

Transfers of genetic merit through multiple-tiered breeding structures into trait expressions for commercial sheep production

BFS Santos^{1,2*}, TJ Byrne¹, PR Amer¹, JP Gibson² and JHJ van der Werf²

¹AbacusBio Limited, P O Box 5585, Dunedin 9058, New Zealand; ²School of Environmental & Rural Science, University of New England, Armidale, NSW 2351, Australia

*Corresponding author. Email: bsantos@abacusbio.co.nz

Abstract

In New Zealand, selection of both replacement females and sires based on performance is typically highly rudimentary in multiplier and commercial flocks. Selection of ewes and rams in these tiers is frequently driven by soundness and overall condition of selected animals and sometimes, based on whether or not the replacement candidate was born in a multiple litter. In breeder flocks, selection is usually supported by knowledge of the genetic merit of candidates. In multi-tiered breeding schemes, genetic progress is disseminated from the nucleus to the commercial tier through the transfer of males. Gene-flow principles can be applied in the optimization of multi-tiered breeding schemes, particularly to define the proportion of genetic superiority expressed in an individual, which also gets expressed in its descendants, in time, across tiers. The opportunity to increase the rate of progress and reduce the genetic lag between tiers in integrated production systems might be exploited by selecting candidates from which performance of the progeny can be predicted. The results of this simulation study demonstrate the long time delays of up to 25 years for genetic expressions to fully flow through a multiple-tiered breeding scheme. There was long time delay before genetic progress realised in the nucleus was achieved in the commercial flocks. For example, it was approximately fourteen years until 70% of benefits of genetic improvement in lambing and slaughter traits were captured in the commercial flocks. This delay was mitigated when performance recording was implemented in the multiplier flock. This gain however, does not have the permanent and cumulative properties of genetic progress achieved in the nucleus flock, and so needs to be continued each year for the benefits to be maintained.

Keywords: gene flow; selection; performance recording; genetic gain

Introduction

Advancements in animal electronic identification and DNA technology have created an opportunity for commercial farmers to capture livestock performance data, and use this to improve farm profitability. In sheep production, these opportunities are still under-utilised as selection decisions based on performance records and the potential to accelerate genetic progress in commercial flocks are not well quantified. Performance recording involves a multidisciplinary approach which initially requires data collection and analysis, eventually expanding to breeding scheme design and optimisation, mating strategies, and adoption of new technologies such as genomics and genomic selection. The implementation of fully or partially recorded parentage and performance should lead to enhanced farm profitability through better selection decisions.

The opportunity to select candidates can be particularly beneficial if the production system is part of a multi-tiered breeding structure that includes a multiplier tier. There is limited scope for selection within purely commercial sheep flocks due to limited opportunities to undertake voluntary culling. In contrast, a greater value proposition of performance recording replacement candidates is likely to exist in the multiplier tier, which disseminates genetic progress from the nucleus to the commercial tier through the transfer of males. This selection manifests as a reduction in the difference in average genetic merit, normally referred to as genetic lag, between nucleus and commercial tiers. In multi-tiered breeding schemes, the implications of selecting

candidates in a more typical commercial environment should also be considered, accounting for the fact that elite ewes and their male offspring are often managed differently to achieve target sale weights, and to facilitate recording of phenotypes.

Within an age-structured population, the genetic contributions can be predicted through modelling the extent of progress that flows through different tiers in time. Hill (1974) developed an age-structured gene flow model to evaluate the selection response in populations with overlapping generations. Bijma & Woolliams (1999) also developed a method to predict genetic gains based on long-term genetic contributions from ancestors to future generations. Amer (1999) proposed a methodology to calculate the proportion of genetic superiority from an individual which is also expressed in the individual's descendants. This methodology accounts for delays until the benefits of genetic improvement are expressed over the lifetimes of the selected animals' descendants.

The main objective of this study was to calculate genetic expressions of trait groups in the different tiers of a three-tiered breeding scheme. This paper also evaluates the extent to which genetic expressions in the commercial flock are affected when selection differential is created in the multiplier tier which supplies breeding males to the commercial flock.

Materials and methods

Multi-tiered breeding structures are characterized by the presence of multiple populations of livestock which

generate, transfer and receive continuous and cumulative genetic improvement. In sheep production, breeding structures are normally composed of two or three tiers. A two-tier programme is composed of nucleus (or elite) flock where genetic improvements are made, and then a commercial tier. It is in the commercial tier that the vast majority of end-products are produced, and this tier relies on the nucleus to provide superior genetic material (generally by male transfer), guaranteeing that genetic improvements are obtained. In three-tier programmes an additional intermediate tier, normally named as the multiplier tier, multiplies stocks from the nucleus in order to support a larger number of commercial flocks with males, or with both males and females.

A three-tiered gene-flow model was developed to conduct the simulations. The model was based partly on methodology proposed by Amer (1999) which used discounted gene-flow principles to quantify the economic value of genetic superiority in individual rams or ewes making a one-way genetic contribution to the commercial production tier. The methodology assumes a given flock age-structure, where P^i is the proportion of animals in age group i for $i = 1$ to n (years), S is a n by 1 vector of probabilities of a ewe surviving and lambing or ram surviving from age group $i-1$ to age group i , and p is the vector of numbers of lambs reaching slaughter age or reproductive age, per ewe lambing in age group i . These assumptions were derived for rams transferred from the multiplier to the commercial tiers using assumptions presented in Table 1. The extent of genetic contribution and the structure of breeding programmes requires consideration of the time and frequency of expression of genetic superiority in resulting daughters, reproductive rates (p) and the culling and survival rates (S) (Dekkers & Gibson 1998). Also important are the d probability of a ewe dying or being culled at i years of age, and the discount rate r which accounts for traits that are expressed at earlier ages and/or more frequently than others.

Table 1 Proportion of ewes and rams in different age groups (P^i), culling and survival rates (S) and reproductive rate (p) used to calculate discounted genetic expressions of replacement ewes in the commercial tier of a multi-tiered breeding scheme.

Age (i)	Multiplier		Commercial		Rams	
	P^i	P^i	S	p	P^i	S
0	0.00	0.00	1.00	0.00	0.00	1.00
1	0.30	0.34	0.78	0.55	0.41	0.80
2	0.24	0.27	0.62	0.65	0.33	0.60
3	0.19	0.16	0.50	0.65	0.20	0.30
4	0.14	0.05	0.40	0.52	0.06	0.00
5	0.10	0.00	0.28	0.36	0.00	0.00
6	0.02	0.00	0.06	0.07	0.00	0.00
7	0.00	0.00	0.01	0.01	0.00	0.00

The calculation of discounted genetic expression (DGE) coefficients accounts for the proportion of superiority transmitted to an individual's descendants through transfer of genes. The expressions of genes in different age classes were calculated through a series of transition matrices with a ten-year planning horizon (h) in years from birth of the self-replacing female (Amer, 1999). The first transition matrix is \mathbf{D} which is based on the probability of a ewe surviving to the next age group. The \mathbf{E} matrix is an $h \times h$ transition matrix of lambs produced for slaughter within age groups. The transition matrix for lambing expressions is \mathbf{F} , while \mathbf{G} is the matrix for cull ewes. The explicit structure of the matrices \mathbf{D} , \mathbf{E} , \mathbf{F} and \mathbf{G} are outlined in more detail in Amer (1999). The vectors of increments of gene-flows by generation (\mathbf{g}_k) account for the ewe's genetic contribution to the progeny, and the sum of their aggregate yearly genetic expressions accumulated over generations is \mathbf{g}_{sum} , calculated as:

$$\mathbf{g}_{sum} = \sum_{k=1}^m \mathbf{g}_k$$

In the current study, genetic expressions for traits expressed at different time points via replacement daughters of a commercial-tier breeding ram were grouped as vectors (with dimension equal to the year of expression) of annually expressed traits (X_{FRA}), traits expressed at end of life or cull traits in ewes (X_{FRC}), traits expressed at birth (X_{FRL}) and at slaughter (X_{FRS}). The equations from which genetic expressions were obtained are:

$$\begin{aligned} X_{FRA} &= \mathbf{g}_{sum} \cdot \mathbf{D}, & X_{FRC} &= \mathbf{g}_{sum} \cdot \mathbf{G}, \\ X_{FRL} &= \frac{1}{2 \cdot l_s} \mathbf{g}_{sum} \cdot \mathbf{F}, & X_{FRS} &= \frac{1}{2 \cdot l_s} \mathbf{g}_{sum} \cdot \mathbf{E}, \end{aligned}$$

where, l_s is the lamb survival from birth to slaughter. Because surplus lambs are generated in the process of breeding replacement breeding ewes, and these lambs express traits at both birth and slaughter, it was necessary to augment the gene flows accounted for by X_{FRA} , X_{FRC} , X_{FRL} and X_{FRS} . A recursive set of calculations was used to calculate the genetic merit of the multiplier flock, as a result of a one-off increase in the genetic merit of rams supplied from the elite tier to mate to multiplier ewes. These equations are

$$\begin{aligned} g_{Li} &= \frac{1}{2} (g_{Si} + g_{Di}) \\ g_{Di} &= \sum_{i=2}^8 \rho_i \cdot g_{L8-i} + k_1 \\ g_{Si} &= k_2 + 0, \text{ for } i \leq 0 \\ &= k_2 + 10, \text{ for } i > 0 \end{aligned}$$

where, g_L , g_D and g_S are the genetic merit levels of lambs, dam and sires in age group \bar{z} in the multiplier population and p gives the age distribution of the nucleus breeding ewe flock. The variables k_1 and k_2 represent selection differentials of ewe lamb replacements in the multiplier flock and in sires from the elite flock that are mated to multiplier ewes. Because it is assumed that k_1 and k_2 are constant over time, they were assigned values of zero and have no material impact on the results.

Genetic merit of the commercial flock was modelled as a function of g_L , which reflects the change in merit over time of rams transferred from the multiplier tier to the commercial tier and the expressions of relevant traits via daughter replacements (e.g., X_{FRA} for annual ewe traits). Where additional lamb traits (birth and slaughter) are expressed directly in progeny of the rams used in the commercial flock, these were also incorporated. For every female replacement generated, there are $2u^{-1}$ expressions of lamb birth traits and $2u^{-1} - 1$ expressions of lamb slaughter traits, where u is the proportion of female lambs born which are kept as replacements.

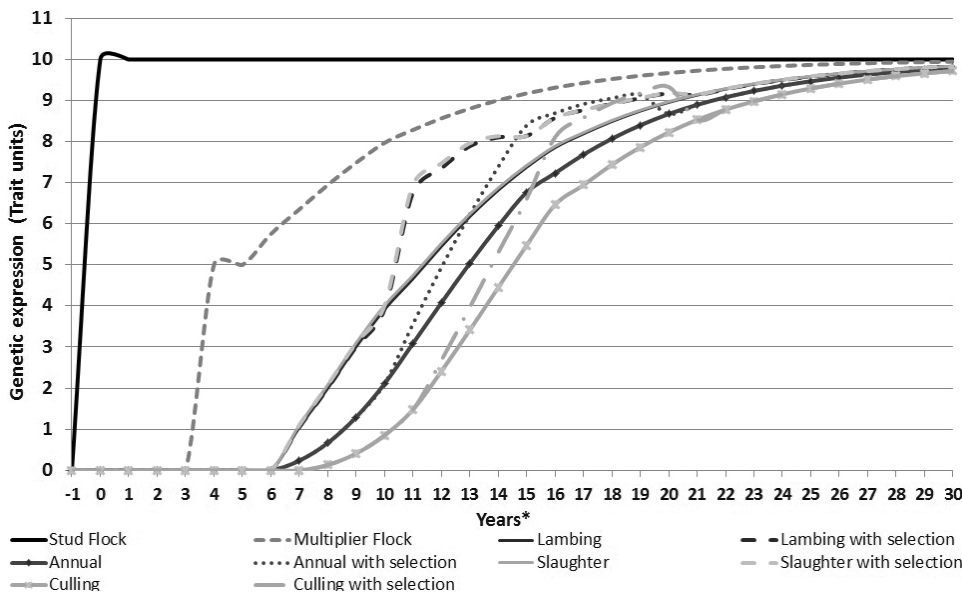
Results are computed which show the timing of expressions of traits in the commercial tier following a one-off annual genetic gain in the nucleus tier at year zero. The ongoing impact of this one-off gain in genetic merit in the nucleus on the multiplier tier is tracked over time. The effect of a further single selection event in the multiplier tier which results in the rams transferred from the multiplier to the commercial tier at Year 10, being ten units of superior genetic merit, is also measured.

Results

The results of this simulation study quantify the expressions of genes based on the flow of superiority in a multi-tiered breeding scheme, in time, across a range of assumptions reflecting the different tiers. Figure 1 presents the genetic expressions in the nucleus after one year of selection resulting in 10 units of genetic gain in the elite flock and illustrates how these gains flow to subsequent tiers. The commercial expressions for trait groups are presented with and without selection differential achieved by selection of rams in the multiplier tier ten years after the initial genetic lift in the nucleus tier. The impacts in the nucleus and multiplier tier are trait neutral, as they reflect

units of genetic gain in lambs born. In contrast, results for the commercial tier represent the timing of actual expressions of the trait, and as such differ for different traits, such that of lamb birth traits impacts occur first, and

Figure 1 Flow of genetic expressions across tiers after one year of selection in the nucleus, with and without selection in the multiplier tier, and timing of expressions of lambing, slaughter, annual and culling traits in the commercial tier¹.



¹Years from one-off selection event in the Nucleus, assuming the one-off selection in the Multiplier tier occur in Year 10.

of cull ewe traits impacts occur last.

For lambing and slaughter traits, impacts in the commercial flock are first observed at Year 7 after the lift in genetic merit of the nucleus. Impacts are first observed between Year 8 and 9 and between Year 10 and 11 for annual and end of life traits, respectively. The impacts for lamb traits increases at a decreasing rate over a further 20-year period as the genetic improvements flow through the population tiers. For ewe traits, the impacts initially accumulate at a slower rate than for lamb traits, then accelerate, before approaching the full impact asymptotically, similarly to lamb traits with a lag.

When a one-off selection differential is introduced in the multiplier tier (Year 10), results demonstrate an additional gain in genetic expressions which reduces the lag between nucleus and commercial flocks. This pattern is present in all trait groups, although the timing at which this additional gain occurs varies across traits.

Discussion

The results of this study demonstrate that implementation of performance recording in the multiplier tier can reduce the very long genetic lag between the nucleus and the commercial flocks in a three-tiered breeding program. This would reduce the existing lag, which, in the absence of selection, is approximately fourteen years until 70% of benefits can be captured in commercial flocks for lambing and slaughter traits. The findings of this

study show that a reduction of three years in genetic lag can be achieved with implementation of selection in the multiplier tier. According to McClintock & Cunningham (1974), differentials in frequency and timing of expression influence decisions on investment in trait selection that normally require additional recording effort, ultimately calling for extra labour and additional costs. For instance, when formulating breeding objectives, weighting factors on traits should reflect the economic benefit of genetic change in the trait simultaneous with the frequency and timing of expressions of the trait over multiple generations (Berry *et al.* 2006). In general the gains promoted by selection decisions are long term, and can last for long periods. Based on results from this study, and as mentioned by Morris & Archer (2007) for reproductive technologies, performance recording in the multiplier tier might be used to achieve faster transfer of elite genes into the commercial population, thereby reducing the genetic lag between the nucleus and commercial herds.

Results presented in this study confirm that the most immediate gains expressed in the multi-tiered breeding scheme are lambing and slaughter traits, followed by annual traits and end-of-life traits. No discounting to account for value of money was considered in the calculation of the genetic expressions in time, although this can easily be applied to the presented results using standard formulae. The results demonstrate a three-year average gain to which one unit of genetic progress is expressed when recording is implemented in the multiplier flock, and the recording investment required to achieve this came ten years later than the investment to achieve the gain in the nucleus. Similarly to lambing and slaughter traits, in annual and end-of-life traits, an average lag decline of three years is achieved when selection is implemented. However, this reduction occurs in traits with even longer genetic lags, eighteen and nineteen years, for annual and end-of-life traits respectively, to achieve 80% of the benefits of one-off increase of ten units in the merit of the nucleus.

These results reflect the impact of a one-off selection event in the nucleus and one-off selection of rams in the multiplier flock. Continuous selection in these tiers would cause the genetic expressions to progressively increase and would result in parallel increases in merit across all three tiers, with the multiplier and commercial tiers lagging behind the nucleus tier. The extent to which the multiplier and commercial tiers lag behind the nucleus tier depends on the level of selection differential achieved prior to ram transfer between the tiers. Bichard (1971) argued that where a self-contained flock has to recoup its testing and selection costs from sales of end-products, such as slaughter lambs, only limited efforts can be made, and therefore, accepting limited rates of genetic progress is the most reasonable option. Where breeding stock is produced, costs can be shared among the total population derived from this stock.

More benefits of recording in the multiplier flock might be captured if multiplier animals identified as being elite, contribute to the nucleus by transfer of animals in a so-

called open-nucleus structure. Other benefits would arise if data from multiplier recording would increase accuracy of prediction of breeding values in the elite flock. According to Horton *et al.* (2014), gains made from selection for meat and wool production are acquired by commercial producers, however, it is essential that the nucleus can recover the extra costs involved with obtaining more accurate information, even though these might be coming from the multiplier flock. Neither of these aspects were modelled in this study, although both will be included in an extension of the model presented here to generate a more comprehensive model which predicts costs and benefits of recording strategies across a three-tiered breeding structure.

The results of this study are part of a wider investigation which aims to develop a model to assess the impact of performance recording and selection decisions, made in the multiplier tier, on the dissemination of genetic progress to commercial units.

Acknowledgements

The authors would like to acknowledge the importance of the Beef + Lamb New Zealand Genetics consortium in funding and supporting this research project.

References

- Amer PR 1999. Economic accounting of numbers of expressions and delays in sheep genetic improvement. *New Zealand Journal of Agricultural Research* 42: 325-336.
- Berry DP, Madalena FE, Cromie AR, Amer PR 2006. Cumulative discounted expressions of dairy and beef traits in cattle production systems. *Livestock Science* 99: 159-174.
- Bichard M 1971. Dissemination of genetic improvement through a livestock industry. *Animal Production* 13: 401-411.
- Bijma P, Woolliams JA 1999. Prediction of genetic contributions and generation intervals in populations with overlapping generations under selection. *Genetics* 151: 1197-1210.
- Dekkers JCM, Gibson JP 1998. Applying breeding objectives to dairy cattle improvement. *Journal of Dairy Science* 81 (2): 19-35.
- Hill WG 1974. Prediction and evaluation of response to selection with overlapping generations. *Animal Production* 18: 117-139.
- Horton BJ, Banks RG, van der Werf JHJ 2014. Industry benefits from using genomic information in two- and three-tier sheep breeding systems. *Animal Production Science*. <http://dx.doi.org/10.1071/AN13265>.
- McClintock AE, Cunningham EP 1974. Selection in dual-purpose cattle population: defining the breeding objective. *Animal Production* 18: 237-247.
- Morris CA, Archer JA 2007. Application of new technologies in New Zealand for beef cattle and deer improvement. *New Zealand Journal of Agricultural Research* 50: 163-179.