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# EFFECT OF GxE ON RESPONSES TO SELECTION IN RECORDED MULTI-TIER SHEEP BREEDING SCHEMES

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## SUMMARY

In multi-tiered breeding schemes, the top tier is frequently maintained under different conditions to that of the commercial tier, which may lead to a genotype by environment interaction (GxE) that affects performance in target environments. Genomic selection might be useful for selection of candidates that perform well across environments in integrated breeding schemes. The results of this study demonstrate that there might be benefits from inclusion of phenotypic and genomic data from lower tiers into an integrated reference population, for situations when there is concern about GxE between the Nucleus tier and commercial populations.

## INTRODUCTION

Integrated breeding schemes are frequently structured in multiple tiers. The nucleus tier pursues rapid rate of genetic gain and overall mean performance, and supplies grandparent stock to multiplier flocks or herds which provide the commercial tier with sound breeding animals as cheaply as possible (Bichard, 1977). Frequently, these tiers are maintained in different environmental conditions and for various reasons, it is common for the environment in the nucleus to be rather different from the conditions in which commercial animals are kept (James, 2009).

Falconer (1952) considered the performance of improved genotypes might be different under a less favourable environment, leading to a genotype by environment interaction (GxE). To mitigate the potential detrimental effects of impaired environment and genetic merit, breeders should target selection of robust animals capable of performing well in challenging conditions. Integrated breeding schemes could be optimised to allow for the existence of GxE among tiers, consequently increasing productivity of the commercial livestock.

DNA technologies, can contribute to better integration of multi-tier breeding schemes. A better estimation of GxE was observed with genomic selection (GS), when compared to conventional selection methods (Mulder, 2016; Silva *et al.* 2014). However, estimates of genomic breeding values based only in nucleus records might be sub-optimal predictors of direct response in the commercial environment. Genomic information and genomic relationships among individuals improve the accuracy of prediction of breeding values in an optimized reference population (Clark *et al.* 2012), and its design determines the selection response achieved in the target subpopulation. Integrated breeding schemes should source information from multiple tiers and environments (Nirea & Meuwissen, 2016).

Our hypothesis is that phenotypes and genotypes recorded on specific multiplier and commercial individuals will increase genetic progress of integrated breeding schemes and minimize the potentially detrimental effects of GxE. The objective of this study was to compare selection strategies and their effectiveness under different levels of GxE, in Australian fine-wool commercial sheep operations that exploit multi-tier breeding structures.

## MATERIALS AND METHODS

A selection index model was used to compare scenarios representing different genetic correlations between nucleus, multiplier and commercial environments and various amounts of recording in the different levels. We compared selection differentials for rams and ewes from the different tiers and the percentage reduction in superiority with increased levels of GxE.

**Breeding scheme.** The breeding scheme was based on an actual fine-wool commercial operation which maintains a multiplier flock that produces rams to mate commercial ewes, all in the same farm. The multiplier tier is composed of commercial ewes historically selected as better performers, based on a phenotypic index, and mated to elite outside nucleus rams by artificial insemination (AI). In this simulation, either pedigree or genomic selection were assumed in the multiplier tier.

**Selection index model.** This study applied selection index theory to quantify responses to selection based on a pre-determined multiple-trait breeding objective. The definition of the aggregate breeding value of selection candidates, across tiers, was calculated as the sum of the products of economic weights ($ew_j$) of the $j$ traits composing the breeding objective and their respective breeding values ($ebv_j$), computed by $H = \sum_1^n (ew_j \cdot ebv_j)$, as described by Hazel *et al.* (1994). Response to selection was calculated for each of the component traits of the breeding objective, computed as the product of the response in index value and the respective regression coefficients of traits on the index, assuming information sources from appropriate selection candidates. Genetic parameters and trait economic weights required for the calculation of the regression coefficients were supplied by Sheep Genetics. Estimated breeding values were based on phenotypes recorded in the Nucleus or in the Multiplier/Commercial tiers, plus genomic predictions with estimates accounting for or not accounting for GxE.

Selection intensities were determined for each pathway (Table 1), accounting for the dilution of intensities when selecting commercial and multiplier candidates due to having two-stage selection, and only a proportion of animals are recorded and/or genomically tested. We also account for differences in intensities when selecting nucleus rams for the multiplier, and multiplier rams used to follow up AI in the multiplier tier itself.

**Table 1. Selection intensity in two-stages in different categories and tiers.**

| Born in | Used at | Sex | Intensity |
|---|---|---|---|
| Nucleus | Nucleus | Males | 2.56 |
| Nucleus | Multiplier | Males | 2.35 |
| Multiplier | Multiplier | Males | 2.35 |
| Multiplier | Commercial | Males | 0.80 |
| Multiplier | Multiplier | Females | 1.09 |

**Genotype by environment interaction.** We modelled GxE by defining a new set of breeding goal traits (indexed as $j'$) expressed in the multiplier and commercial tier environment, which are genetically different from but correlated with the equivalent traits expressed in the nucleus environment ($j$). The correlations ($r_{GxE}$) represented the level of GxE, and ranged from 1.00 to 0. 50. The correlation for goal traits with other traits ($i$) was calculated as $r_{i,j'} = r_{j,i} \cdot r_{GxE}$ , where $r_{j,i}$ is the correlation between traits $j$ and i within an environment. The calculations assumed equal phenotypic variances and heritability of traits expressed in the nucleus and in lower tiers. We also compared the potential effect of "unknown" GxE incidence by directly multiplying the direct response of each goal trait without GxE (i.e. $r_{GXE}$=1), by the trait economic value and this product further multiplied by the respective correlation representing the levels of GxE.

## RESULTS AND DISCUSSION

**Selection differentials.** As GxE increased, trait selection responses decreased. The superiority of nucleus candidates for goal traits was reduced most by the increasing levels of GxE, -\$0.43 and -\$0.19 per 0.05 increase in GxE from the value of \$10.59 and \$4.53, for males and females respectively, in the absence of GxE (Figure 1a). Selection differentials were larger when GS was used (Figure 1a), compared to pedigree selection (Figure 1b). This might be caused by the additional genomic information which makes GS more accurate. With genomic selection, the level of GxE had a small effect on selection differentials in multiplier tier males (Figure 2a) and females (-\$0.04 and -\$0.03 per 0.05 increase in GxE, respectively) and also in replacement commercial females (-\$0.07). The loss of selection differential remained high however, with pedigree selection (Figure 2b). When GxE was present, but not accounted for in genetic evaluation and selection (i.e. GxE unknown), its detrimental effects were larger, -\$0.48 per 0.05 increase in GxE for nucleus males. In this case (pedigree selection), selection differentials in all tiers were reduced by increased levels of GxE.

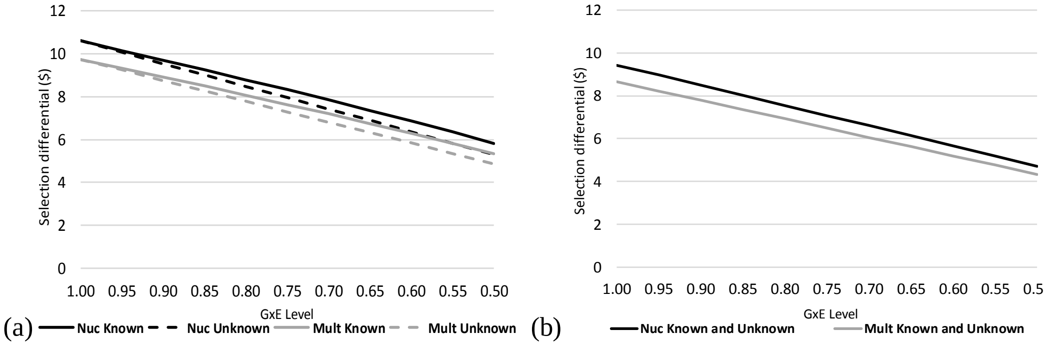

**Figure 1- Superiority (in breeding objective terms) of nucleus born rams selected for use in the nucleus (Nuc) and multiplier (Mult) at different levels of known and unknown GxE, based on genomic (a) and pedigree selection (b).**

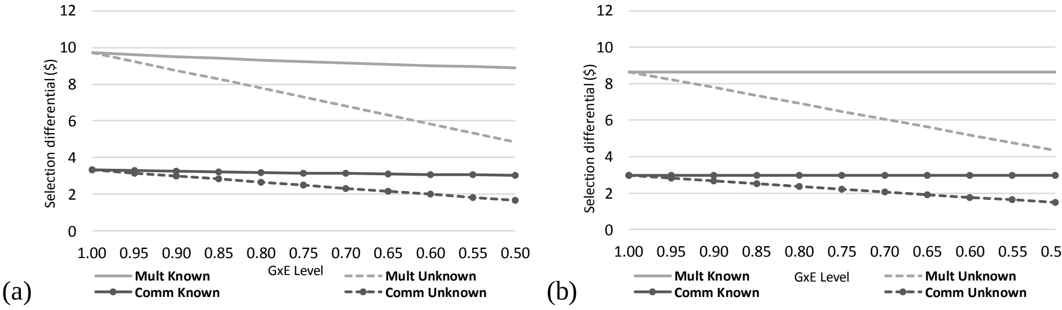

**Figure 2- Superiority of multiplier born rams used in the multiplier (Mult) and commercial tier (Comm) at different levels of known and unknown GxE, based on genomic (a) and pedigree selection (b).**

**Reduction in selection differentials.** The reduction in selection differentials when expressed as a percent reduction relative to the no GxE situation was linearly related to the increase in the value of $r_{GxE}$ (Table 2). Comparing across tiers the reduction was greatest for the nucleus, and was slightly bigger in pedigree selection when compared to GS, -5% versus -4% per 0.05 increase in GxE, respectively. Selection differentials with pedigree selection in the multiplier and commercial tiers were unaffected because information sources are recorded in the target environment. GS resulted in small reductions in selection differentials due to GxE in the nucleus. However, in the multiplier and commercial tiers the GxE reduces the value of genomic information relative to the performance records, which are measured in the target environment.

According to Nirea & Meuwissen (2016), a genetic correlation <1 between environments is the result of a combined action of multiple environment challenges. Estimating genomic breeding values from a reference population that includes records from multiple environments might be an alternative way to address GxE in a breeding program, and this should be explored. The results of this study (Table 2) demonstrate that there would be more value from inclusion of phenotypic and genomic data from lower tiers into an integrated reference population as the genetic correlation between the Nucleus tier and commercial populations increases. In Australia, commercial farmers often source rams from nearby environments, similar to their own. While this should minimise problems of GxE, it limits the pool of selection candidates. Environment specific reference populations boosted in size and commercial relevance by training data, i.e. phenotypes and genotypes, from multiple tiers could allow more accurate and appropriate sourcing of high merit rams from other production regions and environments. In this case, genomic selection could be used to provide wider scope for identifying elite individuals from other regions and reduce the detrimental impacts of GxE on realised genetic progress.

**Table 2. Percent reduction in selection superiority for both rams and ewes across different tiers at different levels of known GxE, based on genomic (GS) and pedigree selection.**

| GXE Level | Nucleus | | Multiplier | | Commercial | |
|---|---|---|---|---|---|---|
| | GS | Pedigree | GS | Pedigree | GS | Pedigree |
| 1.00 | - | - | - | - | - | - |
| 0.90 | -8.23 | -10.05 | -2.18 | 0.00 | -2.18 | 0.00 |
| 0.80 | -16.95 | -20.11 | -4.12 | 0.00 | -4.12 | 0.00 |
| 0.70 | -25.91 | -29.89 | -5.81 | 0.00 | -5.81 | 0.00 |
| 0.60 | -35.35 | -39.95 | -7.26 | 0.00 | -7.26 | 0.00 |
| 0.50 | -45.04 | -50.00 | -8.47 | 0.00 | -8.47 | 0.00 |

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