

Use of MOET in Merino breeding programmes: a practical and economic appraisal

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Abstract

Commercial application of multiple ovulation and embryo transfer (MOET) technology will be subject to practical constraints and economic rationalism. This study examines use of MOET in its most profitable arena: to breed stud rams which will disseminate genetic improvement widely through multiplier studs to commercial flocks. A deterministic prediction is used to evaluate schemes based on an open nucleus MOET group within a Merino parent stud, taking account of genetic merit and inbreeding. Selection is based on clean fleece weight with an assumed heritability of 0.4. Embryos are collected at a rate equivalent to 3.45 live lambs per donor. Benefits of MOET were calculated from the discounted expressions of rams sold, and compared with the costs incurred.

As the proportion of the flock born from MOET increases, the rate of genetic gain increases rapidly at first, but diminishing returns are observed. The costs of MOET increase linearly with the number of lambs produced, so the optimum proportion of MOET lambs is for practical purposes always less than 100%.

Some use of MOET was profitable provided the stud sells sufficient stud rams each year. Sensitivity tests found that other parameters had only a small impact on the optimum level of MOET. In general however, changes which increased the rate of genetic gain (heritability, flock size) or increased its value (wool price, lower discount rate) increased the optimum number of MOET lambs.

The results should provide guidelines to optimum investment in MOET for the wool industry. An across flock genetic evaluation scheme is probably necessary to motivate this investment.

Keywords: breeding programmes, deterministic models, MOET, sheep, wool.

Introduction

The reproductive technology of multiple ovulation and embryo transfer (MOET) can be used to increase the reproductive rate of elite females in the livestock species. Within a breeding programme the generation of large numbers of offspring from superior females has the potential to increase the female selection differential and reduce the female generation intervals, thereby increasing the rate of genetic improvement. MOET has been available for sheep for some time although success rates are lower than for cattle (Maxwell, Szell, Hunton and Ryan, 1990). Compared with cattle, the cost of MOET in sheep is high relative to the value of individual

animals and the cost may exceed the benefits from faster genetic improvement in many situations. Indeed, for the Australian meat sheep industry, McClintock and Nicholas (1991) concluded that investment in MOET is unlikely to be profitable. However, the structure of the Australian wool industry, the size of the national flock and the relatively low reproductive rate of Merino ewes suggest that substantial benefits may accrue through the use of MOET in wool sheep breeding programmes (Wade and Goddard, 1994; Wray and Goddard, 1994).

The Merino breeding industry has a hierarchical structure (Banks, 1987). Parent studs supply rams to daughter and general studs which produce rams for use in commercial flocks. In practice, it may be only the special flock within the parent stud that produces predominantly stud rams, while other parts of the

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parent stud produce many commercial flock rams. The hierarchical structure means that genetic improvements made in the special flock of a parent stud have an effect on many sheep, albeit after a lag in time. For instance, Wade and Goddard (1994) estimate that a ram used in a special parent stud flock may leave 49743 discounted expressions of his genotype. Consequently, it is in these flocks that use of MOET is most likely to be profitable. This is investigated in the present study by examining the costs and benefits of the use of MOET in stud flocks which produce rams that are used in daughter or general studs.

Past studies of the use of MOET in sheep breeding (e.g. Smith, 1986; Wray and Goddard, 1994) have assumed that all matings in the flock use MOET. However it may be that a mix of MOET and natural mating or artificial insemination (AI) provides better results, from an economic and practical point of view. Therefore in this paper breeding programmes are investigated in which the best ewes are used as donors and the next best are used for natural mating.

A large range of flock sizes have been studied. The small flocks could represent individual studs, while the large sizes might represent a group of studs serving a segment of the industry. The benefits from genetic improvement have been calculated from the improved production of commercial sheep and therefore represent the benefits to the whole industry. The individual stud owner who decides to invest in MOET will only be able to capture part of these benefits, and then only if the price for which he sells rams reflects their genetic merit.

Response to selection in a complex MOET scheme can be difficult to predict. Wray and Goddard (1994) used stochastic simulation to assess a range of schemes involving natural mating, MOET and semen sexing. Stochastic simulation is computationally demanding and this limits the range of alternatives which can be tested in a finite time. Runs are replicated but the variability of the mean may limit precision in determining the effects of minor changes in the schemes. Deterministic prediction of response to selection in complex breeding programmes draws on a large body of established and less established genetic theory but the predictions inevitably require that certain assumptions be made and simplifications tolerated. This need not devalue the results, provided that the limitations are understood. The major benefit of deterministic prediction is that the demand for computer time is substantially less than for stochastic simulation, so that a greater range of factors can be varied. In addition, the exact

deterministic predictions facilitate the comparisons and understanding of scheme alternatives.

In this study deterministic predictions of genetic response and inbreeding were used to make economic evaluations of breeding programmes which use MOET within an open nucleus group and natural mating or AI in the remainder of a stud flock.

Material and methods

A computer program was developed to provide deterministic predictions of genetic progress and economic benefits for a stud flock which elected to adopt a MOET programme over a 14-year period. This is considered a medium time scale for genetic improvement of wool sheep, but the benefits continue after the programme while ram sales continue. This is important, to justify the expenditure on MOET in the later years of the programme. In our examples the level of genetic merit at year 14 and the constant market for stud rams were assumed to continue for an infinite period.

The generations were overlapping; parents were selected on phenotype once before their first breeding and then remained in the breeding flock for a fixed time (there were no deaths at any age). Phenotypic selection was performed for clean fleece weight which had a heritability of 0.40 and a phenotypic standard deviation of 0.5 kg. The best ewes were used as MOET donors while the next best ewes were mated naturally and remaining ewes were available for use as embryo recipients. All ewes and rams born into the flock were equally available for selection on merit into the MOET or natural mating groups regardless of whether they were themselves born as a result of MOET or natural mating. Once selected, animals remained in the same breeding group for their lifetime.

The structure of the flock is analogous to the structure of a classic open nucleus breeding scheme described by James (1977). His methods provide the basis of the deterministic predictions used here and his notation is used where possible. Therefore the MOET group will be referred as the nucleus group (N) and the natural mating group as the base group (B). The flock size (n) and the proportion of the flock in the nucleus group (p) were defined in terms of lambs born per year, and the required numbers of ewes were calculated accordingly, depending on female reproductive rates. Four variables defined the source of all breeding animals: v , the proportion of nucleus rams born in the base, w , the proportion of base rams born in the nucleus, x , the proportion of nucleus ewes born in the base, and y , the proportion of base ewes born in the nucleus.

A range of combinations of transfer rates were examined and the optimum values of v , w , x , and y found for any response criterion to within 0.0002, allowing for fractions of animals to be selected from any source. These simplifications were made to allow the response functions to vary in a systematic way, without irregularities due to practical but artificial constraints.

Response variables calculated were as follows:

(1) Asymptotic rate of genetic gain (G^*) assuming an infinite population size, expressed in phenotypic standard deviation units

$$G^* = 0.8 \frac{r\sigma_A}{\sigma_P} \left[\frac{(w+y)C_N + (v+x)C_B}{(w+y)L_N + (v+x)L_B} \right]$$

(after James, 1977)

where r is the accuracy of selection, and σ_A and σ_P are the genetic and phenotypic standard deviations. This calculation of G^* is relevant to a steady state open nucleus scheme at equilibrium, and G^* is assumed to be equal for nucleus and base groups, which differ in mean genetic merit by a constant lag of A^* (James, 1977). The transitional rates of genetic gain and genetic lags in early generations were ignored, but James (1977) shows that equilibrium will be rapidly attained in an open nucleus system. L_N and L_B are the average generation intervals in nucleus and base groups. The scaling factor 0.8 is included to account approximately for the reduction in genetic variance due to selection, the so-called 'Bulmer effect' (Bulmer, 1971). The factor 0.8 was found to be appropriate to the mating ratios and family sizes examined (Wray and Hill, 1989) and was confirmed by stochastic simulation results. Mueller and James (1983) found that allowance for the Bulmer effect reduced predicted gains proportionately by around 0.2 for open nucleus schemes, but had very little effect on the optimal design or ranking of alternatives, which justified the use of a simple scaling factor. Most of this loss of variance was observed at the time of initial parent selection and so the effect is assumed to be constant throughout the breeding programme. C_N and C_B denote the weighted average selection intensities in nucleus and base groups respectively, standardized into phenotypic standard deviation units, calculated as

$$C_N = \frac{1}{2} [(1-v)D_{MN} + v d_{MN} + (1-x)D_{FN} + x d_{FN}]$$

$$C_B = \frac{1}{2} [wD_{MB} + (1-w)d_{MB} + yD_{FB} + (1-y)d_{FB}]$$

(after James, 1977)

where D variables are selection intensities for animals born in the nucleus, and d variables are selection intensities for animals born in the base, with subscripts denoting sex (M or F) and the destination group (N or B). Selection intensities were calculated assuming an infinite population size and those for animals selected to the base took account of the prior selection of animals to the nucleus. The genetic lag between nucleus and base groups (A^*) in phenotypic standard deviation units was given by

$$A^* = 0.8 \frac{r\sigma_A}{\sigma_P} \left[\frac{L_B C_N - L_N C_B}{(w+y)L_N + (v+x)L_B} \right]$$

(James, 1977).

(2) Response in performance to year 14 (R_{14}) accounting for loss of genetic variance due to inbreeding and reduced for inbreeding depression. Assume

$$G_t = G_{t-1} + 0.8 \frac{r_t \sigma_{At}}{\sigma_P} \left[\frac{(w+y)C_N + (v+x)C_B}{(w+y)L_N + (v+x)L_B} \right]$$

where G_t is the mean genetic merit, r_t is the accuracy and σ_{At} is the genetic standard deviation in year t . For mass selection $r_0 = \sigma_{A0}/\sigma_P = h = \sqrt{h^2}$, that is, the square root of the heritability. $\sigma_{At} = \sigma_A(1-F_t)^{1/2}$ and $r_t = \sigma_A(1-F_t)^{1/2}/(\sigma_P^2 - F_t\sigma_A^2)^{1/2}$. G_1 and G_2 were set to zero, so that the merit of foundation parents would not confound the results. The level of inbreeding in year t , was calculated as $F_t \approx (t-2)\Delta F$, where ΔF is the annual increase in inbreeding. This assumes that offspring born in the first 2 years were not inbred. This increase in inbreeding was predicted as

$$\begin{aligned} \Delta F = & \frac{g^2}{8L^2} \left[\frac{(1+C_N^2 W_{NS})}{N_S} + \frac{(1+C_N^2 W_{ND})}{N_D} \right] \\ & + \frac{(1-g)^2}{8L^2} \left[\frac{(1+C_B^2 W_{BS})}{B_S} + \frac{(1+C_B^2 W_{BD})}{B_D} \right] \\ & + \frac{2g(1-g)}{8L^2} \left[\frac{A_S(1+C_N^2 W_{NS})}{N_S B_S} \right] \end{aligned}$$

(1) (Appendix 1)

where: N_S , B_S = number of nucleus sires and base sires entering the breeding flock each year. Sires used in the nucleus are also available to be used in the base and the number of common sires entering the flock each year is denoted A_S . N_S may be less than, equal to or greater than B_S ; N_D , B_D = number of dams entering the nucleus and base each year (the groups

are exclusive); W_{NS} , W_{BS} , W_{ND} , W_{BD} = factors related to the effects of selection on inbreeding for each class; $L = gL_N + (1 - g)L_B$; $g = (w + y)/(v + w + x + y)$.

Then the response in performance to year 14 is calculated as

$$R_t = G_t - DF_t$$

Inbreeding was assumed to depress performance by proportionately 0.005 of the mean for each 0.01F. If the coefficient of variation for clean fleece weight is 15%, the inbreeding depression in phenotypic standard deviation units, $D = 0.5 \times 100/15 = 3.33$.

(3) Profit to infinity from a 14-year MOET programme as net present value (P_{14})

$$P_{14} = ES \sum_{t=3}^{\infty} b^t(R_{t-2} + I_s) - pnC \sum_{t=0}^{13} b^t$$

where E is the number of discounted expressions per ram sold, S is the number of rams sold per year, V is the value of one phenotypic standard deviation of fleece weight, n is the number of lambs born annually in the flock, p is the proportion born from MOET, C is the cost of producing a MOET lamb, b is used to denote $1/(1 + a)$ and a is the discount rate. Appendix 2 shows that the level of inbreeding in commercial sheep lags behind the stud by approximately the same length of time as does additive genetic merit. Therefore net genetic gain (additive genetic gain less inbreeding depression) can be used in the calculation of commercial benefit from a breeding programme.

Multiple ovulation and embryo transfer was performed in year 0 to 13, and resultant lambs were born in years 1 to 14. The rams were sold and their first progeny were born on their 2nd birthday, from year 3 onwards. A set number of rams was sold each year. The rams sold in years 3 to 14 were the best not required as sires and had an average standardized selection differential of I_s . After the breeding programme ended in year 14, breeding and sale animals were selected at random so that the genetic merit of the flock and the level of inbreeding remained constant from year 15 onwards ($R_t = R_{14}$ and $I_s = 0$). The time horizon was infinite in order to allow for returns from the genetic gains made towards the end of the 14 years. For practical purposes, income after year 25 makes very little contribution. The number of discounted expressions per ram sold (discounted to the time of the birth of its first progeny) was taken from scheme C of Wade and Goddard (1994). This is a three-tiered model with parent and daughter studs supporting a commercial level of one million ewes. In this scenario, each ram used at daughter stud level would contribute $E = 1855$ discounted expressions.

Flock rams are of relatively little value (143 discounted expressions), so were not considered. The value of E was not varied, but alternative values of S , V and C were tested in a sensitivity analysis.

Economic comparisons were only made between flocks with the same number of lambs born per year. Consequently, there was no attempt to estimate costs other than for MOET (e.g. fleece measurement, management) which were assumed to be fixed to flock size.

Alternatives considered

Breeding schemes were set up along the lines of Wray and Goddard (1994). The standard scheme was a flock where 345 lambs were born per year. This required 100 MOET donor ewes or 320 naturally mated ewes, or a combination of both. Each year 100 stud rams were sold, allowing for about 35% culling, although culls would be available for sale as flock rams. In the standard arrangements animals, selected on the basis of hogget fleece weight, were mated to produce their first progeny at 2 years of age, and annually thereafter. Rams were mated once, while nucleus ewes were culled after two matings and base ewes were culled after three matings. Eight rams were used in the MOET group and five rams were used in the base group regardless of size. These were the numbers of sires recommended by Wray and Goddard (1994) for small MOET and natural flocks. A brief examination (data not shown) found that this was near optimal with respect to R_{14} for the schemes tested, although the response surface was very flat and its exact undulations depended on the details of the scheme. The optimum number of sires would increase slightly for larger flocks. AI allowed rams to be used simultaneously in MOET and natural groups. Net wool price was estimated at \$5 per kg clean. Naturally mated ewes produced 1.08 live lambs and multiple ovulated ewes produced 3.45 live lambs per year in our model. This is a high but possible rate for natural joining in Australian Merinos. Although optimistic, the MOET rate should be achievable in the future, or would be possible at present with one flush and subsequent natural mating of the donor ewes. At a success rate of 3.45, the costs of preparing donors and six recipients per donor is approximately \$162 per lamb born in a large scale operation (McClintock and Nicholas 1991).

Within these arrangements, a number of factors were varied: (i) MOET success rates and multiple flushing; (ii) natural mating success rates; (iii) number of sires used in the base; (iv) heritability of the trait; (v) discount rate; (vi) price of wool and cost of MOET.

To test the validity of the algorithms and assumptions employed in the prediction program,

results were compared with simulation results for certain similar schemes. The simulation program described by Wray and Goddard (1994) was adapted to the standard scheme outlined above, except that all ewes were bred three times. The best ewes were selected as MOET donors and the next best for natural mating. In the simulation the best ewes were selected as donors each year across age groups, while in the deterministic prediction, ewes were selected for either MOET or natural mating before first breeding and remained in that group for life. In the simulation program adults died at a rate of 5% per year, while complete survival was assumed in the prediction. The mean reproductive rates are the same, but the prediction assumes equal family size within each group, while in the simulation litter size follows a Poisson distribution. The prediction optimized internal transfer rates on G^* but in the simulation transfer rates were determined by selection on estimated breeding values (EBVs).

For the prediction to arrive at an optimum G^* and R_{14} for each p value (the proportion of lambs in the flock born to MOET), around 450 000 combinations of transfer rates were tested. To scan the full range of p values, and determine the point of greatest net returns, about 1 h of computing time was required on a Sun-clone Sparc3 workstation. This compares favourably with the 2 h required to complete 200 replicates of a single combination (i.e. one p value) using the simulation program.

Results

Valuation: comparison of deterministic prediction and stochastic simulation

A representative comparison of simulation and prediction results is presented in Table 1. The small differences in assumptions are expected to produce some variation in results between the two methods,

but the results for G^* were very close, and the internal transfer rates are quite similar. For ΔF , the simulation results are compared with predictions which ignore the effects of selection (equation (A1.1) with (A1.2) or which attempt to account for the effects of selection (equation 1). Both predictions of ΔF contain assumptions and as shown in Table 1, equation (A1.2) tends to underestimate, while equation (1) tends to overestimate, the observed ΔF . However equation (1) was generally closer, and was adopted as the standard prediction.

Optimization of transfer rates

(1) *Asymptotic genetic gain, G^** . Optimization of transfer rates with respect to the rate of genetic gain gave selection intensities which produced equal truncation levels for each class of animal (nucleus ewes, base ewes, nucleus rams, base rams) between the two sources, nucleus and base. Optimization of transfer rates revealed a flat surface for G^* near the optimum, as reported by James (1977). The optimum transfer rates are difficult to predict because of the interrelationships between the rate of gain and the genetic lag between the nucleus and base groups, but in practice would be achieved by selecting across the whole flock on estimated breeding value. Stochastic simulations run under these conditions produced very similar transfer rates and rates of genetic gain. In the basic scheme (345 lambs born per year, 100 rams sold per year) with $p = 0.58$, the optimum open nucleus arrangement with respect to G^* saw 17% of nucleus rams and 23% of nucleus ewes born in the base group, while 85% of base rams and 66% of base ewes were born in the nucleus. This gave $G^* = 0.230$, and $\Delta F = 0.0064$. The predicted returns from such a scheme were \$4.997 million.

(2) *Response to year 14 reduced for inbreeding depression, R_{14}* . The inclusion of inbreeding in a response criterion should lead to a better breeding design. In

Table 1 A comparison of prediction and simulation results†

p	Simulation								Prediction						
	v	w	x	y	G^*	s.e.	$\Delta F(\times 10^2)$	s.e.	v	w	x	y	G^*	$\Delta F (\times 10^2)$	
														Eq (A1.2)	Eq (1)
0.00					0.180	0.003	0.48	0.03					0.185	0.42	0.63
0.25	0.43	0.60	0.46	0.30	0.215	0.003	0.61	0.07	0.44	0.59	0.45	0.32	0.216	0.35	0.73
0.50	0.26	0.76	0.30	0.58	0.230	0.004	0.53	0.07	0.28	0.74	0.31	0.58	0.225	0.33	0.65
0.75	0.11	0.90	0.14	0.82	0.232	0.003	0.55	0.07	0.15	0.86	0.17	0.78	0.227	0.31	0.60
1.00					0.220	0.003	0.50	0.05					0.225	0.31	0.57

† Population of 345 lambs born per year; eight MOET sires and five natural sires; age structure is one adult age group for nucleus males, one for base males, three for nucleus females and three for base females. Standard errors for v, w, x , and y were in the range 0.000 to 0.007.

Table 2 *Confounding effects of MOET and flock structure†*

Scheme	MOET lambs	G^*	$\Delta F (\times 10^2)$
All natural	0	0.185	0.63
All MOET	345	0.233	0.61
Simple flock	200	0.204	0.49
Closed nucleus	200	0.216	0.53
Open nucleus	200	0.230	0.64

† See text for definitions.

reality this had only a small effect on the transfer rates and other response variables. In every case, optimization of transfer rates for R_{14} gave a lower rate of accumulation of inbreeding than optimization for G^* , mostly due to a higher number of base animals selected into the nucleus. The value of G^* was reduced by a smaller amount than the reduction in ΔF . The gain in R_{14} was greatest when the nucleus was small, i.e. there was most potential to relieve inbreeding. Proportional reductions of inbreeding of 0.1 with a 0.01 reduction in genetic gain were observed at $p < 0.1$, but most schemes of interest had $p > 0.4$ and the differences were generally small. Allowance for inbreeding increased the value of a scheme, mostly because of the higher R_{14} value, and partly because a small number of the rams previously needed for breeding were available for sale. In the example of the basic scheme at $p = 0.58$, optimization of intra-flock transfer rates with respect to R_{14} gave an arrangement where 18% of nucleus rams and 23% of nucleus ewes were born in the base group, with 81% of base rams and 63% of base ewes born in the nucleus. This produced a very slight reduction in G^* from above, and ΔF was reduced by 0.003 of its value. The predicted returns from the scheme rose slightly to \$4.998 million.

(3) *Profit to year 14, P_{14}* . The transfer rates for optimization of R_{14} were found also to approximate the economic (profit) optimum, despite the potential advantages of earlier gains under discounting. The economic advantage of a higher rate of genetic gain and a higher level of inbreeding was trivial in all cases. Optimization of internal transfer rates with respect to P_{14} was not pursued, but P_{14} was used to compare schemes of the same size and different proportions of MOET.

Optimization of the proportion of MOET with respect to P_{14}

In the basic scheme, the predicted G^* for a naturally mating flock (i.e. $p = 0.0$) was 0.185 phenotypic standard deviations per year. For a flock entirely reproduced by MOET ($p = 1.0$), $G^* = 0.233$ (Table 2). This use of MOET slightly decreases the rate of

accumulation of inbreeding, due to the greater number of sires used for MOET. For any given quantity of MOET described by p , G^* could be predicted and the net return calculated. For the basic scheme, the quantity of MOET which maximized net return was $p = 0.58$. At this point, 58 donor ewes were enlisted to produce 200 lambs, while 135 naturally mated ewes produced the remaining 145 lambs. A simple flock of this description, where donors were chosen at random from the 193 ewes, gave $G^* = 0.204$ and $\Delta F = 0.0049$. Arranging the flock into a closed nucleus increased this potential to $G^* = 0.216$.

The open nucleus arrangement with internal transfer rates optimized with respect to R_{14} gave $G^* = 0.230$, and $\Delta F = 0.0064$. The predicted gross return from selling 100 rams per year, discounted to present value, was \$4998218. The total discounted costs were \$271216, while the discounted gross returns from a naturally mated flock of the same size was \$4052729. This left the discounted net benefit of using MOET in this way as $4998218 - 4052729 - 271216 = \674273 .

By amortization, a net present value of \$674273 is equivalent to annual payments (an annuity) at the time of ram sales of \$91500 over 15 years or \$67500 over infinity. As this is being recouped from 100 rams sold per year, the values are \$915 and \$675 respectively per stud ram sold. This is the net value of these rams in terms of the additional wool ultimately grown in commercial flocks, so is the premium above the value of average rams. Similar treatment of the total costs gives around \$370 per ram sold in the first 15 years, or \$275 per stud ram sold to infinity. This means that if the rams are sold at a premium of \$400 to \$600, seller and buyer will share the benefits of the superior genotype.

The returns from MOET come slowly over time. Assuming the returns are received at the time of sale of rams and the breeder can capture all the benefits, then the returns from the above scheme first exceed those from a natural-mating scheme in year 4, and break-even occurs in year 10. An alternative assessment of the investment is the internal rate of return on investment, defined as the discount rate required to equate benefits with costs. The standard scheme, described in the preceding paragraphs, had an internal rate of return of 0.229, which would be considered moderate for a long-term investment, in relation to the investment risks.

Effect of number of rams sold

As the number of rams sold increases, the expected returns and the net gains associated with performing MOET increase. Figure 1 shows the expected costs and returns from a flock of size 345, with different

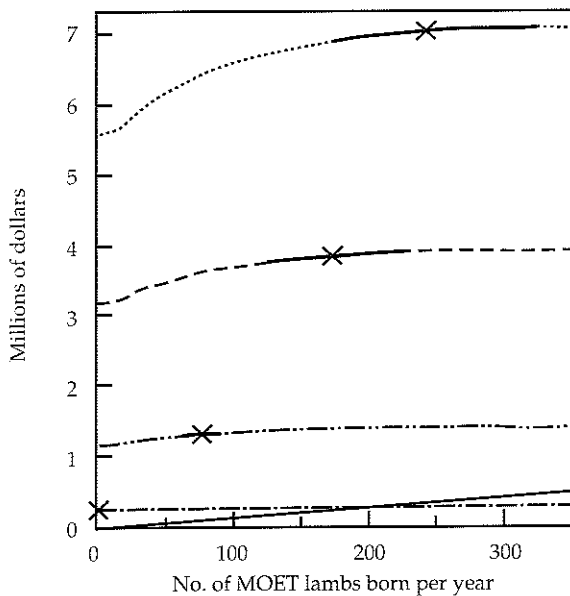


Figure 1 Net present value of costs (—) and returns for a flock of 345 lambs born per year selling five (---), 25 (---), 75 (---) or 150 (---) stud rams per year. MOET was performed for 14 years and achieved an average of 3.45 lambs per donor. The point of greatest net benefit for each curve is shown (X), and the range with 0.95 of maximum benefits indicated by heavy solid curve.

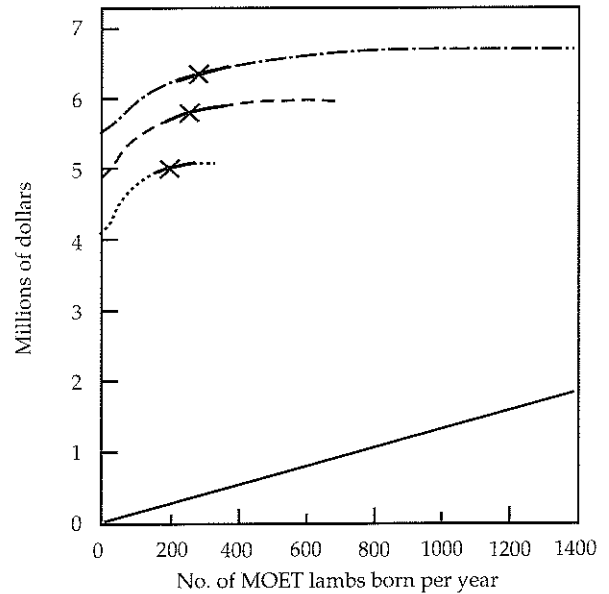


Figure 2 Net present value of costs (—) and returns for a flock selling 100 rams per year. Flock size 345 (---), 690 (---), and 1380 (---) lambs born per year. MOET was performed for 14 years and achieved an average of 3.45 lambs per donor. The point of greatest net benefit for each curve is shown (X), and the range with 0.95 of maximum benefits indicated by heavy solid curve.

market sizes across the range of p values. The expected returns clearly increase as the demand for rams increases, as does the value of performing MOET. The optimum quantity of MOET increases, from zero MOET lambs when five rams are sold to 76, 173 and 242 MOET lambs respectively when 25, 75 or 150 rams are sold.

Effect of flock size

It is recognized that the size of stud flocks will be determined mainly by the number of rams to be sold, with allowances for culling. However, the predicted rate of genetic gain increases with flock size and the way in which MOET would be performed is also likely to change. Figure 2 shows the expected returns and costs for schemes selling 100 rams per year from flock sizes of 345, 690 and 1380 lambs born per year. The greatest returns occurred when 200 lambs ($p = 0.58$), 259 lambs ($p = 0.38$) and 286 lambs ($p = 0.21$) were born to MOET for each flock size respectively. The net benefit from MOET was greatest for the smallest flock size, due to the lower rate of genetic gain in the absence of MOET. The figure also shows that at least 0.95 of the net returns to MOET were achieved over a reasonably wide range (167 to 273 lambs born to MOET for a flock size of 345). Each of these extremities had the same expected net return,

but clearly the costs of MOET would be substantially less at the lower end, with important implications for risk.

A combination of the effects of number of rams sold and flock size is shown in Figure 3. The expected returns and costs for flocks of 345 or 690 lambs born per year selling 50, 100 or 200 stud rams per year are given for the spectrum of p values. In general, there was only a small difference between flock sizes, but a large difference between different sizes of market, in terms of both the expected returns and the proportion of MOET performed to optimize net returns.

A greater range of schemes are shown in Table 3. For each combination of flock size and number of rams sold, the results are given for a naturally mated flock and for the level of MOET which optimizes net returns. The cost of that MOET is shown and the benefit of MOET was calculated as the gross returns less costs (P_{14}), minus the returns from the naturally mated flock. The optimum level of MOET increased at a rate slightly less than proportional to the number of rams sold. The cost of MOET was simply proportional to the number of MOET lambs, but both gross and net returns increased at a rate greater than

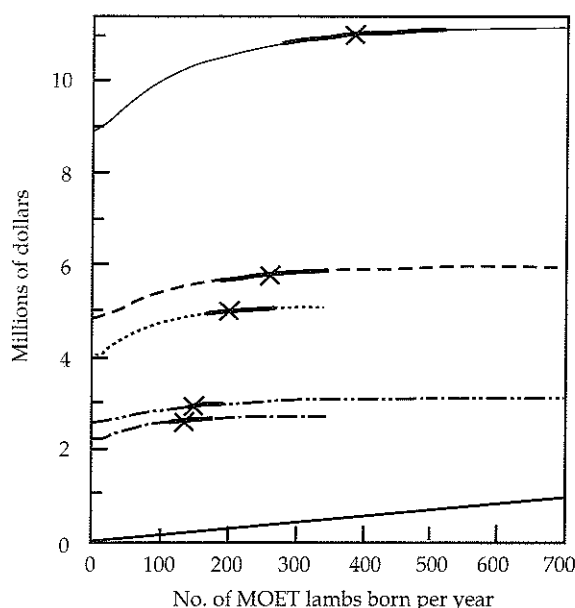


Figure 3 Net present value of costs (—) and returns for a flock size $n = 345$ selling $s = 50$ rams (---), $n = 690$, $s = 50$ (- - - -), $n = 345$, $s = 100$ (.....), $n = 690$, $s = 100$ (— · — · —) and $n = 690$, $s = 200$ (——). MOET was performed for 14 years and achieved 3.45 lambs per donor. The point of greatest net benefit for each curve is shown (X), and the range with 0.95 of maximum benefits indicated by heavy solid curve.

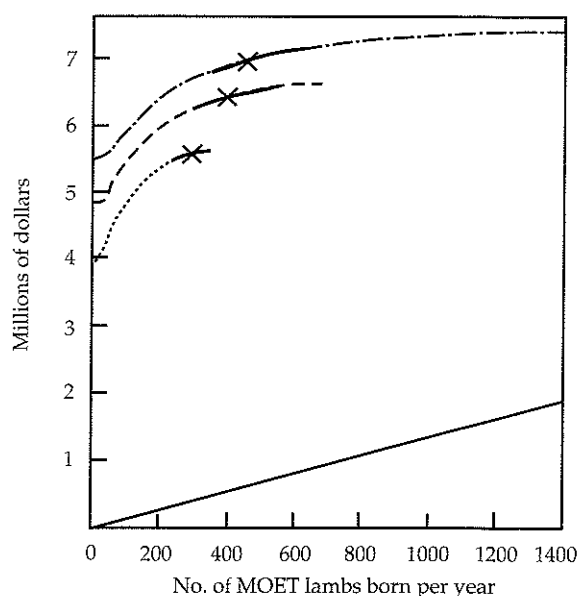


Figure 4 Net present value of costs (—) and returns for a flock selling 100 rams per year. Flock size 345 (.....), 690 (— · — · —), and 1380 (- - - -) lambs born per year. MOET was performed for 14 years and achieved 10.35 lambs per donor. The point of greatest net benefit for each curve is shown (X), and the range with 0.95 of maximum benefits indicated by heavy solid curve.

the number of rams sold. Consequently the ratio of benefits from MOET to costs increased as the number of rams sold increased.

Effect of flushing rates and multiple flushing

Figures 4 and 5 show the same results as Figures 2 and 3 for the case where 10.35 lambs were born per

donor. This could have been achieved by repeated superovulation and flushing of each ewe. The costs were assumed to be the same as previously (\$162 per lamb born). In each case, the increase in returns from using MOET was steeper than before, which led to optima where a greater proportion of the lambs were born to MOET. Despite this, the range within which

Table 3 A range of optimized MOET schemes

No. of rams sold	No. of lambs born	MOET lambs	G^*	$\Delta F (\times 10^2)$	Returns (\$AU'000)	Costs (\$AU'000)	Benefits of MOET (\$AU'000)
25	345	0	0.185	0.63	1 171	0	
25	345	76	0.217	0.71	1 316	103	43
100	345	0	0.185	0.63	4 053	0	
100	345	200	0.230	0.64	4 998	271	674
100	1 380	0	0.217	0.68	5 465	0	
100	1 380	286	0.253	0.66	6 333	388	480
400	1 380	0	0.217	0.68	19 078	0	
400	1 380	738	0.266	0.62	22 712	1001	3 634
400	5 520	0	0.244	0.75	24 183	0	
400	5 520	1042	0.285	0.67	28 364	1412	2 769
1600	5 520	0	0.244	0.75	85 195	0	
1600	5 520	2726	0.297	0.66	105 799	3694	16 911
1600	22 080	0	0.268	0.82	104 360	0	
1600	22 080	3792	0.313	0.71	123 069	5139	13 570

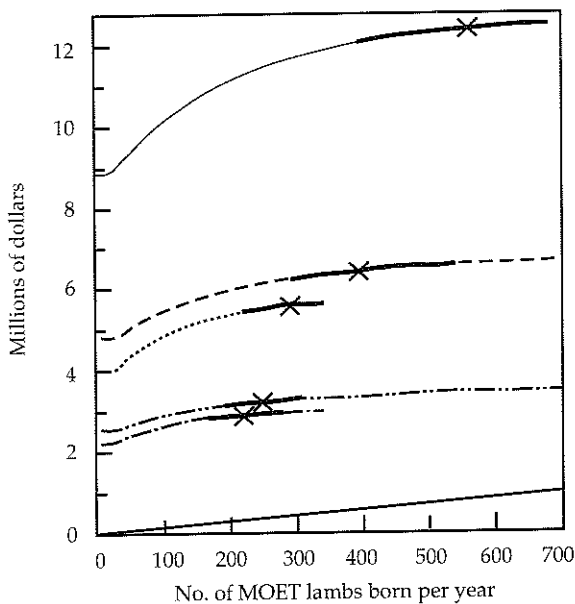


Figure 5 Net present value of costs (—) and returns for a flock size $n = 345$ selling $s = 50$ rams (— · — · —), $n = 690$, $s = 50$ (— · — · —), $n = 345$, $s = 100$ (.....), $n = 690$, $s = 100$ (— · — · —) and $n = 690$, $s = 200$ (— · — · —). MOET was performed for 14 years and achieved 10.35 lambs per donor. The point of greatest net benefit for each curve is shown (X), and the range with 0.95 of maximum benefits indicated by heavy solid curve.

0.95 of the maximum benefits of MOET were achieved became slightly wider in terms of lambs born to MOET. Due to the much higher reproductive rate, the number of donor ewes at optimum was always less than before.

The effects of increasing flock size or increasing the stud ram market were approximately equivalent to those enjoyed at the lower flushing rate, but among the schemes illustrated in Figures 4 and 5, the overall

benefit of MOET at optimum was proportionately 0.68 to 0.86 higher than with 3.45 lambs born per donor. The higher increases were observed in the bigger flocks and within flock size, when fewer rams were sold.

Sensitivity analyses

Table 4 demonstrates the likely sensitivity of predictions to variation or error in the basic parameters, namely the cost of MOET, the discount rate, the heritability of the trait, and the natural reproduction rate achieved. Similarly to Table 3, the benefit of MOET is calculated relative to a naturally mating flock under the same conditions but only the results of a fully optimized scheme are shown here. As the cost of MOET increased, it was desirable to perform somewhat less of it. Conversely, if the price of wool were to rise (results not shown), more MOET could be justified. The ratio of MOET cost and wool price determines the optimum number of donor ewes. Therefore, if MOET costs \$81 per lamb and wool sold for \$2.50 per clean kg, the ratio is equal to the original, and the optimum number of MOET lambs would again be 200, giving a benefit of $674237 \times 0.5 = \$337118$. Reducing the discount rate increased the importance of future expenditure and income. Because income was in excess of costs and costs generally preceded the returns, this made the scheme appear more profitable, and a higher level of MOET was justified. Conversely, if the discount rate was 0.15, although MOET was still a viable proposition, it would not be adopted to the same extent and the benefits were much reduced. For a trait of lower heritability, the potential response to selection was reduced, as was the value of MOET. At a higher heritability, the response in a natural mating flock was quite high, but the benefit of using MOET was also high. A higher level of inbreeding was predicted, due to increased co-selection of relatives. The natural reproduction rates tested had relatively little effect on the adoption of MOET, although the

Table 4 Sensitivity of MOET schemes to variance of assumptions

No. of rams sold	No. of lambs born	MOET cost	Discount rate	h^2	Natural reproduction rate	Optimum MOET lambs	G^*	$\Delta F(\times 10^2)$	Returns (\$AU'000)	Costs (\$AU'000)	Benefit of MOET (\$AU'000)
100	345	162	0.10	0.4	1.08	200	0.230	0.64	4 998	271	674
100	345	81	0.10	0.4	1.08	252	0.232	0.63	5 050	171	827
100	345	324	0.10	0.4	1.08	138	0.226	0.67	4 876	374	449
100	345	162	0.05	0.4	1.08	266	0.232	0.62	14 627	469	2639
100	345	162	0.15	0.4	1.08	114	0.223	0.68	1 682	124	98
100	345	162	0.10	0.2	1.08	141	0.113	0.55	2 294	192	248
100	345	162	0.10	0.6	1.08	231	0.347	0.70	7 713	313	1130
100	345	162	0.10	0.4	0.80	228	0.230	0.63	5 008	309	1043
100	345	162	0.10	0.4	1.40	173	0.230	0.65	4 991	234	439

Table 5 *The effect of sire selection intensity in the base of an optimized MOET scheme*

No. of rams sold	No. of lambs born	Base sires	MOET lambs	<i>v</i>	<i>w</i>	<i>x</i>	<i>y</i>	<i>G</i> *	$\Delta F(\times 10^2)$	Returns (\$AU'000)	Costs (\$AU'000)	Benefit of MOET (\$AU'000)
1600	5520	5	0					0.244	0.75	85 195	0	
1600	5520	5	2726	0.08	0.91	0.22	0.58	0.297	0.66	105 799	3694	16 911
1600	5520	10	0					0.231	0.36	86 661	0	
1600	5520	10	2705	0.08	0.89	0.23	0.57	0.295	0.61	105 833	3666	15 506
1600	5520	3%	0					0.169	0.02	66 812	0	
1600	5520	3%	3591	0.05	0.90	0.15	0.72	0.294	0.53	106 075	4868	34 395

rate of gain in a flock using only natural mating would be affected rather dramatically.

Table 5 shows the effect of varying the number of rams used in the base group. To demonstrate this effect, a larger flock size was used and the number of rams used in the base was either 5, 10 (both possible by artificial insemination) or 3% of the number of base ewes (appropriate for natural joining). In considering the results it is important to understand the corresponding schemes without MOET. The returns for an all natural flock were greatest (among these alternatives) when 10 sires are used. Benefits were reduced if five sires were used due to inbreeding, and if a 3% mating ratio was used, due to the loss of selection intensity. The three schemes with optimum use of MOET gave very similar rates of gain and levels of response, but the number of donors and the benefits varied because of the divergence of the non-MOET alternatives. This is an important result. If widespread use of AI is not practical, the potential benefit : cost ratio for MOET schemes is substantial.

Discussion

Although the results are presented in terms of selection for clean fleece weight, they could apply to any trait or combination of traits which can be assessed at the same time as fleece weight and which have a similar heritability and inbreeding depression. The dollar values for individual schemes will not be accurate, due to the many assumptions involved in their calculation. However the relative values of alternate schemes should be helpful in determining the most efficient breeding designs. The sensitivity analyses support this claim by showing that the results are broadly robust to the assumed parameters.

Potential returns from MOET in Merinos

Benefits from MOET were calculated relative to a naturally mated flock of the same size. This may be a little misleading as part of the benefit of the MOET

schemes tested is due to the formation of a nucleus within the flock. However, in the cases studied, formation of an open nucleus without use of MOET would give little benefit, especially because the nucleus does not use better rams than the base so there is little opportunity for assortative mating.

The results show that the use of MOET can be profitable to the industry as a whole, provided that the benefits can be extended to a large number of commercial sheep via the pyramidal stud structure. This means that MOET is most likely to be useful in the larger Merino bloodlines where it is possible for individual rams to leave many descendants over many flocks.

As MOET is introduced into a natural mating flock, the genetic gain increases rapidly at first but then tends to plateau as the proportion of MOET bred lambs approaches 100%. This means that the economic optimum is nearly always less than 100% MOET. This has consequences for the likely shape of the top tier of the breeding structure; rather than one or two flocks devoted wholly to MOET, the optimum structure will see several flocks which each use some MOET.

The optimum level of MOET use is affected by all the variables studied but the most important is the number of stud rams sold. The results are summarized in Figure 6. The optimum number of lambs born from MOET is approximately twice the number of stud rams to be produced for stud use and sale. This approximation falls within the range which gives 0.95 of maximum benefit in most cases studied here and could be a useful rule of thumb. This is still dependent on the assumptions made and it does not mean that all the stud rams sold should be drawn from the male MOET lambs. A sound genetic evaluation system is required to rank rams from the MOET and natural groups and maximize genetic gain. This rule of thumb could be improved upon by use of the dynamic selection rules proposed by Wade and Goddard (1994). They

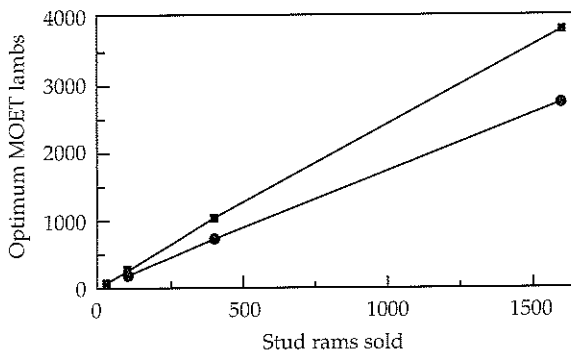


Figure 6 The optimum size of MOET operation according to the size of market for stud rams where 14.5% (●) or 58% (■) of rams born are sold as stud rams.

suggest a method for deciding whether the benefit of replacing a natural embryo with a transferred embryo from a superior donor is greater than the cost. Their method would account for factors such as wool price, cost of MOET and offspring per donor (as is done here) but would take into account the actual sheep available for selection each year. The exact number of MOET donors used would vary between years. On average this approach might lead to designs similar to the best designs reported here but this needs to be tested in further research. An extension of the dynamic selection rules could include the inbreeding consequences of selection decisions.

Factors which increase the benefits from the breeding programme (higher wool price, higher heritability, lower discount rate, higher MOET success rate, larger flock size) or decrease costs (lower MOET cost) cause the optimum number of MOET lambs to increase. Factors not tested here which also increase genetic response would be expected to show similar effects. For example, Wray and Goddard (1994) showed 0.03 to 0.08 proportional improvements from using best linear unbiased prediction (BLUP) genetic evaluations in similar flock structures. Provided the same rams may be used in both the base and the nucleus, the genetic lag between nucleus and base is small and the optimum design involves a significant proportion of base born rams and ewes being used in the nucleus. The optimum transfer rates are difficult to predict but selection across nucleus and base on estimated breeding value should closely approximate the optimum with respect of G^* . Conceptually, a slight bias towards selection of animals born in the base would lead to a lower inbreeding rate and hence to maximum R_{14} and P_{14} , but this has not been tested.

If AI is used to mate the very best rams to the MOET donors but the next best rams are used by natural mating in the base (Table 5), the proportion of base born animals used in the nucleus declines. The design in Table 5 would allow the best rams from many flocks to be selected for use by AI across donors in all flocks. McClintock and Nicholas (1991) point out that if the price of AI semen is high, use of MOET can reduce the cost per lamb by producing more lambs per dose of semen.

Potential adoption of MOET techniques

If there are to be industry benefits from careful use of MOET in major parent studs, it is important to know whether the techniques are likely to be adopted in a free market environment. The benefit generated by MOET, as calculated here, is not the benefit the parent stud might enjoy alone, but the benefit to the industry (or a section of it).

The value of stud rams available for sale was calculated as the net present value of all the returns from using those rams. This is the value of the rams to the industry as a whole, and the benefit of MOET indicates the value of the rams in excess of rams which could be produced by natural breeding, having subtracted the costs of MOET. For MOET to be adopted, it must be possible for these benefits to be distributed among the participants, being the parent stud breeder, the daughter stud breeders and the commercial growers.

The parent stud breeder must be able to sell the rams at a price which at least covers the cost of breeding. One of our examples shown suggests the rams from that particular MOET scheme would need to attract a premium of \$300 to \$400, on average over years, above the price of an average stud ram to cover these costs. While discounting takes account of the fact that costs precede returns, there are also cashflow considerations. Optimum investment in MOET should occur if the price for which rams are sold reflects their genetic merit. Then parent stud breeders should receive a share of the full value of the rams they sell, appropriately discounted for the time it will take for commercial expressions of the superior genes. The ram buyers (daughter stud breeders) will benefit because they do not pay the full discounted value of rams and can attract higher prices for flock rams they sell. For this to occur, a system of comparing the breeding value of rams across studs is essential. The cost of such evaluation has not been included here. In this study rams have been given their full discounted value, which reflects the benefits which can accrue to parent stud breeders, daughter stud breeders and commercial producers.

The value of genetic improvement in the stud has been calculated assuming that it causes an increase in the value of rams without changing the number of rams sold. If other competing studs also increase the genetic merit of their sheep by investing in MOET, competition between studs may force the price of rams down toward their cost of production. In that case the benefits from MOET will concentrate at the daughter stud and commercial levels. It will still be preferable for a stud to invest in MOET while returns exceed costs, as the alternative is to fall behind the competitors and suffer reduced prices and loss of market share. The appropriate investment in MOET will depend on the industry's ability to compare and value rams fairly across studs, which in turn requires a valid genetic evaluation system between flocks. Commercial competition and elasticities of supply and demand will then determine how the industry benefit is distributed among participants.

McClintock and Nicholas (1991) undertook a major review of advanced breeding techniques for the Australian meat (beef and lamb) industries. Their conclusions were that MOET was unlikely to be a worthwhile investment because a MOET scheme must produce a very large number of herd bulls or flock rams to be feasible. Because of the size of the Australian Merino flock, the wool industry may not have the same constraints. In particular, the existence of a defined daughter stud level justifies investment to produce high value natural service rams. McClintock and Nicholas (1991) assumed that herds or flocks used 100% MOET and did not utilize a pyramidal stud structure to multiply the number of animals which benefit. They preferred a higher discount rate (15%) and a short time horizon (10 years). The discount rate required is one adjusted for inflation so 10% does not seem unreasonable, but 15% allows more loading for risk. Bird and Mitchell (1980) argue that a time horizon should not be used as well as discounting. A 10-year time horizon implies that the genetically superior breeding stock available at year 10 are not worth any premium, which is unlikely to be true if genetic superiority prior to year 10 is valuable.

The rates of genetic gain reported in this paper may present an optimistic outlook for the application of MOET in Merino breeding programmes. Risk will remain a critical factor for breeders. However, careful attention to breeding design and the practicalities of accelerated genetic improvement will reduce risks and increase returns. Co-operative breeding arrangements, particularly with across-flock evaluation at low cost, may limit the financial exposure of individual breeders and further improve the realized genetic gains from MOET. Alternatively, a stud operation which includes parent stud and daughter stud segments (and perhaps commercial

sheep as well) will be less dependent on ram sales and can reap the benefits of genetic improvement internally.

Acknowledgements

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References

- Banks, R. G.** 1987. The breeding structure of the Merino industry and its influence on genetic progress. In *Merino improvement programs in Australia* (ed. B. J. McGuirk), pp. 125-135. Australian Wool Corporation, Melbourne.
- Bird, P. J. W. N. and Mitchell, G.** 1980. The choice of discount rate in animal breeding investment appraisal. *Animal Breeding Abstracts* **48**: 499-505.
- Bulmer, M. G.** 1971. The effect of selection on genetic variability. *American Naturalist* **105**: 201-211.
- James, J. W.** 1977. Open nucleus breeding schemes. *Animal Production* **24**: 287-305.
- James, J. W.** 1978. Effective population size in open nucleus breeding schemes. *Acta Agriculturae Scandinavica* **28**: 387-392.
- McClintock, A. E. and Nicholas, F. W.** 1991. The implications of advanced breeding techniques. *Australian Meat and Livestock Research and Development Corporation Project Report US.016*.
- Maxwell, W. M. C., Szell, A., Hunton, J. R. and Ryan, J. P.** 1990. Artificial breeding: embryo transfer and cloning. In *Reproductive physiology of Merino sheep: concepts and consequences* (ed. C. M. Oldham, G. B. Martin, I. W. Purvis), pp. 217-237. University of Western Australia, Perth.
- Mueller, J. P. and James, J. W.** 1983. Effects of reduced variance due to selection in open nucleus breeding systems. *Australian Journal of Agricultural Research* **34**: 53-62.
- Robertson, A.** 1961. Inbreeding in artificial selection programmes. *Genetical Research, Cambridge* **2**: 189-194.
- Smith, C.** 1986. Use of embryo transfer in genetic improvement of sheep. *Animal Production* **42**: 81-88.
- Wade, C. and Goddard, M. E.** 1994. How much is a genetically superior ram worth? *Australian Journal of Agricultural Research* **45**: 403-413.
- Woolliams, J. A., Wray, N. R. and Thompson, R.** 1993. Prediction of long-term contributions and inbreeding in populations undergoing mass selection. *Genetical Research, Cambridge* **62**: 231-242.
- Wray, N. R. and Goddard, M. E.** 1994. MOET breeding schemes for wool sheep. 1. Design alternatives. *Animal Production* **59**: 71-86.
- Wray, N. R. and Hill, W. G.** 1989. Asymptotic rates of response from index selection. *Animal Production* **49**: 217-227.
- Wright, S.** 1931. Evolution in Mendelian populations. *Genetics, USA* **16**: 97-159.

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Appendix 1

Inbreeding in an open nucleus flock

James (1978) showed that the rate of inbreeding in an open nucleus scheme could be approximated as

$$\Delta F = g^2 \Delta F_N + (1 - g)^2 \Delta F_B \quad (A1.1)$$

where g is a function of the transfer rates between nucleus and base, $g = (w + y)/(v + w + x + y)$. ΔF_N and ΔF_B are the rates of inbreeding in the nucleus and base, if each had been closed. James (1978) assumed a rate of inbreeding in the nucleus and base appropriate to a randomly selected population with a Poisson distribution of family sizes before selection. If X denotes N or B then

$$\Delta F_X = \frac{1}{8X_S L^2} + \frac{1}{8X_D L^2} \quad (\text{Wright, 1931}) \quad (A1.2).$$

However, rates of inbreeding are higher when selection is practised (Robertson, 1961) and in an attempt to account for this we assume

$$\Delta F_X = \frac{1 + C_X^2 W_{XS}}{8X_S L^2} + \frac{1 + C_X^2 W_{XD}}{8X_D L^2}$$

which is an approximation to equation (4) of Woolliams, Wray and Thompson (1993) which is appropriate for mass selection and assumes that family size prior to selection follows a Poisson distribution.

Including L^2 in the denominator heuristically adapts their discrete generation equation to overlapping generations, where

$$W_{XS} = \frac{h^2}{4} \left[\frac{X_S}{X_D} + \frac{4}{(1 + k_X h^2)^2} \right]$$

and

$$W_{XD} = \frac{h^2}{4} \left[1 + \frac{4}{(1 + k_X h^2)^2} \right]$$

are factors to account for the effect of selection on inbreeding. Variance reduction factors, k_X , vary only slightly and are difficult to determine for nucleated flocks, so 0.75 is used throughout. Predictions are robust to this approximation.

Sires may be used simultaneously in both nucleus and base. Accounting for this common use of sires in the derivation shown by James (1978) results in the covariance between selection differentials of sires, which was previously assumed to be zero, becoming non-zero. (In the notation of James (1978), $\text{Cov}[C_{SN}, C_{SB}] = \text{V}[C_{SB}]$.) This results in equation (1).

This final equation results from extension of equations from other situations and is based on intuition rather than formal derivation. Predictions of rate of inbreeding achieved by this equation are compared to rates of inbreeding observed in simulations of open nucleus breeding programmes and it was found to provide significant improvement in prediction compared to equations A1.1 and A1.2 (see Table

1). In general, equations A1.1 and A1.2 are under estimates and our equation gave over estimates of inbreeding relative to simulation results.

Appendix 2

Cumulative discounted merit in the commercial flock

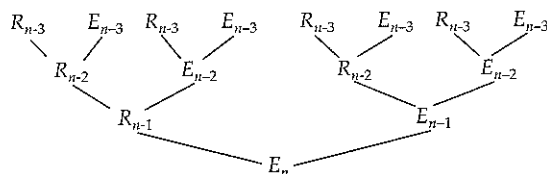
It is the additive genetic merit and inbreeding of animals in the commercial flock that determines the value of the breeding programme to the industry but this paper has attempted only to estimate these quantities for the stud flock. The additive genetic merit and inbreeding of the commercial flock follows that of the stud but after a time lag.

The purpose of this Appendix is to show that inbreeding is passed on to commercial flocks in a manner similar to additive genetic merit. Therefore it is appropriate to use the net genetic merit (additive genetic merit less inbreeding depression) of a ram, along with the expected discounted expressions and the value of the trait, to calculate the benefits of his use.

Consider a discrete generation model of a closed stud flock which provides rams to commercial flocks.

(a) Inbreeding in the commercial flock

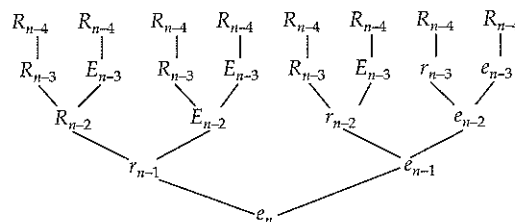
The pedigree of an animal born in the stud in generation n is



where: R_i = any stud ram born in generation i ; and E_i = any stud ewe born in generation i . Assume the number of rams per generation = N , and the number of ewes per generation approaches infinity. Then the inbreeding of E_n is approximately $1/8N$ from each generation of ancestors i.e.

$$F_n \approx \sum_{i=0}^{n-2} \frac{1}{8N}.$$

The pedigree of an animal born in the commercial flock in generation n is



where: r_i = any ram born in the stud in generation i and used in the base; and e_i = ewe born in the commercial flock in generation i .

Inbreeding only occurs through stud rams. Ancestors in generation $n-3$ cause $(2)(1)/32N = 1/16N$, in generation $n-4$ cause $(4)(3)/128N = 3/32N$, and in generation $n-5$ cause $(8)(7)/512N = 7/64N$ inbreeding, i.e.

$$f_n \approx \sum_{i=1}^{n-2} \frac{2^i(2^i-1)}{2^{2i+3}}.$$

As n becomes large $f_n \approx F_n - 1/4N = F_n - 2\Delta F$. That is, inbreeding in the base lags two generations behind inbreeding in the stud.

(b) *Cumulative net genetic merit in the commercial flock*

Let G_i (g_i) = additive genetic merit of animals born in generation i in the stud (commercial); F_i (f_i) = inbreeding of animals born in generation i in the stud (commercial); $R_i = G_i - DF_i$; $r_i = g_i - Df_i$; D = inbreeding depression per unit of inbreeding.

The discounted value of animals born in the commercial flock in generation i is $g_i b^i$.

The discounted value of all commercial animals resulting from the breeding programme is

$$\sum_{i=1}^{\infty} r_i b^i = \sum_{i=1}^{\infty} b^i (g_i - Df_i) = \sum_{i=1}^{\infty} b^i g_i - \sum_{i=1}^{\infty} b^i Df_i \quad (A2.1).$$

The additive merit of animals born in the commercial flock depends on the merit of rams used. Assuming no selection of rams or ewes in the commercial flock $g_i = G_{i-1}/2 + G_{i-2}/4 + \dots + G_0/2^i$.

Therefore

$$\sum_{i=1}^{\infty} b^i g_i = \sum_{i=1}^{\infty} b^i \sum_{j=1}^i \left(\frac{1}{2} \right)^j G_{i-j}.$$

Reversing the order of summation this is equal to

$$\sum_{j=0}^{\infty} G_j \sum_{i=1}^{\infty} \left(\frac{1}{2} \right)^i b^{i+j} = \sum_{j=0}^{\infty} G_j b^j \sum_{i=1}^{\infty} \left(\frac{1}{2} \right)^i b^i = \sum_{j=0}^{\infty} G_j b^j E \quad (A2.2)$$

where E is the number of discounted expressions of the genotype of rams born in generation j and used in the base, discounted to the time of their birth. (Note that this is a slightly different definition to that used in the main paper where the discounted expressions of a ram are discounted to the time of birth of his first progeny.)

Also from part (a)

$$\begin{aligned} f_n &= F_n - 2\Delta F = \frac{1}{2}(F_n - \Delta F) + \frac{1}{4}(F_n - 2\Delta F) + \dots \\ &= \frac{1}{2}F_{n-1} + \frac{1}{4}F_{n-2} + \dots = \sum_{i=1}^n \left(\frac{1}{2} \right)^i F_{n-i} \quad (A2.3). \end{aligned}$$

Substituting (A2.2) and (A2.3) into (A2.1):

$$\begin{aligned} \sum_{i=1}^{\infty} r_i b^i &= \sum_{j=0}^{\infty} [G_j b^j E] - \sum_{j=1}^{\infty} \left[b^j D \sum_{i=1}^j \left(\frac{1}{2} \right)^i F_{j-i} \right] \\ &= \sum_{j=0}^{\infty} G_j b^j E - \sum_{j=1}^{\infty} b^j D \sum_{i=1}^j \left(\frac{1}{2} \right)^i F_{j-i}. \end{aligned}$$

Reversing the order of summation this is equal to:

$$\begin{aligned} \sum_{j=0}^{\infty} G_j b^j E - \sum_{j=0}^{\infty} DF_j \sum_{i=1}^{\infty} \left(\frac{1}{2} \right)^i b^i &= \sum_{j=0}^{\infty} G_j b^j E - \sum_{j=0}^{\infty} DF_j E \\ &= \sum_{j=0}^{\infty} b^j E (G_j - DF_j) = E \sum_{j=0}^{\infty} b^j R_j. \end{aligned}$$

That is, the discounted value of genetic improvement in the commercial flock is the discounted value of improvement in the stud times the discounted expressions of the merit of each generation of rams sold from a stud to a commercial flock. This discussion has assumed only two tiers — stud and commercial. However, the same conclusion would hold for three levels — parent stud, daughter stud and commercial flock.