Merinos and 15 traits for maternal breed analyses.

As noted above, analyses at the lamb level (eg for lambing ease or lamb survival) require full lamb (sire and dam) pedigree in order to appropriately consider both direct and maternal effects concurrently. Therefore, the direct effects for lamb survival may be better estimated from subsets of the data where this information is present, and has the advantage of providing information towards sire breeding values when lamb details are obtained. Unfortunately, full pedigree is frequently not available in Merino flocks, due in part to an historical focus on highly heritable traits where maternal effects (and therefore mothering up) were less important. Full-pedigree is also frequently censored on dead lambs, which are the informative animals within a contemporary group, diminishing the amount of useful data available for genetic evaluations. Therefore, there may be many fewer phenotypes available for any analysis of lamb survival considered at the lamb level compared to rearing ability established at the ewe level. Finally, factors that are most informative regarding the survival of individual lambs (eg birth weight, prevailing weather conditions, or lambing complications – potentially specific to only one lamb in a litter, but often recorded identically against all) are also frequently unavailable, which further reduces the utility of a lamb survival analysis conducted at the lamb level. Establishing a genomic reference population for lamb survival, including genotyping dead lambs, may assist with further developments in this area.

Evidence for genetic improvement

In sheep populations with full pedigree and a history of accurate recording and selection emphasis on reproductive performance, it is possible to demonstrate significant improvements for all reproductive component traits (Figure 2), based historically on selection indices including NLW. This outcome reflects mothering up at lambing, such that young selection candidates receive breeding values, predominantly from connection to their dam's records. Rates of genetic gain in these flocks are actually comparable to the litter size changes that have been observed in other species, for example pig populations. Changes in conception and rearing ability are smaller relative to changes in LS. However, it was not possible to select on any components directly prior to the release of component trait breeding values in 2019-2020, and the variability of conception and rearing ability traits is lower than the variability for LS. Therefore, selection pressure would be expected to be larger for LS than other traits. Despite this, small positive changes can be observed in breeding values for conception and rearing ability within some flocks with positive trends in NLW.
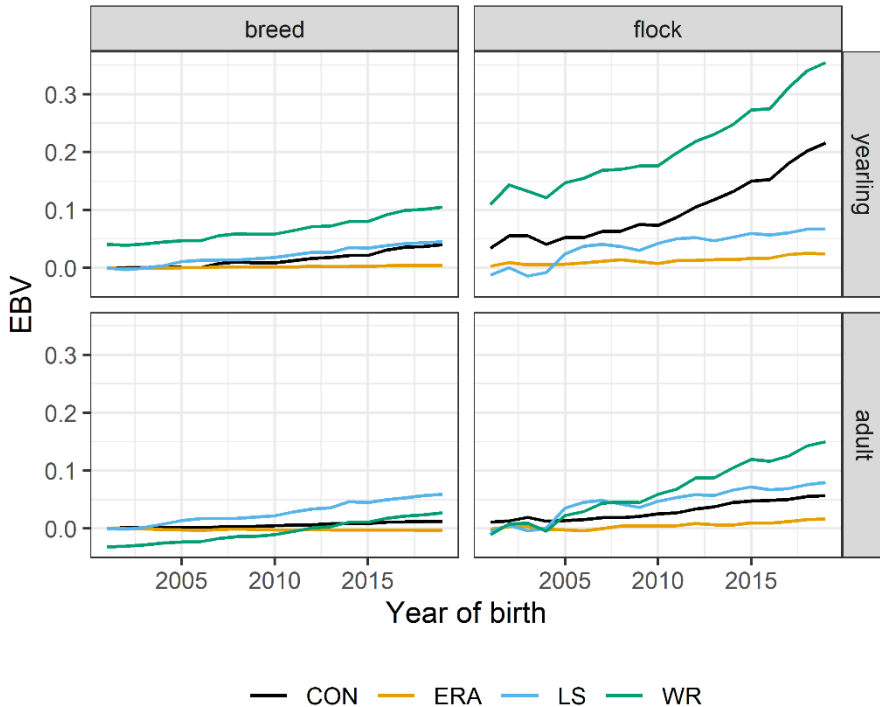
Figure 2. Genetic trends for conception (CON), litter size (LS), rearing ability (ERA) and the derived weaning rate (WR) in maternal breeds, averaged across all flocks (breed) or within an example flock (flock) with a long history of recording reproductive traits

In contrast, in the national population, genetic trends in reproductive performance are much smaller, even in traditionally maternal breeds, because of widespread ineffective recording and variation in effective selection for reproductive performance (Figure 2).

Summary

As with any species, change in reproductive performance through selection is achievable in the sheep industry with accurate data and pedigree recording, advanced statistical methodology such as BLUP, leverage with genomic data and with appropriate selection emphasis. A new genetic evaluation system has recently been implemented for both maternal breeds and Merinos based on ewe records for conception, litter size, rearing ability, body condition and maternal behaviour scores. This system makes use of additional correlated traits, genomic data and single step methodology to produce breeding values for these traits. Genotyping has a role to play for improving accuracy of breeding values. However, obtaining phenotypic data that identifies all lamb losses and which assigns lambs to dams (at birth) in large flocks remain key logistical challenges for sheep breeders. New technologies may assist in this regard.

Acknowledgements

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