

SELECTION STRATEGIES FOR THE GENETIC IMPROVEMENT OF REPRODUCTIVE PERFORMANCE IN SHEEP

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SUMMARY

Selection strategies for the genetic improvement of reproductive performance of sheep in Australia are discussed in the context of current and emerging industry practice. The predicted rates of gain in reproductive rate are compared with varying amounts of pedigree and performance records of relatives. The paper also considers the merits of exploiting indirect as well as direct selection, including selection on the component traits of reproductive rate.

INTRODUCTION

The Australian sheep industry appears to be in a rebuilding phase (based on a marked reduction in sheep slaughterings in the last 2 years, ABS 2010a), in response to high lamb and sheep prices. This follows a long period of decline from a peak of 173.1 million head in 1990 (ABS 1990) to a minimum of 67.7 million in 2010 (ABS 2010b) due to a combination low wool prices, drought, competition from other enterprises, welfare concerns and lifestyle choices. Unfortunately the low reproductive performance of Australian sheep, which has averaged only 78% lambs marked per ewe joined over the last 30 years (ABARE 2010), will limit the rate of increase in the sheep population unless there is considerable improvement.

With a large increase in the relative value of sheep meat compared to wool production since the 1990s (e.g. Swan *et al.* 2007), there has been a marked increase in the proportion of ewes in the national flock, increasing from 55% in 1989-90 to 80% of the flock in 2007-08 (ABARE 2009). These dramatic changes have made flock reproduction rate a more important profit driver for sheep producers, even for those still primarily focussed on wool production.

Optimising ewe nutrition has been the main focus of efforts to increase sheep reproduction rate in recent years, driven mainly by the large-scale Lifetime Wool project (Oldham *et al.* 2011).

Achieving genetic gain in reproduction rate is hindered by low selection accuracy, due to low heritability of the trait and the fact that direct measurement is limited to females and to older animals only. Using information on relatives could increase accuracy considerably, but pedigree information, especially on the dam side is often lacking, particularly in Merino breeding programs. Supplementing direct selection for reproduction rate with indirect selection based on correlated traits (sometimes referred to as indicator traits) may also help boost accuracy and genetic gain. Brown (2007) suggested that lamb ease and gestation length could be useful indirect indicators of lamb survival as a component of reproduction rate and Brien *et al.* (2010) predicted large increases in selection accuracy for lamb survival by using novel indirect traits measured on newborn lambs.

Finally, reproduction rate is itself a composite, made up of a number of components, including fertility, ovulation rate, and embryo and lamb survival. Could more genetic gain in reproduction rate be achieved by selecting on these component traits, rather than on reproduction rate directly?

This paper discusses the usefulness of various selection strategies, including increased use of information from relatives, as well as the potential benefits of exploiting indirect as well as direct selection and the use of genomic selection. It also discusses the efficiency of selection on component traits of reproductive performance in comparison to selection for the number of lambs

weaned per ewe joined. The relative economic value of reproduction rate and its calculation is currently under discussion within the Sheep CRC and whilst an important topic, will not be discussed here.

TRAIT DEFINITION AND CURRENT RECOMMENDED STRATEGIES

Ponzoni (1986) defined reproduction rate as the total number of lambs reaching weaning per ewe over her lifetime in the flock. Sheep Genetics, the genetic evaluation scheme for the Australian sheep industry, uses the number of lambs weaned (NLW) per lambing opportunity as the reference for reporting an Australian Sheep Breeding Values (ASBVs), with records from multiple lambing opportunities considered as repeated measures of that trait. This study will focus on the Sheep Genetics version of reproduction rate as the number of lambs weaned per ewe joined (i.e. per lambing opportunity).

Breeding values for NLW have the highest accuracy in cases of whole-flock recording with complete pedigrees (sire and dam) on all offspring with both alive and dead lambs being recorded. The latter is important as it allows targeting of lambs weaned per ewe joined to include lamb survival as a trait definition. Lamb survival decreases if selection is based solely on litter size at birth (Swan 2009), or if NLW does not include information on dead lambs. Scrotal circumference of rams can be recorded as an indirect indicator of NLW of female relatives (Apps *et al.* 2003).

PREDICTED GAIN IN NLW

For typical Merino ram breeding flocks with no dam pedigree records, Mortimer *et al.* (2010) predicted gains in the percentage of lambs weaned of -2.60%, -2.19%, -1.11%, 0.46% and 2.06% over 10 years using the standard MERINOSELECT indices of Merino 14%, Merino 7%, Merino 3.5%, Dual Purpose 7% and Dual Purpose 3.5%, respectively. Therefore, even with indices with a high relative economic value for NLW, such as in Dual Purpose 7% and Dual Purpose 3.5%, predicted genetic gain in NLW in the absence of any dam records for NLW is not large.

We compared the predicted rates of genetic gain in Merinos for differing selection strategies under multi-trait selection, using MTINDEX, a spreadsheet model developed by J. van der Werf (see http://www.personal.une.edu.au/~jvan_derw/software.htm). Although the predictions are for Merinos, the results are likely to be applicable to all breeds. Selection was assumed to be from within a closed flock, with no outside introductions. Results are shown in Table 1. The selection index option used was Dual Purpose 7%. This places 34% of the selection emphasis on NLW. The genetic parameter estimates used are those of Sheep Genetics and of Brien *et al.* (2010) for estimates involving lamb survival. Other assumptions included the proportion selected as parents being 3% for males and 66% for females, with 70% emphasis in selection placed on the selection index. The age structure included 4 age groups for breeding females and 2 age groups for sires.

The core selection criteria for males included yearling clean fleece weight, fibre diameter, coefficient of variation of fibre diameter, staple strength, body weight, fat and eye muscle depth, with females selected on a slightly reduced set of core criteria (excluding yearling staple strength). Additional selection criteria were added for selection scenarios 2 to 9, as outlined in Table 1. We have assessed the impact of a change in selection strategy for NLW on gain for other traits by monitoring the predicted gain in the overall index and for lamb survival.

Net reproduction rate (NLW/100 EJ) is predicted to genetically increase by 3.5 over 10 years from index selection, in the absence of NLW records on dams, with most of the gain coming from a correlated response to an increase of approximately 5 kg in adult body weight. This contrasts with the lower estimate of 0.46% for NLW over 10 years predicted by Mortimer *et al.* (2010) using the same index, but with minor differences in base selection criteria. We are unclear why there is such a considerable difference in predictions between the two studies, but it may relate partly to differences in the assumed genetic parameters.

Table 1. Predicted genetic gain over 10 years in the number of lambs weaned per 100 ewes joined (NLW/100 EJ), selection index (\$) and lamb survival to weaning per 100 lambs born (LSW/100 LB), using the MERINOSELECT Dual Purpose 7% selection index

| Option | Selection criteria and records used (males) | | | | NLW accuracy* | Genetic gain over 10 years | | |
|--------|---|-----------|------------|---------------|---------------|----------------------------|------------|------------|
| | Dam NLW | Half sibs | Progeny | Other records | | NLW/100 EJ | Index (\$) | LSW/100 LB |
| 1 | No | No | No | - | 0.13 | 3.5 | 39.68 | -0.2 |
| 2 | No | No | No | SC** | 0.20 | 6.4 | 43.21 | 0.0 |
| 3 | Yes | No | No | SC | 0.24 | 7.9 | 46.93 | 0.4 |
| 4 | Yes | No | No | SC, LE** | 0.25 | 8.4 | 47.54 | 0.5 |
| 5 | Yes | No | No | SC, LE, LSW** | 0.29 | 10.5 | 50.09 | 0.4 |
| 6 | Yes | 10 | No | SC, LE, LSW | 0.35 | 10.9 | 43.24 | 0.5 |
| 7 | Yes | 10 | 10 for NLW | | 0.50 | 9.8 | 38.61 | 1.1 |
| 8 | Yes | 10 | 20 for LSW | SC, LE, LSW | 0.40 | 11.4 | 50.63 | 0.7 |
| 9 | Yes | 10 | 30 for LSW | SC, LE, LSW | 0.50 | 16.2 | 51.52 | 1.9 |

*from multi-trait evaluation of males

**SC – scrotal circumference, LE – lambing ease, LSW – lamb survival to weaning

Adding a scrotal circumference record on yearling rams to the selection index boosts accuracy to 0.20 and predicted genetic gain in NLW to 6.4 lambs weaned per ewe joined over 10 years. Accuracy (and genetic gain) is further increased to 0.24 with the addition of dam NLW records. A further increase in accuracy (to 0.29) and in genetic gain in NLW to 10.5 is predicted when lambing ease and LSW records are added to the selection index, with most the gain predicted due to LSW records (not shown).

With 10 female half-sib NLW records added to the selection index (Option 6), accuracy for NLW is increased to 0.35 and genetic gain to 10.9 over 10 years, despite the increase of 1 year in generation interval to allow for the collection of NLW records. However, index gain declines by \$6.85 (option 6 compared to option 5) with other traits benefiting less from improvements in accuracy than NLW and are not enough to offset higher generation interval. In Option 7, sires progeny-tested for NLW are assumed to be a minimum of 5 years of age when their progeny are born and despite higher accuracy, even genetic gain in NLW is less than Option 6, with index gain further disadvantaged compared to earlier options.

Whilst progeny-testing for NLW is counter-productive with only 10 progeny per sire, progeny-testing for LSW, as explored in Options 8 and 9, can be achieved at a much earlier sire age and the trait is expressed in both sexes, unlike NLW. Rates of genetic gain for NLW are predicted to be 11.4 and 16.2 lambs weaned per 100 ewes joined for selection indexes incorporating 20 and 30 progeny records for LSW, respectively. Index gain slightly exceeds the best of the earlier options (Option 5), indicating that higher gains in NLW are not associated with lower gains for other traits.

In all but Option 1, lamb survival is predicted to either remain genetically unchanged, as in Option 2, or progressively show greater gains as more information is added from relatives and especially when sires are progeny tested for NLW and LSW. This contrasts to genetic reductions in lamb survival predicted for some selection strategies considered by Brien *et al.* (2010). In this study, the genetic correlation assumed between yearling body weight and NLW is 0.15, whereas an estimate of 0.30 was used in Brien *et al.* (2010). This explained some of the differences in the predictions of genetic gain for lamb survival between the two studies, with most of the remainder explained by differences in economic values assumed for NLW.

Genomic selection. Using index selection relevant for fine wool Merinos, Van der Werf (2009) predicted improvements in accuracy for NLW of 20% and 36%, respectively if genomic selection was available that could explain either 3% or 6% of the additive genetic variance for the trait, equivalent to either $h^2/2$ or h^2 for NLW. These improvements are similar in magnitude to those when comparing Option 5 and 6 with Option 4 in Table 1 above and are clearly useful if the technology of genomic selection becomes available.

RECORDING ISSUES

Pedigree recording. The need for ewe pedigree is obvious when large genetic gains in NLW are desired (Table 1). However, as shown in Table 2, of those flocks submitting data to Sheep Genetics, only 16% provide reproduction records for genetic evaluation. Only 18% of Merino flocks participating in Sheep Genetics supply reproduction records, as alluded to earlier. More of the Border Leicester and Coopworth flocks, breeds that have traditionally emphasised maternal traits, supply reproduction records (44% and 52%, respectively). Table 2 may overstate the situation, as some flocks with reproduction records have incomplete recording of their ewe flock.

Table 2. Flocks in Sheep Genetics with reproduction records, 2005 to 2010

| Breed or breed type | Active flocks | Flocks with reproduction records | % |
|---------------------|---------------|----------------------------------|-----|
| Terminals | 595 | 46 | 8% |
| Border Leicester | 84 | 37 | 44% |
| Merino | 205 | 37 | 18% |
| Coopworth | 52 | 27 | 52% |
| TOTAL | 936 | 147 | 16% |

The low submission rate of reproduction records acts as a major barrier for flocks, particularly Merino flocks, to make appreciable genetic gains in reproduction rate. The cost and effort of collecting detailed lambing records, reported to be around \$10 per lamb, is the most likely reason for sheep breeders not collecting ewe pedigree information (Richards and Atkins 2007). Some sheep breeders rely on mothering up techniques after lambing time, but due to cross-fostering of lambs (Alexander *et al.* 1983), accuracy of assigning the correct pedigree is likely to be considerably lower than identifying lambs with their dam at lambing and the practice is not recommended for formal genetic evaluation. Shepherd[®], a commercially-available parentage test based on DNA markers, is available, but at a cost of \$20 to \$30 per lamb is currently more expensive than collecting pedigree records at lambing and cost remains a barrier to wider adoption. With advancements in marker technology, such as SNPs, there may be opportunities to reduce the unit cost of pedigree determination via DNA testing and thereby boost the prospects of better adoption by industry.

Pedigree matchmaker, a system of assigning pedigree by physical movement associations between lambs and their dam using electronic tags with a radio-frequency identification (RFID) technology, offers a potential option of obtaining dam pedigree records, for as little as \$3 to \$4 a lamb (Richards and Atkins 2007). Accuracy of 90-96% in assigning pedigree after 4-5 weeks of observations of lambs and ewes have been reported (Richards and Atkins 2007). This is approaching the 95% accuracy achieved from detailed recording of pedigrees during lambing as practiced in the Sheep CRC's Information Nucleus (Brien *et al.* 2010). Further testing and validation of pedigree matchmaker is underway by the Sheep CRC.

Data quality. To provide the best opportunity to genetically improve traits, it is critical that data be of the highest quality. For improving NLW, apart from errors in pedigree, the most likely weakness in data quality is the potential to inadequately record dead lambs as well as live lambs. Even with careful data collection, dead lambs may be missed because of removal of carcasses by predators or have their pedigree incorrectly recorded because of the difficulty of assigning the correct dam. In these situations, records of foetal numbers from ultra-sound scanning of ewes during pregnancy can be used to minimise the error rate.

Sheep Genetics have quality control procedures to minimise any bias from inaccurate recording procedures, but there is no substitute for starting with high quality data. Nevertheless, it remains problematic that not all recording software is set up as a full inventory system for all stages of reproduction, starting with mating, then scanning, lambing, marking and weaning.

IMPLICATIONS OF CROSSBREEDING

Analysis. While the Australian sheep industry remains dominated by Merino ewes (ABARE, 2009), crosses to a range of terminal and maternal breeds have become more widespread and composite breeds are also becoming more common (Walkom *et al.* 2011). In these circumstances, many animals evaluated under a pure breeding system will ultimately be used as parents within a crossbreeding system and evaluation systems will also need to be able to account for animals being assessed under crossbreeding. With reproductive traits displaying considerable heterosis, not only from breed crosses, but from across strain and bloodline crosses within breeds (Atkins 1987), it is important that evaluation systems are able to appropriately account for industry practice.

Sheep Genetics is currently developing evaluation systems to cope with crossbreeding, including the effects of heterosis. Early indications are that this will be difficult because of the structure of field data where crossbreds are rarely compared head-to-head with straightbreds. This has made it very difficult to separate heterosis from additive genetic effects which in turn leads to poor prediction of progeny performance from estimated breeding values.

Different breeds and crosses. Do selection strategies for reproduction rate need to differ for different sheep breeds and crosses? There is evidence for across-breed variation for the main components of reproduction rate, such as fertility, litter size and lamb survival (Walker *et al.* 2003) and breeds may have different genetic strengths and weaknesses for each component. With two or more breeds involved in crossing systems or incorporated into a composite, there may be scope for variation in the optimal selection strategy across breeds and breed combinations. For lamb survival, there is variation in underlying reasons for lamb losses. In crossbreeding, dystocia is probably the largest cause of lamb loss, whereas in straight-bred Merino matings, it is more likely to be starvation/mismothering/exposure (Hinch 2008). In these cases, optimal selection strategies may differ for NLW in relation to desired changes in lambing ease and birth weight, for example.

SHOULD SELECTION BE FOR NLW OR FOR ITS COMPONENTS?

To genetically improve reproductive rate, ideally all indicator and component traits of reproductive rate are identified, and their genetic and phenotypic relationships with reproductive rate estimated. However, is this achievable and worth the effort compared to just evaluating NLW as a composite trait? Also, do component traits of reproductive rate have any inherent value in their own right and therefore need to be considered as distinct part of the breeding objective?

From a genetic gain perspective only, selection on components of NLW may be better than direct selection for NLW when they have larger heritabilities and coefficients of variation than NLW and a high genetic correlation with NLW. Values for these parameters are given in Table 3.

Table 3. Heritability (h^2) and coefficient of variation (CV) for fertility, litter size, lamb survival and NLW. Genetic correlations (R_g) with NLW are also shown (Safari *et al.* 2005)

| Trait | h^2 | CV (%) | R_g with NLW |
|---------------------------------------|-------|--------|----------------|
| Fertility | 0.08 | 52 | 0.73 |
| Litter size | 0.13 | 34 | 0.62 |
| Lamb survival - as a trait of the ewe | 0.06 | 40 | 0.63 |
| - as a trait of the lamb | 0.03 | 46 | - |
| NLW | 0.07 | 64 | - |

Fertility has a similar h^2 and CV to NLW. Although h^2 for litter size is approximately double that for NLW, CV is only a little over one half. For lamb survival as a trait of the ewe, although h^2 is similar to that for NLW, CV is only around 63% of the size. Fertility, litter size and lamb survival all have strong genetic correlations with NLW. On balance therefore, one would not expect a big advantage in genetic gain for NLW by selecting for its component traits rather than by applying direct selection, although the result may vary with mean reproduction rates, the production system in use and the specific genetic parameter estimates.

Where reproduction is not directly recorded and NLW is low (0.7 to 1.2), Swan (2009) argued that using NLW in the breeding objective and in reporting EBVs is a reasonable approach. However, the preferred alternative when reproduction is recorded is to include the components of reproduction rate in the breeding objective, modelling litter size and lamb survival in particular as separate traits. Part of the reasoning for this is that the components of reproduction rate represent distinctly different but interacting events (Swan 2009).

It is quite possible for ewes to have largely similar EBVs for NLW, but have quite different genetic merit for its components. An extreme example is comparing sheep carrying the *FecB* mutation (the Booroola gene, Davis 2005), which are characterised by high litter size, but low lamb survival, with other non-carrier sheep that have equivalent EBVs for NLW with more moderate merit for litter size and lamb survival. Under extensive grazing conditions where lamb survival is often compromised, the latter sheep are preferable, despite similar EBVs for NLW. In other words, lamb survival has its own intrinsic value, both from reproduction efficiency and animal welfare perspectives. As predicted in Option 1 in Table 1 and by Brien *et al.* (2010), where only NLW is part of a multi-trait breeding objective, lamb survival may genetically decline, although these predictions need to be tested against what is occurring in commercial breeding programs. If selection for reproductive rate is on the basis of selection on its components, more control over the size and direction of genetic change in lamb survival in particular could be practised.

Afolayan *et al.* (2007) considered the merits of direct selection for a composite trait (the total weight of litter weaned per ewe - TWWj) versus selection based on its components (fertility, litter size, rearing ability or lamb survival as a trait of the ewe and average lamb weight weaned). The authors concluded that an optimal index of the 4 component traits was predicted to result in a 17% higher response in TWWj than direct selection for the trait itself. In this case, reliable genetic parameters and trait records were available from the Maternal Central Progeny Test project (Afolayan *et al.* 2007) to develop an appropriate selection index. Litter size, with a slightly higher heritability than TWWj (0.19 vs. 0.17) was by far the major contributor to predicted gain based on component traits (Afolayan *et al.* 2007) and this may partly explain the result.

In a review, Snowden and Fogarty (2009) conclude that in most circumstances, selection to improve reproductive efficiency and ewe productivity would benefit from selection for litter-weight weaned, rather than for a single component trait. They argue that such selection should maintain a biological balance and increase the animal's adaptation to the production system.

If a sheep breeder is submitting sire and dam pedigrees to Sheep Genetics, most of the records necessary for selection based on the components of NLW are already available. The area of weakness in utilising component selection is the lack of reliable genetic parameters, especially the paucity of precise estimates of genetic correlations among components of reproduction and with other production traits. Further, as stated earlier, field recording of dead lambs is often lacking or incomplete, so including lamb survival as part of genetic evaluation is likely to be more difficult.

Sheep Genetics has under consideration the development of recording systems to capture more comprehensive reproduction data, based on RFID electronic tag technology, making it easier for breeders to collect the required information, including mating, scanning, lambing and weaning records (Swan *et al.* 2007). Under this scenario, it would be feasible for litter size records from scanning, together with weaning records, for example, to be utilised by the breeder to select on components of NLW, with or without detailed collection of pedigree records at lambing time.

Finally, an alternative approach is to combine selection directly for NLW with selection on its component traits. Further work is needed to quantify the benefits and costs of all these alternatives.

CURRENT GENERATION GAINS

In addition to genetic gains, gains in the current generation can be exploited by all sheep breeders, regardless of whether they breed rams or rely on ram purchases. It has been long-recommended that dry ewes be culled from the flock on the basis of being twice-dry rather than once-dry, with benefits in flock reproductive rate in the order of 4% (Lee, *pers. comm.*). This recommendation has been on the basis that repeatability is low and any improvement in reproductive rate of the whole flock from culling young ewes after only 1 mating opportunity will be diluted by introducing a higher proportion of maiden ewes (normally of lower reproductive rate than parous ewes) required to maintain breeding flock numbers. Another option put forward recently is to retain the better performing ewes, say the top 50% of each age group for net reproductive rate, for 1 to 2 years longer (Lee *et al.* 2009). Modelling predicts increases of 4% and 7% in flock reproduction rate after 5 and 10 years use of this approach, respectively (Lee, *pers. comm.*). However, the potential advantages of retention of older ewes remain to be fully explored.

CONCLUSIONS

A key limitation to achieving genetic gain in reproduction rate in the Australian sheep industry is the low level of maternal pedigree recording, particularly in Merino breeding programs. Finding a cheaper way of accurately determining maternal pedigree is a priority. This could be provided with further developments in DNA marker technology and by refinement and wider validation of Pedigree Matchmaker. With full pedigrees, information from relatives enhances gain predicted for reproduction rate, although progeny testing for NLW is counter-productive. An alternative is to progeny-test for lamb survival, which is not sex-limited and can be achieved on younger sires. These enhancements appear achievable without detriment to genetic gain in other traits. Genomic selection for NLW could make a similar improvement in accuracy and genetic gain as the addition of 10 half-sib records, but without the disadvantage of increasing generation length.

The increased prevalence of crossbreeding in the Australian sheep industry poses a challenge to genetic evaluation, especially for reproductive traits that express considerable heterosis. This challenge appears difficult to overcome. Some variations in selection strategies for reproductive rate may be appropriate to cater for different breeds and breed combinations, for example where the causes of lamb loss may vary widely.

Finally, refinements of breeding objectives and selection criteria for reproductive rate are desirable. For the former, lamb survival has value, from an economic and welfare perspective and should be included in the breeding objective. For selection criteria, more work needs to be undertaken to determine if more genetic progress in reproductive rate can be made by considering

its component traits, alone or in combination with net reproductive rate itself. This includes the development of more precise genetic parameters, particularly genetic correlations among reproductive trait components and with other production traits. With the widespread availability of ultrasound scanning records on foetal numbers and further adoption of RFID electronic identification systems, selection on component traits for reproduction rate is more feasible.

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