STRATEGIES TO MAXIMISE SELECTION PROGRESS IN DAIRY CATTLE

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SUMMARY

The basic principles for maximising progress using the infinite alleles model are largely understood. However this is not the case when individual alleles can be identified in conjunction with continuous variation, nor when constraints on inbreeding are applied. Accounting for linkage disequilibrium does not alter the relative merits of progeny testing and MOET nucleus schemes. The reduction in the rate of progress at equilibrium in progeny testing is similar to the reduction in the total genetic variance. However in MOET nucleus schemes the reduction in progress is greater than the reduction in genetic variance alone since the value of ancestral information is also reduced by linkage equilibrium.

BLUP selection enhances progress and removes the distinctions between MOET nucleus schemes and progeny testing schemes. When the female family size is increased, factorial mating gives extra progress when constrained by inbreeding. When accuracy is low, as in MOET nucleus schemes or the use of young unproven bulls indicator traits would prove useful. Cloning has potential for reducing genetic lags, but not as yet for increasing the progress of leading herds; sexing of embryos and semen can improve progress through more effective use of the allocated resources.

INTRODUCTION

The maximisation of genetic progress has become more and more tractable for animal breeders over the last decade. This has principally been achieved through the development of statistical and computational techniques for estimating breeding values. However the single-minded pursuit of progress is not without its risks and consequences - not only in management, but through the effects of more rapid inbreeding and loss of genetic variation for production and disease resistance.

Therefore the first section of the paper reviews the basic principles upon which genetic progress is maximised, together with the risks and consequences and the second section will examine how genetic progress may be maximised further, risks notwithstanding, given the current procedures for evaluation and the likely developments over the next decade.

BASIC PRINCIPLES

The selection objective may be complex and composed of a range of traits of varying economic importance but it will be assumed that it is clearly defined. This problem has historically led to 3 selection procedures to achieve the objective; tandem selection whereby each trait is selected on in turn; multiple culling levels whereby breeding livestock have to satisfy threshold requirements on each trait; or, index selection in which measurements of each trait are combined linearly to give an aggregate value upon which selection is then practised. It has been clearly shown that for linear economic functions of the traits the efficiency of these procedures rank 'index', 'multiple culling' and 'tandem' in descending order. Thus it is sufficient in discussing the maximum selection progress to consider progress in a single trait i.e. the aggregate genotype.

Progress assuming the infinite-loci model

Throughout the phenotypes of the base population (t=0) are assumed to be normally distributed with variance \( V_0 = 1 \) and unless otherwise stated the infinite-loci model of Bulmer (1980) with no linkage or epistasis will be assumed. The breeding values of the base
population are assumed normally distributed with variance $V_A(0) = h^2$ and under the model the regression of the breeding value of an individual ($A_c$) measured prior to selection on its parents ($A_s$ and $A_d$) remains invariant with

$$A_c = \frac{1}{2} A_s + \frac{1}{2} A_d + A_m$$  \hspace{1cm} (1)$$

where $A_m$ is a Mendelian sampling term normally distributed with mean zero and variance $1/2 h^2 (1-F)$ and $F$ is the mean inbreeding coefficient of its parents. The regression of breeding value on phenotype ($Y$) in generation $t$ is

$$A = h^2(t) Y + e$$  \hspace{1cm} (2)$$

where $h^2(t) = V_A(t)/V_p(t)$ and $e$ is normally distributed with mean zero and variance $(1-h^2(t))V_A(t)$. Under normality this regression is preserved by truncation of the population.

Genetic progress in generation $t$ is given by

$$\Delta G(t) = (i_M r_{IAM}(t) + i_F r_{IAF}(t))\sqrt{V_A(t)}/(L_M + L_F)$$  \hspace{1cm} (3)$$

where $i$ denotes standardised selection differential, $r_{IA}$ selection accuracy (the correlation between the index used and the true aggregate breeding value), $L$ denotes generation interval and the subscripts $M$ and $F$ denote males and females respectively. Strictly speaking, for overlapping generations this defines the asymptotic rate of progress but this will suffice for the current purpose.

Selection progress is thus increased by increasing selection differential, i.e. by decreasing selection proportion to a limit that is determined by the practical reproductive rate of the male and female. It is principally by this route that the major improvements in selection progress were made over the last 40 years through the increase in male reproductive rate made possible by AI and the freezing of semen, and where more modest gains are possible through the use of ET to increase the female reproductive rate. Secondly the accuracy of estimating the breeding value can be increased through i) controlling the environment, ii) reducing measurement errors, iii) good design of testing schemes, iv) incorporating as much information on relevant traits and on relatives as possible, and v) by fitting as good models as possible. The use of information from relatives and computational power to fit appropriately large statistical models are ways in which BLUP and individual animal models will help speed genetic progress. However increasing gain through accuracy cannot be viewed in isolation: for example, accuracy on females can be improved by recording many lactations before breeding decisions are made but this in turn increases the generation interval and hence from (3) reduces progress. Thus there is a compromise to be made between accuracy and generation interval, and this lies at the heart of much of the debate on ways to maximise genetic gain in dairy cattle (e.g. MOET and progeny testing).

Finally genetic progress can be increased by increasing $V_A$. At first sight this may seem impossible given the base population and also given the selected parents. However by the use of positive assortative mating genetic variation in the offspring can be increased. From (1) for any generation

$$V_A(t) = \frac{1}{4} (V_{AS} + V_{AD}) + 2 \text{cov} (A_s, A_d) + \frac{1}{2} h^2 (1-F)$$

where $V_{AS}$ and $V_{AD}$ are the variance of breeding values amongst selected sires and dams of the previous generation. Thus by introducing a positive covariance between the expected
breeding values of the mates and thus, in consequence, between the true breeding values of the mates, \( V_A \) is increased. By analogy it is also true that if the covariance is negative, through negative assortative mating, then progress will be reduced.

Smith and Hammond (1987) confirmed the work of others that assortative mating is particularly useful when \( h^2 \) is high and selection intensity is low, but extra progress exceeds 10% only when \( h^2 > 1 \) and \( i < 0 \). These authors questioned the value of assortative mating when distributions are non-normal. However it can be shown (proof not given) that positive assortment is never counter-productive when

i) for each sex, prediction error variances of expected breeding values for individuals are identically distributed.

ii) the breeding value of the offspring is the average of its parents with deviation distributed in any form but independent of the parental breeding values.

iii) inbreeding is either negligible or uniform in the population.

Assumption (ii) include (1) as a special case. Thus if there are two 'discordant' pairs \((S_1,D_1)\) and \((S_2,D_2)\) i.e. with expected breeding values \( E(A_{S1}) < E(A_{S2}) \) but \( E(A_{D1}) > E(A_{D2}) \), then selection progress is at least as good if the pairs are rearranged to be concordant.

**Linkage disequilibrium**

The infinite model predicts that truncation selection will reduce the genetic variation present in the population (Bulmer, 1980). Let an asterisk denote variance after selection and \( I(t) \) the regressed index of selection.

\[
V_A(t)^* = V_A(t) + (1-r_{IA}^2(t))V_A(t)
\]

and from (1), with \( k = i(i-x) \) so that \( V_A(t)^* = (1-k)r_{IA}^2(t)VA(t)\)

\[
V_A(t+1) = \frac{1}{2}(h^2 + V_A(t)) - \frac{1}{4}(k_{IA}^2(t) + k_{IA}^2(t))V_A(t)
\]

Thus \( V_A(1) < V_A(0) \) and Bulmer continues to show that the recurrence relation (4) converges rapidly for truncation selection. Thus most genetic variation is predicted to disappear in the first round of selection. From the assumptions of the infinite model the decline in genetic variance can only be explained by linkage disequilibrium induced by selection. Furthermore, the model predicts that upon ceasing selection genetic variance is progressively restored, the shortfall reducing by 50% per generation.

The effects of the linkage disequilibrium in the infinite model are i) loss of progress through lower \( V_A(t) \) and ii) a reduction in the correlation between individual performance and that of its sibs due to a smaller contribution of genetic variance from the parents.

Since increasing selection intensity increases progress but also reduces genetic variation and, as a consequence, subsequent genetic progress, there is an a priori case that maximal selection progress may be obtained from a trade-off between \( i \) and \( V_A(t) \). However, it can be shown (proof not given) that under a model described by (1) with the same conditions given for assortative mating (hence including the infinite model) selection progress is always maximised by selecting the best individuals.

**Progress with finite-loci models**

It is unfortunate that the clear results for the infinite-loci models do not apply generally to models with finite loci. Examples can be found to show i) positive assortative
mating is not always beneficial; ii) $V_A(t)$ need not decrease with selection; iii) progress is not greatest by selecting the best. The key to all the conditions for the results in the infinite-loci model is the homogenous distribution of the offspring about the mean expected breeding value of their parents, a condition that is broken by the Mendelian sampling terms when specific alleles are considered in homozygous or heterozygous conditions. Thus strategies for maximising gain will depend specifically on gene frequencies and gene effects. The optimal strategies for selection when quantitative variation is combined with even one major gene are also unclear. This situation may become a reality of proposals to map the complete bovine genome are pursued.

**Inbreeding**

Unlike linkage disequilibrium, whatever the allelic model, inbreeding causes a permanent reduction in the genetic variance of a homogeneous population. It is this loss that ultimately brings genetic progress to a halt, apart from new mutational variance arising. Inbreeding is unavoidable in finite populations and is usually, but not always, exacerbated by genetic selection. All the methods for increasing progress described previously such as higher selection intensities, including the use of ancestral information and assortative mating will increase inbreeding when used with mass selection.

Thus from the narrow viewpoint of future selection progress there is a need to trade off progress with inbreeding. Faster inbreeding will also cause greater drift in neutral traits some of which may become of economic importance as a result (e.g. susceptibility to disease) and will also lead to a greater variance in the response of the selected traits. Furthermore there is the economic loss in the present to consider. Hudson and Van Vleck (1984) although suggesting that current levels of inbreeding were not of concern, estimated a 21kg drop in milk yield per cent inbreeding with reductions in longevity and calving interval. The possible hidden costs of reduced growth and greater disease and mortality, well-documented in other species, were not measured.

The consideration of inbreeding introduces a further concept: the time horizon over which genetic gain is to be maximised - one generation, n generations for some n, or a weighted average over generations such as would be produced by discounted benefit techniques. Smith (1969) considered adjusting intensity of mass selection to maximise response over a fixed n generations and Demple (1974) showed that when $n \to \infty$ so response is greatest using within-family selection rather than mass selection.

**PROGRESS IN THE DAIRY POPULATION**

Two major themes over the last decade concerning dairy cattle have been i) the relative advantages of MOET nucleus herds and progeny testing and ii) BLUP and individual animal models.

**MOET and progeny testing**

Progeny testing is a robust system of improvement that overcomes the sex-limitation of dairy improvement. It is characterised by selecting bulls with high accuracy but with a long generation interval. Nicholas and Smith (1983) and Woolliams and Smith (1988) examined what impact multiple ovulation and embryo transfer could have in a nucleus herd. By increasing the reproductive rate of the cow selection intensity could be increased. Moreover the increase in the number of close relatives (principally full-sibs) meant that information on their performance could help in increasing the accuracy of female selection. For males, the extra information from full-sib sisters provided more information on the breeding value of its dam, whilst the female paternal half-sibs provided information on its
Their conclusions were that sufficient information was obtained by 4 years of age, after the 1st lactation of the females, to allow selection to take place (thus reducing the generation interval below that of progeny testing) and to give rates of change within the nucleus comparable to those from progeny testing. This was termed the 'Adult' (A) Scheme. Furthermore these authors showed that by selecting progeny at 2 years of age using ancestral information (i.e. aunts, half-aunts and grand-dams) and then using MOET, progress was further enhanced. This was termed the 'Juvenile' (J) scheme, and can be characterised by low accuracy and low generation interval, with the Adult scheme characterised by medium accuracy and medium generation interval. This is an example of the trade-off between  \( r_{AI} \) and \( L \) required to maximise progress.

Since the publication of these results it has been a subject of dispute as to whether or not the advantages given by Woolliams and Smith (1988) could be realised in practice. Simulations carried out (Juga and Maki-Tanila, 1987; and latterly Ruane and Thompson, 1990) suggest that progress obtained in A schemes is perhaps only 60-65% of that proposed.

A major cause of the shortfall was identified as a loss of between family variation i.e. linkage disequilibrium. Proponents of MOET had not explicitly accounted for the loss in genetic variation and, furthermore, MOET uses ancestral and collateral information whose value is also reduced by linkage disequilibrium. However a fair comparison of progeny testing and MOET must also take into account the loss of progress below initial expectation that is bound to occur in models of progeny testing. This has been shown by simulation (Meyer and Smith, 1990) and by complex deterministic models (Meuwissen, 1989). These systems have therefore been compared again using the original structures of Woolliams and Smith (1988), with progress estimated both initially and in equilibrium (which is quickly reached before inbreeding would become a serious consideration). Results are shown in Table 1; two values of \( h^2 \) (0.25 and 0.35) are used since the published estimates of progress may be appropriate if estimates of \( h^2 \) used are interpreted as coming from a base population already under selection using progeny testing.

**Table 1** Rates of progress (base phenotypic s.d./annum) in progeny testing and MOET nucleus schemes

<table>
<thead>
<tr>
<th>Heritability (( h^2 ))</th>
<th>0.25</th>
<th>0.35</th>
<th>0.25</th>
<th>0.35</th>
<th>0.25</th>
<th>0.35</th>
</tr>
</thead>
<tbody>
<tr>
<td>Progeny testing A*</td>
<td>0.133</td>
<td>0.166</td>
<td>0.100</td>
<td>0.125</td>
<td>0.75</td>
<td>0.75</td>
</tr>
<tr>
<td>B</td>
<td>0.133</td>
<td>0.166</td>
<td>0.102</td>
<td>0.125</td>
<td>0.77</td>
<td>0.75</td>
</tr>
<tr>
<td>Adult MOET N*</td>
<td>0.118</td>
<td>0.151</td>
<td>0.092</td>
<td>0.115</td>
<td>0.78</td>
<td>0.76</td>
</tr>
<tr>
<td>H</td>
<td>0.158</td>
<td>0.198</td>
<td>0.120</td>
<td>0.148</td>
<td>0.76</td>
<td>0.75</td>
</tr>
<tr>
<td>Juvenile MOET N</td>
<td>0.170</td>
<td>0.218</td>
<td>0.134</td>
<td>0.169</td>
<td>0.79</td>
<td>0.77</td>
</tr>
<tr>
<td>H</td>
<td>0.225</td>
<td>0.282</td>
<td>0.175</td>
<td>0.217</td>
<td>0.78</td>
<td>0.77</td>
</tr>
</tbody>
</table>

*\( A = 50 \) effective daughters; \( B = \) bulls tested to constant accuracy
+\( N = 8 \) calves/donor, 8 donors/sire; \( H = 16 \) calves/donor, 16 donors/sire
The relative rates of progress predicted are very similar whichever set of parameters is used, all being reduced by 20-25% when linkage disequilibrium is introduced. Increasing h² exacerbates the effect of disequilibrium in all schemes. Table 2 shows V_A(t) is reduced most in progeny testing, and least in juvenile schemes. However whilst progress in progeny testing is reduced in line with the true h² at equilibrium ((3) in Table 2), progress in MOET schemes is further reduced, particularly in J schemes. This reflects the reliance of MOET schemes on ancestral or collateral performance rather than individual or offspring performance. The reduction in value of ancestral information can be judged by the extra reduction in h² estimated from paternal half-sibs in ((4) Table 2) compared to the true heritabilities at equilibrium. The reduction in progress of J schemes, relying as they do entirely on ancestral information, is very similar to the reduction in the half-sib estimate of h². A schemes are intermediate.

Table 2 Genetic variance at equilibrium (V_A(∞))

<table>
<thead>
<tr>
<th>Heritability (h²)</th>
<th>(1)V_A(∞)*</th>
<th>(2)V_A(∞)/h²</th>
<th>(3)h²(∞)/h² from paternal half-sibs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Progeny testing</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A*</td>
<td>0.184</td>
<td>0.250</td>
<td>0.74</td>
</tr>
<tr>
<td>B</td>
<td>0.180</td>
<td>0.250</td>
<td>0.72</td>
</tr>
<tr>
<td>Adult MOET</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N*</td>
<td>0.206</td>
<td>0.280</td>
<td>0.82</td>
</tr>
<tr>
<td>H</td>
<td>0.199</td>
<td>0.272</td>
<td>0.80</td>
</tr>
<tr>
<td>Juvenile MOET</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>0.228</td>
<td>0.310</td>
<td>0.91</td>
</tr>
<tr>
<td>H</td>
<td>0.224</td>
<td>0.310</td>
<td>0.89</td>
</tr>
</tbody>
</table>

*See Table 1; +For cows

The equilibrium half-sib estimate of h² in progeny testing when initial h² = 0.35 is very close to 0.25, suggesting that simulation studies for milk production might be more appropriate using 0.35 as the heritability of an unselected base population rather than 0.25.

In summary, the relative merits of progeny testing and MOET schemes are not greatly affected by linkage disequilibrium. However it is now possible to match the simulations of A schemes to the deterministic predictions: this study suggests a 22% reduction through linkage disequilibrium and Woolliams (1989) found a 15% loss through the finite correlated selection intensities - putting those together suggests that in the absence of inbreeding only 0.66 of the predicted progress will be realised, in close accord with the simulations.

BLUP and individual animal models

For the purposes of this paper BLUP methodology will not be discussed. Some of its key properties are i) the unbiased predictions of breeding value which means that for any individual, no matter how good the predictions are, further information is as likely to increase the prediction as decrease it, ii) the simultaneous estimation of genetic and
environmental fixed effects, iii) the accounting of all available genetic information however distant genetically or geographically and iv) the provision of expected breeding values for comparison across age groups.

This last point (in conjunction with the first) means that progress can be made by selecting the best individuals of the population no matter what age, no matter how much information is available (individuals with little or no information will only be found at or very close to the mean genetic level of the whole population). It might be advocated that selection should only be from amongst those groups with the highest accuracy. However it is very clearly shown that extra progress is obtained by simulations in pigs (Belansky and Kennedy, 1988) and perhaps more importantly for dairy cattle by the deterministic model of Meuwissen (1989) - in all of these truncation was applied at the same point across all generations irrespective of accuracy. One important consequence is the removal of the requirement to adhere to a rigid strategy that selects individuals at given ages with given accuracies to obtain the required trade-off. Thus the distinction and controversy over MOET and progeny testing disappears. Using BLUP this trade-off is engineered automatically and flexibly. This is shown by results of Meuwissen (1989), given in Table 3. The age distribution uses both young unproven bulls (ages 2-5) and proven progeny-tested bulls (ages 6+). However, since the truncation of BLUP estimates of varying accuracy breaks the conditions for maximum progress to come from the selection of the greatest expected breeding values, BLUP selection may not prove to be optimal.

Table 3 Results of Meuwissen (1989) showing the age distribution (%) of bulls used for breeding in the nucleus and commercial populations, derived from BLUP models

<table>
<thead>
<tr>
<th>Age</th>
<th>Bulls for</th>
<th>Nucleus cows</th>
<th>Commercial cows</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>42</td>
<td>73</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>5</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>38</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>9</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>8+</td>
<td>3</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

Maximization of progress using BLUP selection

Given the use of BLUP across whole populations, what are the optimal population structures to identify merit as quickly as possible? What is the role of MOET?

Four routes will be explored i) increasing the female reproductive rate, ii) mating design, iii) juvenile predictors, iv) embryo technology.

Embryo Transfer. Meuwissen (1989) has provided a structure and deterministic model of a sufficient complexity to optimise breeding schemes encompassing progeny testing, embryo transfer and nucleus herds of a variable degree of openness. Evaluation in this model mimics BLUP in its use of information and selection across age groups. Initial results (Meuwissen, 1990) suggest that multiple ovulation and embryo transfer in a nucleus herd increases progress by up to 16% in what are termed practical schemes with increases in family size over the range that is currently feasible yielding most of this additional progress.

Mating design. Initial proposals for MOET nucleus schemes used full-sibs primarily because it is the result in practice of obtaining all eggs from a single flush - an ideal that is not always
One penalty arising from the production of full-sibs in schemes using family indices is the increased potential for inbreeding through the high correlation of the index amongst them. Nicholas and Smith (1983) attempted to overcome this by restricting bull selection to one per full-sibship thereby reducing the selection proportion n-fold (where n is the number of male full-sibs).

Woolliams (1989b) considered the effect of changing the mating design within the nucleus in order to replace full-sibs with maternal half-sibs. This would be most effectively achieved by mating donor cows to a different bull at each flushing. In ideal circumstances the number of offspring per cow and per bull would remain constant but would result in fewer full-sibs. Table 4 summarises some of the findings. The rested mating design is that used by Nicholas and Smith (1983) with restrictions on the usage of male full-sibs. Results showed that accuracy was marginally reduced by this change. However it was found that greater selection intensities could be applied without incurring additional penalties of inbreeding. Thus for the same rate of inbreeding, expected progress was greater, or alternatively, the same progress could be achieved with less inbreeding. In the absence of selection the mating designs considered by Woolliams (1989b) had identical inbreeding rates, however the imposition of selection created differences in the inbreeding rate. The influence of mating design within a MOET nucleus was not large in the absence of any consideration of inbreeding (including the use of full-sib males) but was relevant to the consideration of progress under constraints on inbreeding.

Table 4 Initial accuracies and rates of progress (phenotypic s.d./annum) together with measures of inbreeding in adult MOET nucleus schemes according to mating design

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>Accuracy</th>
<th></th>
<th>Measure of annual inbreeding rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Male</td>
<td>Female</td>
<td>ΔG</td>
</tr>
<tr>
<td>Nested</td>
<td>3.83</td>
<td>0.56</td>
<td>0.66</td>
<td>0.102</td>
</tr>
<tr>
<td>Factorial</td>
<td>3.83</td>
<td>0.55</td>
<td>0.65</td>
<td>0.117</td>
</tr>
<tr>
<td></td>
<td>4.18</td>
<td>0.55</td>
<td>0.65</td>
<td>0.107</td>
</tr>
</tbody>
</table>

The application considered by Woolliams (1989b) was in closed MOET nucleus schemes, however the principles may well be found to apply to the mating design of any nucleus herd employing MOET. The previous section suggests this will still be relevant in population structures that are optimised for BLUP selection.

Juvenile prediction of dairy merit

Woolliams and Smith (1986) considered the impact of a juvenile predictor of dairy merit on genetic progress in conjunction with a variety of breeding schemes. With the computational power available and the amount of performance recording it is only conceivable that such a predictor would be used in conjunction with yield data. When used with a system requiring a progeny test of the bull prior to widespread use the predictor was of value only when combined with MOET. In this case the predictor was used to select which bull from a full-sib family would enter the progeny test. With a co-heritability of 0.27 (an optimistic figure) the predictor gave an additional 10% progress. However the benefits were considerably greater when combined with MOET nucleus schemes (see Table 5) and are
very similar for initial and equilibrium rates of progress (results not shown). The extra progress comes partly from increased accuracy in estimating breeding values of both females and male full sib-ships but approximately half the benefit comes from using the within-family variation among male full-sibs (previously unused) i.e. by offering an informed choice instead of a random one. The value of the predictor was dependent on the accuracy of the scheme in its absence; the value of the extra information being inversely related to the amount of other information, thus juvenile schemes benefitted most. The juvenile predictor has further advantages when inbreeding is a consideration since it shifts the balance of information away from ancestral sources towards the individual’s own performance.

Table 5 The benefits of a juvenile predictor expressed as the proportional increase in initial AG resulting from its incorporation into indices

<table>
<thead>
<tr>
<th>$h^2$</th>
<th>0.1</th>
<th>0.25</th>
<th>0.5</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_G$</td>
<td>0.25</td>
<td>0.5</td>
<td>0.75</td>
</tr>
<tr>
<td>Adult</td>
<td>1.03</td>
<td>1.06</td>
<td>1.11</td>
</tr>
<tr>
<td>Juvenile</td>
<td>N</td>
<td>1.06</td>
<td>1.16</td>
</tr>
</tbody>
</table>

*h$^2$ = heritability of indicator trait, $r_G$ = additive genetic correlation; + See Table 1

The results of Table 5 are for nested mating designs. The benefits of juvenile predictors in factorial mating systems will not be as dramatic. This is because factorial mating systems improve response by recovering some of the loss of selection intensity that results from the selection among male full-sib families, which is also a part of the improvement given by juvenile predictors. However the additional accuracy from the predictor will still improve progress.

BLUP selection was not considered by Woolliams and Smith (1988). However Table 3 suggests that a very significant proportion of matings would use young unproven bulls. As with factorial mating the benefits of juvenile predictors will depend on the size and usage of full-sib families but additional accuracy will improve progress.

Embryo technologies

Cloning a female dairy cow gives the opportunity to increase the accuracy of evaluation more, and more rapidly, than multiple lactations. Through this route Nicholas and Smith (1983) concluded that cloning would improve rates of progress in MOET nucleus schemes. However their analysis assumed that resources were expandable to accommodate the clone families. Woolliams (1989a) concluded that when resources are fixed the extra accuracy was (in most cases) more than offset by the loss of selection differential through the reduction in the number of distinct genotypes. Exceptions to this were found when the number of sire families as reduced to accommodate the clones but this route would exacerbate inbreeding.

Distinct from enhancing progress, the production of large clone families through nuclear transfer, possibly in combination with embryo stem cells, would produce a genetic lift (a reduction in the time lag between the best of the population and the other sub-populations) through more rapid dissemination of merit. This course is not without risks.
which have yet to be quantified. Other benefits include more efficient detection of genotype by environment interactions.

The prospects arising from other embryo technologies were reviewed by Woolliams and Wilmut (1989). They considered in vitro maturation (IVM) and fertilisation (IVF) of oocytes, embryo sexing and freezing, embryo stem cells nuclear transfer (including cloning) and gene transfer. They concluded that embryo sexing, like semen sexing, would be useful in enhancing progress through the more effective use of embryo transfer resources. However although semen sexing has obvious benefits in the conduct of progeny testing, embryo sexing would have practical difficulties that could reduce the robustness of progeny testing. IVM and IVF could improve progress through increasing the female reproductive rate to allow more complex mating designs, however their use will depend greatly upon future improvements in their reliability.

CONCLUSIONS

It is clear from the discussion of Woolliams and Wilmut (1989) and discussions of earlier sections of this paper that the different routes for improving progress are not independent; developments in one route towards increasing progress will sometimes devalue, sometimes enhance developments in another. For example, using embryo sexing in MOET nucleus schemes has obvious advantages in saving resources when only a single member of a full-sibship is used but when factorial mating is introduced, perhaps in combination with a sibship scheme (Ruane and Thompson, these proceedings), or when within-family variation can be utilised using a juvenile predictor, the benefits are reduced.

In conclusion with current technology the maximisation of selection progress in dairy cattle will be brought about through (i) BLUP selection, (ii) the use of MOET to increase the reproductive rate of high-merit cows, and (iii) more attention to mating design to restrict inbreeding. Future developments in physiological and embryological understanding may find a role in increasing progress depending on their reliability and acceptability, and will require careful integration into breeding structures.

REFERENCES