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Comparison of two-stage selection breeding programmes for terminal sire sheep

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ABSTRACT

Two-stage selection is a technique used in animal breeding to make the use of expensive measurements economically viable in a breeding programme. Selection candidates are first screened using inexpensive, but imperfect, predictors of their genetic merit. A selected subset are then evaluated using more accurate, but expensive, measurements and the final selection is made. This study compared the assessment of carcass composition traits using either computed tomography (CT) scanning or progeny testing (with 10 or 20 progeny per sire; PT10 and PT20, respectively) in the second stage of two stage selection systems using quantitative genetic theory. Stage 1 selection was assumed to be based on live weight and ultrasonic predictions of carcass merit. For a genetic correlation of 0.7 between ultrasonic and CT/PT measures, the economic return peaked for progeny test at \$2.70 and \$2.38 per commercial ewe when 10 and 5% of the male selection candidates were evaluated in PT10 and PT20, respectively. CT had a greater return at \$3.52 per commercial ewe when 20% of the male selection candidates were evaluated using CT. The results show that given the moderate heritability of carcass composition traits, the reduction in generation interval and the lower cost of evaluation of CT outweighs the increased accuracy of selection and higher mating ratios associated with progeny testing.

Keywords: sheep; two-stage selection; meat; computed tomography; progeny test.

INTRODUCTION

Two stage selection is a technique used in animal breeding to enable the collection of expensive measurements of animal performance, or to pre-screen animals to allow for culling when the particular measurements are collected late in the animals life. In the case where the second stage measurements are expensive to collect, the first stage selection candidates are screened using inexpensive, but imperfect, predictors of the trait under selection. The best-performing subset are then evaluated using more accurate, but expensive, measurements and the final selection is made. This allows the use of technology that would not be physically or economically feasible over the entire group of selection candidates. For sheep meat traits, computer tomography (CT) scanning and progeny testing are two examples of expensive evaluations whose use is becoming increasingly common in the New Zealand meat sheep industry.

The cost of these two technologies varies from hundreds to several thousands of dollars per ram evaluated. It is therefore important that the two-stage selection process has been optimised so that these technologies can be used cost effectively, and so that economically optimum rates of genetic progress can be achieved. In particular, the critical factor in determining the effectiveness of a two stage selection programme is determining the optimal proportion of animals to measure using the second stage measurement. The optimum proportion is influenced by the correlation between the first and second stage measurements, and the proportion of rams required at the final selection. Other key factors include the heritability of the traits

under selection, the cost of recording animals at the second stage, and the expected economic benefits from genetic improvement. Evaluating a greater proportion of animals than the optimum at the second stage gives no additional selection benefit while increasing the total cost. Evaluating a lower proportion of animals reduces the total cost, but reduces the final intensity of selection. Often the proportion of animals evaluated at the second stage is not made on the basis of an economic optimum, but rather on a fixed level of investment.

Optimisation of two-stage selection programmes has been difficult in the past because the required calculation of a double integral for the distributions of the first and second stage measurements is numerically intensive. Alternative strategies have been developed which are less numerically intensive, but these have not been widely used. Advances in computing power have now made calculation of the double integral feasible. This paper compares the cost effectiveness of optimised CT scanning and progeny testing in two-stage genetic selection programmes for meat quality traits. It uses the double integral of a bivariate normal distribution to compare the genetic gain that can be made considering differences in selection intensity and generation interval between the two approaches.

MATERIALS AND METHODS

A model was designed to evaluate and optimise two stage selection programmes based on quantitative genetic theory. This model was used to compare the economic benefits of improving carcass composition in a terminal sire breeding programme using two expensive but accurate second stage measurements. The two

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technologies chosen for evaluation were individual selection using (CT) scanning, as well as progeny testing using carcass dissections, with either 10 or 20 progeny evaluated per sire (PT10 and PT20, respectively).

A breeding programme was modelled that supplies rams for use in a large commercial flock or flocks. All benefits from genetic improvement in the commercial flocks were assumed to be captured by the breeding programme. The two stage selection process was applied to rams used to mate ewes within the breeding programme. It was assumed that the accuracy of selection among rams to mate to commercial ewes was unaffected by the two stage selection process, rather, it was the overall average genetic merit of all rams available that changed.

The intensity of selection (i ; the number of standard deviation units that selected animals are better than their contemporaries) after two-stages of selection was based on a standard bivariate normal distribution (SBN) with a given correlation between the two indexes as follows:

$$SBN(x, y, \rho) = \frac{1}{2\pi\sqrt{1-\rho^2}} e^{-\frac{1}{2(1-\rho^2)}(x^2+y^2-2\rho \cdot x \cdot y)}$$

where x and y are indexes of estimated breeding values after the first and second stage selection measurements have been taken respectively, and ρ is the correlation between the two indexes.

In a two stage selection process, there is a truncation point applied at each round of selection, above which the animals are selected. The truncation point (on a standardised scale with mean 0 and standard deviation of 1) for the second round of selection (T_y) can be calculated from the proportion of sires that are retained for breeding purposes within a nucleus breeding flock as follows:

$$propn_y = \frac{1}{ewes} \cdot \frac{2}{fert}$$

where $ewes$ is the number of nucleus breeding ewes and $fert$ is the fertility of the nucleus flock (lambs weaned per ewe mated). For the purposes of this study, $fert$ was set to 130%.

The truncation point for the first round of selection (T_x) should be optimised to ensure that the very best animals are not inadvertently culled, but is often dictated by other factors such as the available finances for the second stage evaluation. Thus, the final selection intensity (i) of the animals after selection at the second stage is computed as:

$$i = \frac{\int_{T_x}^{\infty} \int_{T_y}^{\infty} SBN(x, y, \rho) \cdot x \, dy \, dx}{propn_y}$$

where $propn_y$ is the proportion of animals selected after second stage. The response after two stages of selection was calculated as:

$$R = \frac{i \cdot r \cdot \sigma_A}{L}$$

Where r is the accuracy of selection when both stage 1 and stage 2 are available to compute estimated breeding values, σ_A is the standard deviation of the breeding values after second stage selection measurements have been taken and i and L are the selection intensity and generation interval, respectively. Accuracy of selection for CT (r_{CT}) and progeny test (r_{PT}) were calculated from the following formulae:

$$r_{CT} = \sqrt{h^2}$$

$$r_{PT} = \sqrt{\frac{n}{n + \left(\frac{4-h^2}{h^2}\right)}}$$

The discounted economic benefit was calculated for a 1000 ewe nucleus used to produce rams to mate across a 62,000 ewe commercial flock. For the CT scanning scenario, nucleus flock replacement rams were used as ram lambs for a single year. The PT scenarios used two-tooth rams for a single year because a year is lost in evaluating the rams. The ewes in the nucleus flock for both CT and PT scenarios were assumed to be lambed first as two-tooths, and retained for four lambings. This gave a generation interval of 2.25 and 2.75 years for CT and PT, respectively. Mating ratios within the nucleus flock were set at 1:60 for ram lambs and 1:100 for two tooth rams, reflecting typical natural mating ratio's for these two livestock classes.

It was assumed that CT measured the weight and yield of primal cuts with the same level of accuracy as a manual dissection that would be used for progeny testing (Afonso, 1992; Young *et al.*, 1996; Jopson *et al.*, 1997). Index selection was based on the weights of lean and fat in the various cuts. For simplicity, it was assumed that these measurements were combined into an index of carcass merit with a heritability of 0.25. This value of 0.25 for the index is similar to, or lower than, the heritabilities determined for a range of sheep meat traits by Waldron *et al.* (1992). The response to selection for each combination of effects was evaluated in a gene flow model which calculated the net present value for a single year of selection and with a horizon of ten years as described by Jopson *et al.* (1995). The discount rate was set at 7%.

The first stage of selection was assumed to be on the basis of ultrasound scanning of the eye muscle width (A) and depth (B) and depth of fat over the eye muscle (C) as defined by Palsson (1939). The correlation (ρ) between ultrasound and second stage measurement (i.e. primal cut composition as determined by either CT scanning or manual dissection) was set at 0.7, based on the genetic correlations between A, B and lean weight in the leg and loin from Waldron *et al.* (1992; range 0.56 to 0.70). The effects on final selection intensity of changing ρ to 0.5

and 0.9 were also considered. The response to selection was calculated for 2, 5, 10, 15 and 20 percent of selection candidates evaluated at the second stage (i.e. T_x).

TABLE 1: Accuracy of selection and generation interval for two stage selection programmes using computed tomography (CT), progeny testing with 10 test progeny (PT10) and progeny testing with 20 test progeny (PT20).

	CT	PT10	PT20
Accuracy of selection (r)	0.50	0.63	0.76
Generation interval (L)	2.25	2.75	2.75

While genetic progress can be optimised on the basis of selection intensity, or selection intensity per year, this is not necessarily the economic optimum. This is especially true given that the second stage measurement is usually expensive to record, and that beyond a certain point, the marginal benefits of evaluating additional animals are outweighed by the costs of measuring those animals. Additional factors influencing the response to selection are the accuracy of selection and the generation interval. The values used for each of these factors are presented in Table 1.

The accuracy of selection was higher for the two progeny testing scenarios than for CT scanning. However, the generation interval is lower for CT scanning compared to progeny testing as a year is not lost evaluating progeny before the rams are used in the nucleus flock. The cost of CT scanning was set to \$380 per ram and the cost of progeny testing was set at \$150 per progeny evaluated in the PT10 or PT20 scenarios, respectively. The cost for progeny testing varies widely depending upon the measurements that are collected. The value of \$150 is based upon mating/recording costs, loss of carcass value and labour costs for dissection of \$15, \$65 and \$70 per lamb, respectively.

RESULTS

The final selection intensity from a two-stage selection programme at various mating ratios, correlations between the first and second stage

measurements, and for differing proportions of animals evaluated as selection candidates for the second stage measurements is shown in Table 2. Evaluation of sub optimal numbers of selection candidates resulted in a loss of selection intensity. The values for 100% screened using the second stage measurement show the selection intensity that would be achieved in a single-stage selection programme. For mating ratios (nucleus rams to ewes) of 1:60, 1:100 and 1:500, these were 2.33, 2.52 and 3.04 standard deviation units, respectively (Table 2). There is no additional genetic response to be gained once the proportion selected for the second stage achieves a critical threshold. At this point there is a very small probability that any animal rejected after stage one selection would have been selected after stage two measurement. For example, for correlation of 0.9 and mating ratio of 1:100 there is almost no gain in selection intensity above 15% evaluated at the second stage of selection (Table 2). The mating ratios of 1:60, 1:100 and 1:500 were selected because they represent ratios used for ram lambs, adult rams or in an intensive AI programme, respectively.

Several trends are obvious from the results, namely the greater the number of ewes an individual ram is mated to, the greater the final selection intensity in a two-stage selection programme. Increasing the correlation between the first- and second-stage measurements also increased the final selection intensity. Most importantly from a two-stage selection point of view, the final selection intensity diminishes rapidly as smaller numbers of animals are evaluated using the second-stage measurement, with the magnitude of the decline increasing with a decrease in the correlation between the two measurement stages. For example, when the correlation between traits was 0.9, there is essentially no difference in the final selection intensity between the 15% and 100% screening levels for the 1:60 mating ratio. However, when the correlation was set to 0.5, around 50% of the animals had to be screened in order to give the same final selection intensity as evaluating all the animals.

TABLE 2: The final selection intensity in two stage selection programmes for various correlations between first and second stage measurements at that various mating ratios.

Correlation (ρ)	0.5			0.7			0.9			
	Mating ratio ¹	1:60	1:100	1:500	1:60	1:100	1:500	1:60	1:100	1:500
% screened using 2 nd stage measurement										
2%	0.41	0.50	0.87	0.7	0.91	1.67	1.27	1.68	2.81	
5%	0.75	0.90	1.41	1.1	1.45	2.28	1.91	2.26	3.01	
10%	1.14	1.33	1.93	1.6	1.90	2.68	2.21	2.46	3.04	
15%	1.42	1.62	2.25	1.8	2.13	2.84	2.29	2.50	3.04	
20%	1.63	1.85	2.47	2.0	2.27	2.93	2.32	2.51	3.04	
50%	2.30	2.49	3.03	2.3	2.51	3.04	2.33	2.52	3.04	
100%	2.33	2.52	3.04	2.3	2.52	3.04	2.33	2.52	3.04	

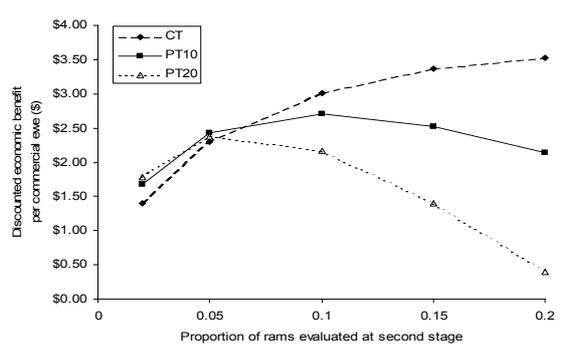
¹Mating ratio of rams to ewes in the nucleus

The costs for second stage evaluation are in Table 3, while the discounted benefits for the CT, PT10 and PT20 scenarios are presented in Figure 1. All three scenarios displayed a curvilinear trend, increasing towards an optimum level before tapering off at higher proportions of rams evaluated in the case of the two progeny testing scenarios. CT scanning gave a marginally smaller return than the two progeny testing scenarios when very low numbers of animals were evaluated at the second stage. However, by the time that 10% of selection candidates were evaluated with CT, the net benefit per commercial dam was in excess of \$3.00 and this continued to rise, albeit at a slower rate, out to \$3.52 when 20% of animals were evaluated. The curve for CT scanning reached a maximum of \$3.56 at 25% of animals evaluated, and declined thereafter (results not presented). The two progeny testing scenarios peaked and then declined. For the PT10 scenario, the peak benefit was \$2.70 per commercial ewe recorded at 10% of rams evaluated after which the benefit slowly declined. The PT20 scenario peaked at \$2.38 for 5% of rams evaluated. The decline after this point was rapid to reach only \$0.40 at 20% of rams evaluated.

TABLE 3: Costs of second stage evaluation for two stage selection programmes using computed tomography (CT), progeny testing with 10 test progeny (PT10) and progeny testing with 20 test progeny (PT20).

	Number	CT	PT10	PT20
Cost per ram		\$380	\$1,500	\$3,000
Total cost (\$x0 ³) (Percent evaluated)				
2%	11	\$4.1	\$16.5	\$33.0
5%	27	\$10.3	\$40.5	\$81.0
10%	55	\$20.9	\$82.5	\$165.0
15%	83	\$31.5	\$124.5	\$249.0
20%	111	\$42.2	\$166.5	\$333.0

FIGURE 1: The discounted net benefits for two stage selection programmes using computed tomography (CT), progeny testing with 10 test progeny (PT10) and progeny testing with 20 test progeny (PT20) at alternative proportions of candidate rams evaluated at the second stage. The correlation between first and second stage evaluations was 0.7, CT and progeny test rams were mated at ratios of 1:60 and 1:100, respectively.



DISCUSSION

Two-stage selection programmes enable the use of expensive technologies that would otherwise not be practical to use. However, optimisation of the selection programme is vital, especially when the cost of the second stage selection technology is very high. The results have clearly demonstrated that the optimum use of a second-stage technology is very sensitive to cost of the technology, and that the cost of additional evaluations can very quickly erode the genetic benefits gained from increased revenue from the genetic gain. When evaluating a breeding programme from a performance perspective, the optimum level of use of the second stage measurement is clearly the point at which selection intensity no longer increases with increasing number of animals evaluated. However, in practice, the economic optimum is at much lower proportion of animals evaluated, and in many cases the proportion is actually determined by having a restriction on the financial resource that can be allocated to the programme.

The three scenarios presented in this paper illustrate how breeding programmes using different technologies can be optimised and evaluated. CT scanning is a well established technique where an individual animal's performance can be non-invasively measured for any number of carcass composition traits (Jopson *et al.*, 1997; Kvame *et al.*, 2004). It has the advantage that the animal can be evaluated and used in the same year meaning that generation interval is minimised. While the cost of evaluation is high, it is substantially less expensive than a progeny test. As a result, the economic benefit continued to rise as the proportion of animals evaluated increased.

Progeny testing has always been a popular method of evaluating rams, and there are a number of progeny tests in operation in New Zealand to rank rams on their performance (Johnson *et al.*, 2002; Campbell *et al.*, 2003). Progeny testing is most useful when the traits of interest can only be measured in one sex, when the measurement can only be measured after the animal is slaughtered, or when heritability is low (Simm, 1998). In the case of meat traits, the heritabilities are moderate and the traits can be measured in both sexes. Progeny testing offers the ability to measure traits that can only be collected after slaughter (e.g. colour and pH), and has increased accuracy of selection compared to CT scanning. However, the increased accuracy of selection comes at a price. The costs of evaluating the progeny are much higher, and the ram is a minimum of two years of age before it has been evaluated and therefore ready for use within the nucleus breeding program. The results for the two progeny testing scenarios showed the optimum proportion to evaluate was very sensitive to cost. While additional genetic improvement could be gained by increasing the number of animals evaluated, the marginal benefit of that improvement was less than the increase in evaluation costs.

The optimisation exercise also enables a comparison between the scenarios. In Figure 1, the economic

benefits are expressed against the proportion of animals evaluated. A direct comparison between the two progeny test scenarios can be made. While the accuracy of selection increases markedly in going from 10 to 20 progeny per sire, the economic benefit of the increase is completely removed by the cost of evaluating the additional animals. Similar returns are made for each of PT10 and PT20 up to the 5% selected for second stage measurement, but the investment required for the PT20 is double that of the PT10 scenario. In comparing the progeny test to the CT scenarios, the gains for CT are far greater due to the reduced cost and generation interval. If the cost of progeny testing was reduced without reducing accuracy of the measurements, it is possible that similar economic gains to CT could be made. If 15% of animals are selected for evaluation using CT, then the same economic benefits could be achieved from progeny testing when the cost per progeny tested ram was reduced to \$870 and \$1530 for PT10 and PT20, respectively (i.e. \$87 and \$76.50 per progeny evaluated, respectively).

An alternative way to compare the scenarios is to evaluate the differences in economic benefit against the investment required to produce the result. Again, the lower cost of CT scanning favours that option over progeny testing. For example, a limited investment of \$32,000 for second stage measurement would restrict second stage evaluation to 2% and 15% of rams for PT20 and CT, for an economic benefit of \$1.78 and \$3.36 per commercial dam, respectively. Likewise, a limited investment of around \$42,000 would purchase evaluation of 5 and 20% of rams for PT10 and CT, for an economic benefit of \$2.43 and \$3.52 per commercial ewe, respectively.

Two-stage selection for carcass composition using CT scanning or progeny testing is effective in increasing rates of genetic progress, and in many of the scenarios tested, there were sound economic benefits. However, the benefits were extremely cost sensitive, so careful planning and optimisation is justified to ensure they are profitable in a commercial setting.

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