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Predicting the benefits of two stage genomic selection in young breeding rams

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ABSTRACT

A two stage selection index model was developed to assess the cost effectiveness of using genomic technologies to assist in selection decisions for retention of ram lambs for breeding within a ram breeder flock. The principle of two stage selection is that many of the benefits of an expensive, but more accurate, measure of genetic merit can be captured while drastically reducing measurement costs. This paper describes the two stage model used, and some of the potential benefits of testing the top 6–50% of selection candidates ranked according to estimated breeding values, prior to ranking on a combined score using genomic breeding values. The model assumes a hypothetical panel of markers and trait predictive accuracies to explore the benefits of selection using both types of breeding values. The value of genetic progress is assessed using selection index theory to predict trait changes according to a selection index recently revised for implementation as the recommended index for dual purpose sheep in New Zealand. Results suggest that maximum benefits were obtained when the top 10–20% of selection candidates were tested, with the level of benefits dependent on both the prediction accuracy and price of the test.

Key words: sheep; genetics; economics; breeding; genomics.

INTRODUCTION

Over the last five years, much research has gone into the development of high density DNA marker chips with a view to their application in livestock improvement programs. These chips contain many thousands of single nucleotide polymorphisms (SNPs), many of which may be linked to traits of economic importance. Associations of large numbers of markers spread across the genome with phenotypes linked to economic traits, has allowed development of marker assisted selection methods, used to predict breeding values for individuals using their combined marker genotypes (Meuwissen *et al.*, 2001).

For intensively farmed livestock species with high reproductive rates of elite males such as dairy cattle, or highly tiered nucleus breeding programs such as pigs and poultry, opportunities for breeding schemes to leverage investment in expensive technologies across very high numbers of commercial animals are attractive. Arguably, this is much less so for sheep, where the breeding industries consists of a large number of specialised ram breeders, each with a relatively small share of the market, and high breeding program costs relative to the sales revenues of breeding males. Thus, there are challenges to make relatively expensive new genomic technologies cost effective for sheep breeding programs. However, the problem of having expensive or difficult selection criteria in animal breeding programs is not new (Cunningham, 1975).

This paper uses a two stage selection index model (Jopson *et al.*, 2004) to predict the response

to selection in dual purpose sheep breeding flocks, when young rams are initially selected according to traditional recorded trait and pedigree information, with the parameters and assumptions based around selection indexes widely used within the New Zealand sheep industry (S-A.N. Newman, Personal communication). A proportion of young rams identified at Stage 1 as being of high genetic merit are then undergo a second round of selection using predictions of genetic merit enhanced using genomic prediction of breeding values. Selection index methods (Dekkers, 2007) are then used to model the potential benefits of recorded trait and DNA marker information in selection decisions for young animals.

MATERIALS AND METHODS

A two stage selection index model as implemented by Jopson *et al.* (2004) was adapted to predict the response to conventional and marker assisted selection in dual purpose sheep breeding flocks. The total merit index was comprised of prolificacy, growth, carcass, wool, lamb survival and internal parasite resistance traits of direct economic importance, with the economic values set according to those proposed for the New Zealand sheep industry (T.J. Byrne, Unpublished data). The initial selection criteria (Index 1) included recorded trait information sources on an animal and its relatives as described below, with the final selection criteria (Index 2) also including SNP predictor information. Genetic and phenotypic correlation matrices are incorporated into the selection index

calculation to account for known positive and negative associations between correlated traits.

A specified proportion of the rams ranked according to Index 1, are then tested and re-ranked prior to final selection using Index 2 (see Figure 1). The effective intensity of selection at Stage 2 is dependent on the correlation between the two indices, and the proportion of animals selected after being ranked at Stage 1 for additional secondary testing. When all the information sources used to determine merit in the first index are also used in the second index, along with new information sources not previously available, the correlation between the first and second indexes can be determined by comparing the superiority of the top proportion of animals ranked on Index 1 divided by the superiority of the same proportion of animals ranked using Index 2. When the two index values are highly correlated, animals high on Index 1 are also likely to be high on Index 2. This situation results in high selection responses but the added value of the second stage of selection tends to be modest. Conversely, when the correlation between the two indexes decreases, animals ranked highly on Index 1 may re-rank down when evaluated using Index 2. As the proportion of animals selected for secondary testing increases, so too does the selection intensity, until the correlation between the first and second index determines that there is no additional benefit from testing more animals, and that all potential high performers are in the secondary test group.

Recorded information sources

Young ram lambs are assumed to have their own trait records along with weaning weight (WWT), predicted carcass weight (CWT) and survival (SUR) records from up to 120 paternal half sibs, and yearling (hogget) fleece weight (HFW) records for 60 paternal half sibs. Information is also derived from their dam and 15 of the sire’s female half sibs, who each have two performance records for NLB, maternal WWT (WWTmat) and survival

(SURmat). Ewes are assumed to have the same records as those of young rams, with the exception that they have no HFW records for themselves or on their half sibs.

SNP predictors

Hypothetical SNP predictors for growth, reproduction and parasite resistance were included as selection criteria within Index 2 for the ram selection candidates, with the predictive accuracy of the DNA test assumed to be either 0.3 or 0.5 for all three traits. The heritability of the SNP predictors was assumed to be 0.95 after allowing for genotype error.

Index correlations

The correlation between each animal’s selection index values incorporating their recorded trait information alone, and selection index values using the recorded trait and SNP predictor information was estimated to be 0.74. The superiority of the top 5% of rams selected using recorded trait information alone was 718 cents, versus 962 cents, when all candidates also have SNP predictor information with an accuracy of 0.5 for the growth, reproduction and parasite resistance traits.

Value estimations

The total industry value of a one selection index unit increase in the genetic merit of lambs born within a breeding program has been estimated according to the superiority of future first and second generation ram progeny sold to commercial buyers. The discounted value of immediate ram sales is calculated according to Meikle and Amer (2003) where the additional value of a ram to a commercial farmer is 260 times the index superiority of the animal expressed in New Zealand dollars, assuming a commercial ram is mated over three years to 100 ewes and 1.45 lambs are tailed per ewe. Total ram sales are then discounted at a rate of 7% per annum for two years to account for the difference between the time of birth and the time of sale, with the discount rate reflecting a typical farm mortgage interest rate

adjusted for an average rate of inflation. In a 1,000 ewe breeding flock, with each ewe selling 0.25 of ram lambs born as breeding rams to commercial farmers, then the additional value of improving the flock by one cent can be calculated as NZ\$562.

A one off increase in a genetic trend leads to an upward shift in merit of all selection candidates for the year cohort and as a result,

FIGURE 1: Principle of two stage selection.

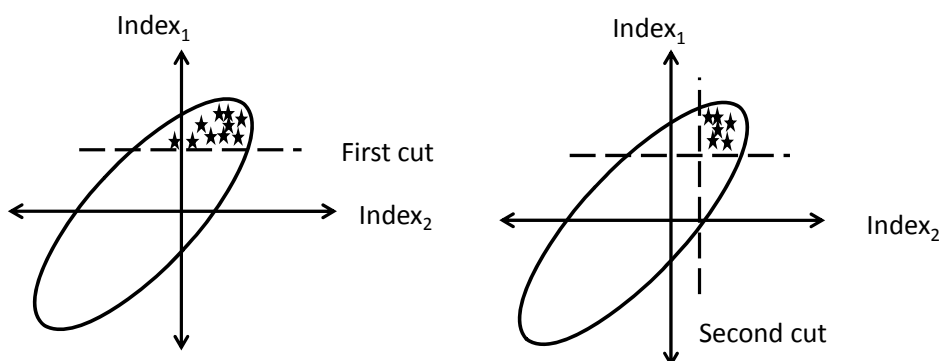


TABLE 1: Superiority of progeny born to improved parents mated in Years 1-6 due to improved selection in Year 1 using SNP predictor information.

Year after selection	Discount rate	Superiority (cents)	Discounted ram sale value
Year 1	0.930	0.112	\$62.74
Year 2	0.865	0.294	\$165.32
Year 3	0.804	0.177	\$99.48
Year 4	0.748	0.135	\$75.70
Year 5	0.696	0.056	\$31.29
Year 6	0.647	0.039	\$ 21.82
Total value of ram sales from superior parents			\$456.35

parents selected in the future out of this cohort will also be superior. This in turn leads to future crops of rams being superior, with the value of the superiority captured in immediate progeny of the selected cohort and grand-progeny of the selected cohort. In order to estimate the future benefits, an average industry breeding program design with an average ram generation interval of 2.28 years, comprising 44% young untested rams (aged one and two years-old), 40% emerging rams (aged two and three years-old) and 16% mature rams (aged three and four years old) was used. The generation interval of the ewes was fixed, based on an average age of 3.6 years when their lambs are born. Within the 1,000 ewe breeding flock the value of improvement in the first and second generation offspring of the selected animals is \$827, resulting in a total value of \$1,389 due to a one cent improvement in the genetic merit of lambs born.

First and second generation benefits

Table 1 shows the increased superiority of ram lambs born over years 1-6, where ewe and ram lamb selection candidates from the year 1 cohort are improved by 1 cent over what they would have been. Superiority of lambs born is calculated according to the proportion of improved rams and ewes used in the breeding program each year, and discounted against time of testing using a discount rate of 7%. The discounted ram sale value is calculated using the formulae as described above. The total discounted ram sale value of 2nd generation descendants has previously been estimated as \$371 (data not shown), with benefits obtained from ram and ewe lambs born in years 1-6 entering the breeding flock and having progeny over that time frame according to the breeding program design already described.

RESULTS AND DISCUSSION

The total industry value of the improved selection decisions made due to the use of SNP predictors with accuracies for all traits including growth, reproduction and parasite resistance, is shown in Figure 2, according to prediction accuracy of 0.3 and 0.5, and the proportion of candidates SNP tested. With the rate of increase in selection intensity reducing as more animals are tested, there is little additional benefit to be gained by testing animals ranked lowly on Index 1, with animals ranked in the bottom 25% unlikely to shift to the top 5% using the additional SNP information. Value is critically dependent on prediction accuracy, with previous studies showing a nonlinear relationship between prediction accuracy and rates of genetic gain (Sise & Amer, 2009). Using a SNP prediction accuracy of 0.5, the potential increase in the annual rate of genetic gain for index merit through application of the test is estimated to be 10%, assuming all animals are tested and dropping to 8% if only the top 15% of animals ranked according to Index 1 are tested. If prediction accuracy for all traits drops to 0.3, then the potential increases in the rate of genetic gain is estimated to be 4% when all animals are tested, and 2% if only the top 15% of animals ranked according to Index 1 are tested.

By using SNP predictors, more information is available to enhance selection decisions for traits with associated SNP tests. However, this does have an impact on other production traits under selection as selection emphasis gets diverted towards the traits with the extra predictive accuracy. Using SNP

FIGURE 2: Total industry value of improved selection of young breeding rams, within a 1,000 ewe breeding flock using single nucleotide polymorphism (SNP) markers with a predictive accuracy of 0.3 and 0.5 for growth, reproduction and parasite resistance.

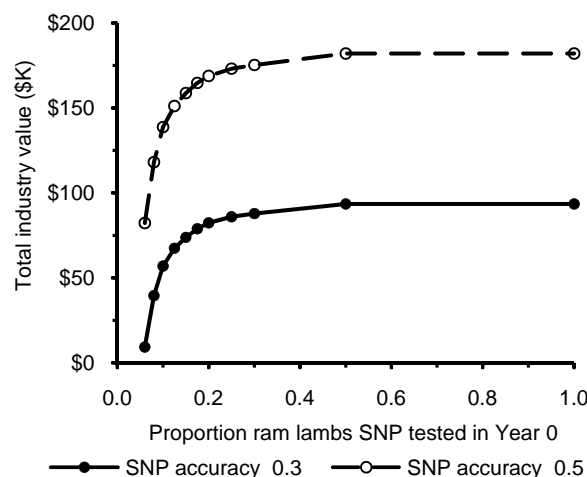
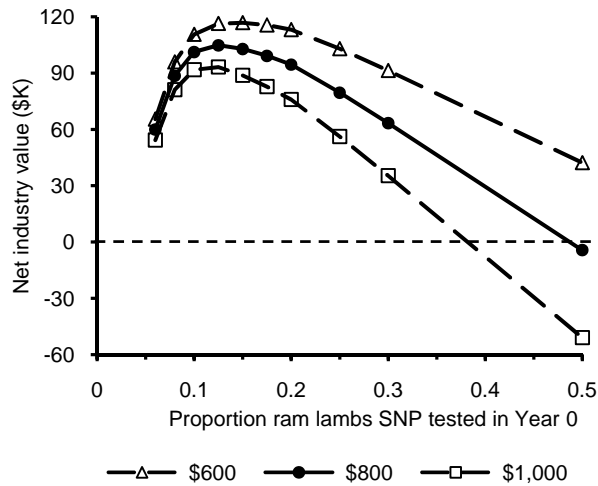


FIGURE 3: Net discounted industry value according to test price, of improved selection of young breeding rams using single nucleotide polymorphism (SNP) markers with a predictive accuracy of 0.5 for growth, reproduction and parasite resistance.



predictors with an accuracy of 0.5 on the top 15% of animals, the overall increase in the rate of genetic gain for reproduction is 33%, but losses of 4% for growth, 6% for survival and 8% for wool relative to selection using recorded trait information, are observed. This is due to the additional information on reproduction, and parasite resistance, diverting selection pressure away from the other traits, including growth. Jopson *et al.* (1995) found that 15% was an ideal proportion of terminal sire ram lamb breeding program candidates to select based on growth rate and ultrasound measurements for more expensive but also more accurate computed tomography (CT) prediction of carcass lean and fat tissue weights.

Figure 3 shows the net industry value of using SNP predictors at a prediction accuracy of 0.5, when the cost of testing is taken into account, with theoretical test costs of \$600, \$800 and \$1,000 per animal evaluated. At a test cost of \$600 per animal, maximum benefits are observed when the top 15% of ram lambs are tested, reducing to 12.5% as test costs increase to \$800 or \$1,000 per animal. With there being a trade-off between testing many animals to gain maximum industry benefits, and test cost, the optimal number of animals to test reduces as test price increases. As test price decreases, more animals can be tested before the cost of testing outweighs the return due to improvements in selection.

Whilst the assumptions used within the model are purely theoretical, an on-going Ovita research program has resulted in the development of Sheep50K, which is marketed by Pfizer Animal Genetics. The current prediction accuracies used by Sheep50K range from 0.3 to 0.5, and are likely to

increase as more phenotype data becomes available to the research team. Future advances in technology, may provide mechanisms to reduce test price, with the optimal proportion of animals to test increasing, resulting in further increases in the rate of genetic gain and industry value from application of the test.

CONCLUSIONS

This study has shown that net industry benefits of SNP predictor tests incorporated into two stage selection strategies are highly dependent on prediction accuracy and test price. While the costs of genomic testing remain high in sheep relative to the value of individual animals, two stage selection strategies are likely to substantially increase the attractiveness of SNP prediction tests to commercial sheep breeders. As a result, they are also likely to increase industry level benefits to sheep farmers.

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