EVALUATION OF GENETIC IMPROVEMENT PROGRAMMES USING MULTIPLE OVULATION AND EMBRYO TRANSFER IN DAIRY CATTLE

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ABSTRACT

The application of embryo transfer to genetic improvement programmes in dairy cattle was investigated. Traditional progeny testing schemes and new Multiple Ovulation and Embryo Transfer (MOET) nucleus schemes were considered.

Previous studies have shown that using MOET to increase the probability of producing a bull calf for progeny testing may increase the response to selection because fewer bull dams, each of higher genetic merit, are needed. This study has shown that the response may be even higher in practice because their daughters (bred by MOET) are of higher genetic merit and consequently, many may be selected as bull dams in the next generation and also, their records can be used to provide a sib test for their brothers.

Compared with an efficient progeny testing scheme in steady state equilibrium, it was shown that responses from setting up an adult MOET nucleus scheme (selection after first lactation) were quite small in the short term but were significant in the long term. For the juvenile MOET nucleus scheme (selection before first breeding), both the short and long term responses were substantial.

Closed adult nucleus schemes with discrete generations of single trait selection were investigated using Monte Carlo simulation. Eighteen schemes, utilising hierarchical mating designs with one son per dam eligible for selection and requiring 128-2048 embryo transfers, achieved 0.6-1.3% annual rates of response with 0.8-2.3% annual rates of inbreeding. Detailed analysis of six of these schemes revealed that simple deterministic predictors, assuming base generation variances and large population sizes, overestimated response by 40-67%. More realistic predictors, accounting for the effects of finite numbers, inbreeding and selection, were within 4%

of the simulated response. It was shown that factorial mating designs increased response and that using more than one male from a selected sibship reduced inbreeding. The combination of these two strategies (factorial sibship schemes) increased response and reduced inbreeding. Variation in family sizes in nucleus schemes brought about by differences in sex ratios, in survival rates and by variation in embryo numbers per donor had little impact on response. The proportion of selected cows that yield no embryos was shown to be of most importance.

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CHAPTER 1

INTRODUCTION

1. REVIEW OF THE USE OF EMBRYO TRANSFER IN THE GENETIC IMPROVEMENT OF DAIRY CATTLE

One of the restrictions to genetic progress in cattle has been the inability of a cow to produce more than one offspring, on average, per year. However, with the development of reliable embryo transfer (ET) techniques in the 1970s, this limitation has been removed.

It is now routine procedure for a cow to be given a hormonal treatment which results in the shedding of a larger number of eggs than normal. Following insemination, the fertilized eggs (embryos) are recovered from the uterus by flushing and subsequently, either directly or after a period of frozen storage, are transferred to recipient cows. On average, six good embryos can be expected from each flush, and a 70% conception rate achieved from embryos transferred (Christie, W., personal communication; Hasler et al., 1987). Although these figures are a significant improvement on those in the past, the full potential of the technique is still unexploited, since there are over 20000 follicles in the ovaries of heifers (Salisbury et al., 1978).

Two distinct methods of applying ET to dairy cattle breeding have been presented in the literature. The first incorporates ET into a conventional progeny testing scheme. The second involves the use of ET in an elite herd, and selection of animals at an earlier age on family information. The aim of this study is to review previous work on the application of the different methods to the genetic improvement of dairy cattle and the evaluation of their

relative merits.

I. USING ET TO INCREASE GENETIC PROGRESS IN A CURRENT PROGENY TESTING SCHEME

In a conventional progeny testing scheme, each sire is evaluated on the first lactation records of many daughters spread over several herds. When these records become available, the sire is usually around six years of age. Of the tested bulls, only the best are used to breed the next generation of young bulls for progeny testing.

These young bulls are bred from a small number of genetically superior cows in the population. Approximately six bull dams are needed to produce each young bull for progeny testing (Hinks, 1978). Most cows in the commercial population are needed to breed female replacements.

Rendel and Robertson (1950) showed that the annual genetic response (ΔG) from a breeding programme operating for a sufficient length of time to be in a steady state could be calculated from $\Delta G = (I_{BB} + I_{BC} + I_{CB} + I_{CC})/(L_{BB} + L_{BC} + L_{CB} + L_{CC})$, where I refers to the genetic superiority of the selected animals and L to the generation interval along each of the four selection pathways. BB and BC refer to the bull to breed bull and bull to breed cow pathways while CB and CC refer to the cow to breed bull and cow to breed cow pathways. I is a product of (a) the accuracy of selection (r), which depends on the information available on the animal being evaluated, (b) the genetic standard deviation (σ_g), which depends on the additive genetic variance of the trait of interest and (c) the intensity of selection (i), which depends on the proportion of animals selected.

Three main ways have been proposed by which a conventional

progeny testing scheme could be improved by ET (i) by increasing the selection intensity on the cow to breed bull pathway, (ii) by increasing the selection intensity on the cow to breed cow pathway, and (iii) by providing further information for evaluation of animals.

1. Using ET on the cow to breed bull pathway

ET is currently used to produce a high proportion of young dairy bulls for progeny testing in some countries e.g. in Canada (58%), the USA (50%) and France (50%), and is used to a lesser extent or not at all in others (Cunningham, 1987).

By using ET on bull dams, the probability of getting a male offspring suitable for progeny testing from each bull dam is greatly increased, depending on the number of eggs transferred. Thus, the number of bull dams selected can be much smaller, and selection intensity and response can be increased. Assuming that the cow to bull pathway is responsible for about 25% of total genetic response, Hill and Land (1976) and Cunningham (1976) shows that additional gains of 2-10% could be obtained from ET, depending on the original selection intensities on bull dams and the increase in reproductive rate.

Hansen (1976) and Petersen and Hansen (1977) studied the effect of using ET on the cow to bull pathway in a population of 500,000 dual-purpose cattle (i.e. selected for both beef and dairy traits). In their scheme, 400 young bulls were tested for daily gain, and 40% of these were selected to be progeny tested for milk fat yield. The number of bull calves per bull dam was varied from 0.5 (normal reproduction) to 10 (with embryo transfer), while keeping the total number of young bulls available for selection constant. They showed that when keeping the relative response per annum for daily gain constant, fat yield could be raised by up to 15% due to increased selection

pressure on bull dams.

However, the degree of improvement depends on the effectiveness of bull dam selection previous to applying ET. Thus, Cunningham (1976) examined a similar situation to that of Petersen and Hansen (1977), but with a more intense selection of bull dams, and found that using ET had a reduced impact on rates of genetic progress. Petersen and Hansen (1977) also showed that these responses could yield considerable economic benefits, but the costs of ET were not taken into account. Inbreeding was not considered in these studies, which could be a problem in the schemes with the highest genetic gains, where as few as 50 bull dams supply the 400 bull calves for performance testing.

Krausslich (1976) similarly modelled a dual-purpose system with young bulls produced by ET. He found that the use of ET could increase genetic gains by 5 to 10%. Furthermore, these could be raised up to 20 to 25% if combined with cyclical inbreeding, where sire-daughter or brother-sister matings would be used to allow selection between partially inbred sons, as proposed by Dickerson (1973). But although the increase in genetic variance due to inbreeding was included, the decrease in genetic variance due to selection (Bulmer, 1971), which would be significant, was ignored.

However, the genetic gains outlined above may be lower in practice, due to uncertainty about the true genetic merit of high-yielding cows. Bradford and Kennedy (1980) pointed out that since potential bull dams lie at the extreme edge of the phenotypic distribution, it is much more difficult to evaluate them accurately than cows at other parts of the distribution. Cunningham (1976) stated that it is doubtful whether the superiority of bull dams selected very intensely can be calculated assuming a normal distribution of underlying genotypic values. Similarly, Van Vleck

(1986) suggested treating cows that are 3 to 5 standard deviations above the herd level with caution, and he emphasised the importance and difficulty of distinguishing between genetically superior cows and those given preferential treatment, and so biasing the records upwards.

2. Using ET on the cow to breed cow pathway

Due to the very high proportion of cows currently needed to breed replacement females, the genetic contribution of the CC pathway is minimal. Thus, considerable scope exists for increasing genetic response by applying ET on this pathway. However, the current high costs of ET rule out this possibility unless ET becomes far less expensive.

Cunningham (1976) stated that using ET on the cow to cow pathway to increase the reproductive rate 20-fold could increase genetic gain by 15 to 30%, assuming the pathway contributes 5 to 10% to the total genetic gain. McDaniel and Cassell (1981) demonstrated that in a 100-cow herd with five ET offspring per cow, the selection intensity in the cow to cow pathway is increased three and seven fold when, without ET, 70 and 90% of cows are needed to breed replacements respectively. Nevertheless, they showed that the economic benefits are negligible when compared to applying ET on the cow to bull pathway.

Van Vleck (1981) calculated the expected net present value of genetic gains made by breeding replacement females with ET, using several discount rates and time periods. He showed that although the net present value of returns was greater when ET was used, the costs of the ET work were far greater. He therefore concluded that the use of ET on the cow to cow pathway could only become economically feasible if these costs were reduced by a large

multiple.

Navarro-Fierro et al., (1986) calculated the increase in milk yield, adjusted for frequency and production of different age classes, over a 20-year period from cows bred using ET. The number of offspring per donor was varied from one up to 100. To measure the response from selecting female replacements only, they assumed that the genetic merit of bulls used was the same with or without ET. They concluded that even after 20 years and with high reproductive rates, the increase in milk yield would not compensate for the direct cost of ET, or indirect costs such as loss in milk production while flushing the best cows.

Using ET on the cow to breed cow pathway in a national breeding programme seems even less desirable than in a single herd. Hill and Land (1976) pointed out that, of necessity, most of the commercial population would become recipients, and that to carry out an operation on such an immense scale would require considerable improvements in ET technology. Van Vleck (1981) also suggested that by using ET over the whole population, the amount of semen used and sold would be substantially reduced, leading to an eventual reduction in numbers of bulls being progeny tested. Thus, genetic progress in the cow to breed offspring pathways would be made at the expense of the bull to breed offspring pathways.

McDaniel and Cassell (1981) suggested that if cytoplasmic inheritance is shown to be important for dairy traits, gains from breeding replacement females by ET would be higher. However, to date the importance of cytoplasmic inheritance has not been proven. Bell et al. (1985) analysed milk records from six herds, all of which had been closed on the female side for at least 30 years, and concluded that cytoplasmic inheritance accounted for 2, 1.8 and 3.5% of the total variation for milk yield, fat yield and fat percentage

respectively. However, Kennedy (1986) showed that these results could be explained by random genetic drift alone. Huizinga et al. (1986) also claimed to have found evidence for the presence of cytoplasmic effects in milk production traits, but as in the study of Bell et al. (1985), random genetic drift was not taken into account. Reed and van Vleck (1987) compared daughter-dam and daughter-granddam heritability estimates, and found no evidence that cytoplasmic inheritance influenced milk production traits of dairy cattle. Analysis of data on cows bred from ET should prove very useful in determining if cytoplasmic effects, and other effects such as dominance, are important in dairy cattle.

3. Using ET for evaluation of animals

The development of ET techniques has opened up new possibilities for evaluating both dams and sires.

(a) Dam evaluation

Since a donor can have several daughters by ET, this allows progeny testing of individual cows. Powell (1981) showed that adding 10 daughter records to a cow index, which had data on the cow (one record), her dam ($r = 0.66$), her sire ($r = 0.97$) and her maternal grandsire, would increase the accuracy of the index by 7 and 13% when the daughters were recorded all in one herd or in separate herds respectively. With 50 daughters, these increases in accuracy rose to 10 and 33%.

When the number of individual records on the cow to be evaluated is increased, the relative effect of adding daughter records is reduced. On the other hand, if a cow is evaluated on her own performance only, instead of on a family index, the benefits from adding progeny test data are much higher (Bradford and Kennedy, 1980). McDaniel and Cassell (1981) concluded that although progeny

records should be used if available, there would be no advantage in delaying selection decisions to wait for them, since the large increase in generation interval would result in an overall reduction in annual genetic gain.

An alternative way that ET can be used in cow evaluation is to increase the number of full- and half-sib records (Powell, 1981). For example, if one sire is bred to four donors, each producing four daughters, then each cow evaluated has three full-sibs and 12 half-sibs. The accuracy of selection from an index including one lactation record of the cow with her full- and half-sib records is about the same as using three records on the cow. The major advantage of this is that the cow selected on the family index is two lactations younger than the cow selected without sib information. Thus, using ET in this manner gives us the opportunity to reduce the generation interval without suffering a loss in accuracy of cow evaluation. This strategy is central to the MOET nucleus schemes considered later.

(b) Sire evaluation

Since sires are currently evaluated with considerable accuracy, there seems, at first glance, to be less scope for improvement using ET. If dam records are included in evaluating sires, progeny testing of dams should increase the accuracy of evaluation (Powell, 1981), but not substantially.

A more useful way in which sire evaluation could be improved is with full- and half-sib data, which would be available much earlier than the sire's progeny test results. After being mated to a wide range of cows from the commercial population when about one year old, males usually have to wait a further four to five years before their daughters complete their first lactation, and the males can be selected. Smith and Ruane (1987) suggested that bulls for

commercial use could be selected from those evaluated on full-sib records when aged about three years, and those evaluated on progeny test data when aged about 5.5-6 years. They found that with 3 to 7 full-sister records available per bull, the genetic merit of the bulls selected for commercial use was 10 to 20% higher than when selection was restricted to bulls evaluated on progeny test data alone. This increased response was a consequence of the reduced generation interval.

(c) Problems

There may well be problems associated with using ET information to evaluate animals. Powell (1981) pointed out that the records of animals born from ET could be subject to bias due to preferential treatment, owing to the relative rarity and expense of ET. Also, accuracy of evaluation may be reduced since management constraints may prevent the spread of a donor's offspring over several herds. Powell (1981) warned that progeny testing of sires could be biased if many of the daughters are bred using ET from a few genetically superior donors. If sib information is used for evaluating animals, there is an increased probability of related individuals being selected, leading to an increase in inbreeding (Burrows, 1984), but with a large breeding population this should not be a serious problem.

II. GENETIC RESPONSE POSSIBLE WITH A MOET NUCLEUS HERD

1. MOET nucleus schemes

Potentially the best way that ET can be used to speed up genetic progress in dairy cattle is by setting up a multiple ovulation and embryo transfer (MOET) nucleus scheme. This involves creating a nucleus herd of elite males and females, concentrating testing and selection in the herd, and selecting at an early age

using family information.

Nicholas (1979) was the first to examine the possible impact of a MOET nucleus scheme on dairy cattle improvement. He showed that rates of gain equal to those possible from an efficient national progeny testing scheme could be made in a 500-cow herd. This idea was later elaborated (Nicholas and Smith, 1983) and since then, MOET nucleus breeding schemes have been the subject of much interest. Practical MOET nucleus herds have been established in Denmark, France and the United Kingdom.

The basic scheme of Nicholas (1979) was similar to that suggested by Land and Hill (1975) for beef cattle. For the beef system, Land and Hill (1975) assumed a fixed number of cows in the herd, with non-selected females used as recipients. Thus, the selection intensity of females was dependent on the number of eggs transferred per donor and on the total herd size. Animals of both sexes were chosen by mass selection with a generation interval of two years, the minimum possible for beef cattle.

Nicholas (1979) examined the effect of using ET and a family selection index on the genetic response for a sex-limited trait in a 500-cow herd comprising both donors and recipients. In all three schemes outlined, females were selected on their dam's first lactation record, with a short generation interval of two years but with a low accuracy of selection ($r = 0.25$). Males were selected on their dam's first record (pedigree selection scheme) or on a family index utilising full-sib, half-sib and dam records, with a generation interval of 3.6 years (sib selection scheme). In the third scheme, the nucleus herd supplied 30 young bulls for progeny testing, and nucleus replacements were bred both from young males selected on their dam's first-lactation record and from the top two progeny tested sires. Each selected male was mated to eight donors.

Nicholas (1979) showed that the genetic response possible was substantially higher from all three schemes than from a progeny testing programme in the herd, and could even be as high as from a national progeny testing scheme. Of the three schemes, the pedigree scheme was always the least effective, and the sib scheme was only superior to the third scheme including progeny testing when the number of eggs per donor was high (leading to an increased selection pressure on males and females).

Annual inbreeding rates ranged from 0.15 to 1.2%, and were highest for the pedigree scheme and lowest with progeny testing of sires. However, these rates are probably underestimated. In all three schemes, each female would have the same estimated breeding value as her full-sisters, since only dam performance is used in evaluation. Similarly, full-brothers would be ranked together in the sib and pedigree schemes. Thus, selection is between full-sib groups rather than between individuals and, due to selecting full-sibs, inbreeding rates would be considerably higher than calculated.

The schemes of Nicholas (1979) were expanded by Nicholas and Smith (1983) into two further schemes. In the first scheme, instead of selecting on the dam's first lactation record only, the pedigree scheme was modified to allow selection of both sexes at 12 months of age using information from the dam's family, i.e. the dam's own record, her sisters' records, her half-sisters' records and her dam's records. This they called the juvenile scheme.

In the sib scheme proposed by Nicholas (1979), males were selected on their full-sibs', half-sibs' and dam's records. This was retained in the second scheme described by Nicholas and Smith (1983). In addition, females were to be selected on the same information plus their own first lactation record, giving a

generation interval of 3.67 years. This they called the adult scheme.

Genetic gains possible were calculated for various numbers of offspring per donor and donors mated per male. They demonstrated that higher rates of genetic gain (by up to 80%) could be made in MOET nucleus schemes compared with a national progeny testing scheme. Rates of improvement in the juvenile scheme were higher than in the adult scheme, emphasising the benefits of reducing the generation interval. By including information on the sire's family, instead of only the dam's, the advantage of the juvenile scheme would be increased even more (Woolliams and Smith, 1988).

Rates of response from these studies were calculated assuming that the MOET nucleus and progeny testing schemes were running for a sufficient length of time, so that both were in steady-state equilibrium. Ruane and Smith (1989) examined the genetic response possible from using bull parents (BB and CB) from an efficient steady-state progeny testing scheme to set up a MOET nucleus breeding herd, and compared it to the response expected if the bull parents were used, as normal, to produce young bulls for progeny testing. They found that the differences in genetic response of animals at birth were small for the adult scheme but substantial for the juvenile scheme over the first 10 years. After 20 years, the genetic response of MOET-bred stock over stock bred in the progeny testing scheme was about 55% (juvenile scheme) and 20% (adult scheme).

Nicholas and Smith (1983) reduced the problem of inbreeding by allowing only one male to be eligible for selection from each donor. This lowered the intensity of selection in males. No restriction was placed on females. In the juvenile scheme, all females in a full-sib group will rank the same and be selected, which

will raise inbreeding rates. In addition to the problem of selecting full-sibs, using a family index will increase inbreeding rates, since related individuals will be evaluated on overlapping information, resulting in relatives being ranked closely together (Burrows, 1984).

Although the theoretical rates of progress predicted for the MOET schemes are quite high, there are factors affecting these rates which were not taken into account. By selecting on a family index in a small population, the selection intensity is reduced (Hill, 1977a). In addition, rates of inbreeding and hence inbreeding depression are both increased. Another danger, due to the small population size, is that of genetic drift leading to the chance fixation of genes and increased variation in the response to selection, so that the response in any individual scheme is uncertain (Nicholas, 1980).

Juga and Maki-Tanila (1987) simulated an adult MOET scheme with 128 females and 32 males eligible for selection each generation. Although not taking account of the reduction in response or variance due to inbreeding, the genetic gain was still substantially lower than predicted from formulae assuming the population to be improving at a constant rate, as used by Nicholas and Smith (1983). For example, with four sires selected, eight donors mated to each sire and eight progeny per donor, the response was reduced by over 33%. The most likely reason for the reduced response is that the extensive use of family information, combined with the small population size, effectively resulted in selection between families rather than between individuals.

If population size is the major limitation to genetic progress, the question must be addressed as to how large the population should be before there is a significant probability of

getting all or most of the expected genetic gains. This problem is discussed by Nicholas (1980). In the juvenile scheme, with much shorter generation intervals and total dependence on family information for evaluating candidates for selection, these problems are likely to be exacerbated.

Annual genetic gain is calculated by summing the genetic superiorities of selected animals and dividing by the summed generation intervals. In a MOET nucleus scheme, where animals are young when selected, there may be an increase in annual genetic gain from further reducing the generation intervals through using part-lactation records of performance, depending on the reduction in genetic merit of selected animals. The genetic and phenotypic correlations between part- and full-lactation milk yield are quite high (e.g. Auran, 1976), and so the potential benefits from selecting on part-records in MOET nucleus schemes should be investigated.

Selection index theory has been used in previous studies for evaluating response in MOET nucleus schemes. In practice, Best Linear Unbiased Prediction (BLUP) methods would be preferred. These would allow for the spread of animals over different spatial and temporal groups, for the genetic trend in the population, and for the inclusion of information on all relatives and ancestors in evaluating animals. Kennedy and Schaeffer (1988) examined the possible effects of new technologies such as ET, cloning, sexing and gene tranfer on the genetic evaluation of animals, and showed how existing BLUP procedures should be modified to deal with them.

Other questions have still to be answered regarding the actual running of the MOET scheme, such as whether selected donors or sires should be eligible for selection for more than one year, and what effect this would have on rates of inbreeding and response. Also, it is extremely unlikely that all transfers would be carried

out together, and so this would probably lead to transferring blocks of embryos over the whole year. It would be important to manage the transfer of embryos so that all offspring could be accurately evaluated and response optimised.

Large variation has been found in the number of eggs recovered from any flush (Seidel, 1981). Thus, a practical problem which should be considered is whether it is preferable to carry out a fixed number of flushes on each donor or to continue flushing until all or a fixed number of donors give a certain minimum number of eggs. The first strategy should lead to increased variation in family size, the second to a slightly extended generation interval.

There will also be variation in the sex ratio within individual families. Like variation in embryo numbers per flush, this may also affect both the accuracy and intensity of selection. For example, if each transferred embryo has a 50% chance of survival to selection, the sex ratio is 1:1 and six embryos are transferred, there is an 18% chance of getting no females for selection.

No studies have yet been carried out on the implications of these two sources of variation of family structure for response in the MOET nucleus scheme. These problems are likely to be more severe in the juvenile scheme than in the adult scheme, because fewer embryos can be recovered from a young, immature donor than from a mature donor (Gordon, 1983).

2. Hybrid MOET-progeny testing schemes

The idea of using the MOET nucleus herd to produce young bulls for progeny testing, as proposed by Nicholas (1979), has been developed by Christensen (1984) and in great detail by Colleau (1985). In the MOET x conventional hybrid schemes of Colleau (1985), the generation interval for females is low, and the nucleus

herd is used to produce all young bulls needed for progeny testing. Only progeny tested sires are used for breeding. He described three schemes. In all three, nucleus females are selected to produce both the young bulls and the nucleus female replacements.

In scheme A, all nucleus females are flushed twice, when 16 and 18 months old, and then put in calf at 20 months. After 6 months of the lactation, donors are selected on their own performance assuming a genetic correlation of unity between a six-month and a full-lactation record. At selection the donors' offspring are 9 months old, and so the generation interval is substantially reduced. This reduction is made possible by transferring embryos from all females, without knowing at the time whether or not they will be selected.

In scheme B, embryos are transferred from donors after selection based on their first lactation record. Thus, the generation interval is almost doubled compared to scheme A, but the number of embryos transferred, and hence recipients needed, is substantially reduced. The third scheme B′, is the same as scheme B, but with an equal number of embryos transferred as in scheme A. These schemes were compared with a highly efficient progeny testing scheme and the juvenile scheme described by Nicholas and Smith (1983), although with a slightly longer generation interval than they proposed.

When the schemes are compared keeping the total number of transfers constant, scheme A is at least 10% superior to the progeny testing scheme over a wide range of donor family sizes and is always better than B′ and B. When the number of offspring born per donor is low, scheme A is superior to the juvenile MOET nucleus scheme, but with high numbers of offspring the juvenile scheme is best.

The reranking of the schemes according to the number of

offspring per donor is due to the higher sensitivity of the MOET nucleus scheme to ET success rates compared with the hybrid scheme. This sensitivity is a consequence of the dependence of genetic gain in the MOET nucleus schemes on only two pathways, both using ET. With the hybrid schemes, the bull to cow and bull to bull pathways are unaffected by variability in ET rates.

Truncation selection reduces the genetic variance in parents by a factor of $1-kr^2$, where r is the accuracy of selection and k is a term which depends on the selection pressure applied and which increases as selection becomes more intense (Bulmer, 1971). Colleau (1985) showed that the reduction in genetic variance for the juvenile MOET scheme was almost negligible compared with that for the progeny testing and MOET hybrid schemes, due to the lower accuracy of selection of animals of both sexes. When the reduced genetic variance was accounted for, he demonstrated that the annual genetic gain in the juvenile MOET nucleus scheme compared with the progeny testing and hybrid MOET schemes was increased by about 25 and 20% respectively. Accounting for the Bulmer effect in the adult MOET nucleus scheme would also increase genetic gains relative to the schemes with progeny testing, but to a lesser degree than the juvenile MOET nucleus scheme, because animals are evaluated with greater accuracy.

Annual rates of inbreeding were much lower in the hybrid schemes than in the juvenile scheme, due to the longer generation interval. Of the three hybrid schemes, the inbreeding rate was highest for A, due to the shorter generation interval on the female side.

Colleau (1986) examined the effect on response of opening up the nucleus in scheme A to foreign genetic material. He showed that if genetically superior bulls, progeny tested in a foreign population

were available for use in the nucleus, this would allow a much more rapid diffusion of their superiority throughout the population than with a conventional progeny testing scheme. This would be a considerable advantage for a country with a population lagging behind in genetic merit that wished to upgrade its stock. Dissemination of superior foreign genes to the commercial herd would be even faster with MOET nucleus schemes (Nicholas and Smith, 1983) than with MOET hybrid schemes since the generation interval on the bull to commercial cow pathway is considerably shorter.

Christensen (1984) and Christensen and Liboriussen (1986) also favoured a hybrid scheme over a pure MOET nucleus scheme. They found that even with high rates of genetic gain in the nucleus, moderate selection pressure on progeny tested bulls was sufficient for their breeding values to be superior to those of young bulls within the nucleus. However the comparison they made was between the average genetic merit of selected progeny tested bulls and of unselected nucleus bulls, which biased calculations in favour of the progeny tested bulls.

3. Other aspects of MOET and dairy cattle breeding

(a) Physiological indicators

Genetic progress for dairy traits has been hampered by the fact that they can only be measured in the female. If it was possible to measure a trait significantly correlated with milk yield in both sexes before reproductive age, this would be advantageous. Studies on thyroxine degradation rates and more recently on blood urea nitrogen levels suggest that such a trait may exist. Woolliams and Smith (1988) studied the effect of an indicator trait, such as blood urea nitrogen level, on genetic response for milk yield. They showed that the possible increase in genetic gain due to using the

indicator trait was greater with MOET nucleus schemes than with progeny testing schemes. In comparing Nicholas and Smith's (1983) adult and juvenile MOET nucleus schemes, the effect of an indicator trait on the juvenile scheme was most favourable.

The increases in response were achieved by adding individual and family measurements of the indicator trait to the family index for milk yield. In the juvenile scheme, even when including the sire's family information, the accuracy of selection is low, leaving considerably more scope for improvement than in the adult scheme. This increased accuracy explains the greater response.

(b) Other factors in MOET nucleus versus progeny testing schemes

The dependence on a single herd in MOET nucleus schemes for genetic progress allows a greater degree of control over selection than in a conventional progeny testing scheme. By controlling the environment, heritability should increase, and so improve the accuracy of breeding value estimation (Christensen and Liboriussen, 1986). However, the possibility of genotype by environment interaction arising must be guarded against by testing and selecting in commercial conditions.

A problem of far greater possible consequence is that of disease occurring in the MOET nucleus herd. To prevent this, stringent health regulations must be applied. Nicholas and Smith (1983) also suggest keeping nucleus stock of different ages in different locations. This should reduce the impact of any outbreak of disease.

Van Tassell and Van Vleck (1987) estimated the actual genetic gain that has been made for milk production in progeny testing schemes, and found that the gap between theoretical and actual progress was substantial. Preferential treatment of animals,

selection for other traits and selection of parents of bulls with lower-than-possible selection intensities and at an advanced age were all responsible for the gap. With a MOET nucleus scheme, these problems can be minimised, and the gap between theoretical and actual genetic progress narrowed.

It should be possible in MOET nucleus schemes to select for economically important traits normally not included in dairy cattle breeding programmes. In the current climate of quotas in milk production, selection for food conversion efficiency and for beef traits may be worthwhile.

In general, the lower the effectiveness of a current progeny testing scheme, the greater the impact that ET can have. It could also be argued that there is a greater need for an efficient breeding scheme to replace it. In a country lacking the infrastructure necessary to run an effective national progeny testing scheme a MOET nucleus scheme, due to its centralised nature would be a useful alternative (Hinks, 1978; Land, 1986).

c) Other advantages and potential developments of ET technology

In this study, the potential impact of ET on genetic gain alone has been examined. It may also prove beneficial in other ways. The problem of getting offspring from high yielding cows that are infertile, due to disease or injury, may be overcome using ET. For example, it may allow brucellosis-positive donors to have brucellosis-negative offspring (Youngs et al., 1986). Also, female carriers of harmful recessive genes causing diseases such as bovine syndactyly can be detected by progeny testing with ET (Johnson et al., 1980).

ET can also be used for the expansion and conservation of rare or valuable stocks. Indeed, the initial role of ET in North

America in the 1970s was in the production of high-priced animals from the continental beef breeds. Many arguments have been put forward for the conservation of rare livestock breeds, such as the advantages it could offer in meeting possible changes in future market requirements. The storage of frozen embryos and their expansion when needed could prove a useful method of conservation (Smith, 1984).

ET can be used to increase the twinning rate by transferring two embryos to each recipient. If one embryo is placed in both uterine horns of an unmated recipient, twinning rates in pregnant recipients of more than 70% can be achieved (Anderson et al., 1979). The net result is an increased number of progeny per donor without having to increase the recipient herd size. Alternatively, it could be used as a strategy to produce the same number of offspring but from a smaller recipient herd. The main disadvantage of twinning is the high proportion of freemartin heifers produced when embryos of opposite sex are transferred together. However, depending on ET success rates, the actual number of fertile females available for selection may not be reduced compared to the situation where each recipient received only one embryo. Embryo sexing would solve the freemartin problem, and twinning could be a very useful breeding strategy.

The technique of splitting bovine embryos has been available since 1981, but has not been used widely so far. Currently, embryos are seldom split more than twice, producing four genetically identical embryos. The net result is a greater number of offspring per donor, despite the lower survival rates of split embryos compared to whole embryos. Currently, the application of this technique to dairy cattle breeding seems limited. The intensity of selection is not increased, since the animals are genetically identical.

However, it can be used to improve the accuracy of selection. Split embryos can also be used to estimate maternal effects, genetic trends and genotype-environment interactions (Brem, 1986).

Some attention has been paid to the potential applications of clones produced by the further development of embryo splitting (Nicholas and Smith, 1983) or cell culture techniques (Van Vleck, 1981). The potential gains described give a very substantial genetic lift. Using selected clones in the commercial herd could increase genetic merit by over 25% (Nicholas and Smith, 1983). Van Vleck (1981) warned that the validity of quantitative genetics theory may be doubtful when selecting animals for cloning which are several phenotypic standard deviations above average.

Nicholas and Smith (1983) suggested one method for selecting cloned animals which should overcome any such problems. Firstly, the best animals in the population would be selected to produce embryos which would be the potential candidates for cloning. Each embryo is then split several times, some are stored and some are transferred. Selection between clones is made on the basis of first lactation records. The remaining cloned embryos of the selected clones are then further multiplied and supplied to the commercial herd. The genetic variance of the breeding population can be maintained by keeping the same numbers of selected females (clones) and males as in a conventional breeding system.

Although it is not yet possible to sex sperm or embryos reliably prior to transfer, these techniques may be available in the near future. In addition to preventing freemartins with twinning, sexing could also reduce the number of embryos transferred and recipients needed. If selection of males is restricted for inbreeding purposes so that only one son per donor is eligible for selection, the number of male embryos transferred can be greatly

reduced.

SUMMARY

The development of a technology which enables us to increase the reproductive rate of the cow will have a considerable impact on genetic improvement in dairy cattle. However, by applying this ET technology to an efficient current progeny testing scheme, little extra gain can be made. Instead alternative breeding strategies must be designed which exploit the novel opportunities the technique presents. Two such schemes are the MOET nucleus and the MOET hybrid breeding schemes. Based on current ET success rates, both schemes should yield rates of genetic response superior to those possible from current progeny testing schemes.

However, by selecting animals in a MOET nucleus scheme from a small population using family information, potential problems such as inbreeding, random genetic drift and reduced selection intensities may be quite significant. These problems are likely to be greater in the juvenile (selection before first breeding) than in the adult (selection after first lactation) MOET nucleus schemes. More work is needed to determine how serious a danger these potential problems represent to genetic progress, and how they can be reduced or overcome.

Improvements in ET technology have been quite considerable in recent years, and should be even greater in the future. Lu et al. (1987) described a reliable in vitro fertilization system for bovine embryos which makes it possible to accumulate large numbers of embryos for reseach purposes at a low cost. Thus, for example, it should soon be feasible to recover much higher numbers of embryos per donor, sex them, and split them as often as required. Breeding schemes using ET will be at an advantage since they will be able to

adopt these new technologies rapidly. These developments will further enhance the merits of the MOET nucleus schemes in which all genetic gains are derived from pathways using ET, compared with the MOET hybrid schemes, where only two of the four pathways depend on ET.

2. UPDATE OF REVIEW

Since the review was written (about nine months after starting the project) there has been continued interest in the use of embryo transfer for the genetic improvement of dairy cattle both in theory and in practice. As an indication of this, a seminar focussing on the topic entitled "new selection schemes in cattle : nucleus programmes" was held in Kiel in December 1988 under the auspices of the European Association of Animal Production.

The seminar revealed that many European countries had set up or were planning to set up breeding schemes involving extensive use of embryo transfer. All the schemes described are likely to be open rather than closed and most will evaluate females over several herds rather than in a single herd. Such schemes were designed to improve the cow to breed bull pathway in the conventional progeny testing scheme and they differ considerably from the MOET nucleus schemes envisaged by Nicholas and Smith (1983).

Most recent theoretical work has been directed towards studies of MOET nucleus schemes. Woolliams (1989) used deterministic methods to examine the implications of altering the population structure on response and inbreeding rates in adult and juvenile MOET nucleus schemes. He found that the designs proposed by Nicholas and Smith (1983) could be improved.

Four sires and 36 dams were selected and the number of sires mated to each dam was changed from one (hierarchical design) to two or four (complete factorial design). With factorial mating designs, the number of sire x dam mating combinations and sibships produced are increased but the sibship size is reduced.

His results were similar for adult and juvenile schemes and depended on whether the number of male candidates was restricted. With one male per sibship eligible for selection and two or four

sires mated to each dam, response was increased by 9-19% compared to the hierarchical design, because of the increased number of male candidates, while inbreeding rates remained constant.

When factorial mating designs were used and there was no restriction on the number of males per sibship eligible for selection, the number of male candidates, and hence response, was unchanged. However, because the possibilities of selecting full sibs were reduced, inbreeding rates were 15-22% lower.

These results were calculated assuming that factorial mating designs had no effect on generation intervals. In some situations they might be extended and consequently the advantages of factorial mating designs would be reduced.

The inbreeding rates predicted were over 6% per generation and were derived using new methods developed to account for the effects of selection. The response rates were calculated accounting for the impact of finite numbers and the family structure on selection intensities but ignoring the effects of inbreeding and selection on genetic variances.

Much work has also been devoted to simulating MOET nucleus schemes. Jansen and Schlote (1987) simulated adult nucleus schemes of various sizes, assuming that milk yield was controlled by 32 independent loci with two alleles per locus.

For comparable schemes, responses were lower than Juga and Maki-Tanila (1987) predicted because candidates were evaluated with less information. Females were selected on their own first lactation records only while males were selected on full sib family means. Compared to responses expected, assuming base generation genetic variances and large numbers of candidates, the reductions in response were of a similar order to those found by Juga and Maki-Tanila (1987). Another simulation study was carried out by

Ruane and Thompson (1989). Their results are described later in this thesis.

Toro and Silio (1989) were the first to simulate juvenile MOET nucleus schemes. Their genetic model was very similar to that of Jansen and Schlote (1987), having 30 independent loci with two alleles per locus.

They showed that the differences between simulated and expected results in juvenile schemes were even greater than found with simulations of adult schemes. Using a pedigree index containing information on both parents, simulated responses were 17-59% lower than expected while inbreeding rates were three to five times higher. Compared to adult schemes of equal size simulated by Ruane and Thompson (1989), increased rates of response were achieved but with considerably higher inbreeding rates.

They also examined various alternative selection strategies. Of these, they showed that using an indicator trait strongly correlated with milk production would be most beneficial. When selecting on an index combining information on milk yield and the indicator trait, response was increased by about 60% and inbreeding rates were reduced by about 40%.

The continued interest in new breeding strategies has led to the reappraisal of traditional progeny testing schemes. Until quite recently, the substantial differences between realised and expected responses in conventional schemes were explained by factors such as preferential treatment or selection for many traits (e.g. Van Vleck, 1986). Deterministic (Meuwissen, 1989a) and simulation (Meyer and Smith, 1989) models now suggest that the reduction in variances due to selection (Bulmer, 1971) can explain much of these differences.

New strategies to increase rates of response in progeny testing schemes have also been suggested. By selecting potential

bull dams before or after their first lactation is completed, Colleau and Mocquot (1989) predicted that response rates could be increased by 17 or 11% respectively. Meuwissen (1989b) showed that if animals of all ages were eligible for selection and evaluated using the individual animal model, rates of response could be increased by 50%.

3. BRIEF OUTLINE OF THESIS

Chapters 2 to 4 model alternative breeding schemes using deterministic methods. Chapters 2 and 3 investigate some of the possibilities of using embryo transfer in conventional progeny testing schemes (on the cow to breed bull pathway). Chapter 4 examines the implications of switching from an efficient progeny testing scheme to a juvenile or adult MOET nucleus scheme.

Chapters 5 to 7 describe a Monte Carlo simulation study of an adult MOET nucleus scheme. Chapter 5 examines the simulation results in detail and compares them to expectations from deterministic models. The effects of employing alternative mating designs and selection strategies are described in Chapter 6. Chapter 7 examines the impact of changing the family sizes.

CHAPTER 2

USE OF SIB TESTING AS A SUPPLEMENT TO PROGENY TESTING TO IMPROVE THE GENETIC MERIT OF COMMERCIAL SEMEN IN DAIRY CATTLE

INTRODUCTION

In breeding young bulls for progeny testing, multiple ovulation and embryo transfer (MOET) is often used to increase the probability of getting a suitable young candidate bull from designated selected contract matings. At the same time a number of full sib sisters, and several half sibs, will be produced. These sibs will have their first lactation records complete when they, and their brother are 3 years of age, some 2.5–3 years before the progeny test on the bull's daughters is available. The object of this study is to consider the use of a sib test as a supplement to the progeny test to improve the genetic merit of semen for commercial use from a bull stud. Use of MOET in breeding herds has been considered by Nicholas and Smith (1983), Colleau (1985), Christensen and Liboriussen (1986) and Woolliams and Smith (1988).

MATERIALS AND METHODS

The average genetic merit of young bulls for progeny testing should be higher than the mean of the previous generation of bulls, if there is a genetic trend in the population, or if there is effective selection of bulls and cows to breed the next group of bulls for testing. The distribution of estimated breeding values (EBVs) about the group mean depends on the accuracy of estimation (r). The standard deviation of the EBV distribution is simply rh (expressed in phenotypic standard deviation (SD) units) with h^2 the

heritability. Concern is with economic merit. Since this is highly correlated with milk yield, a heritability of 0.25 has been used for economic merit.

Rather than use semen only from progeny-tested bulls, it should be better to use the bulls with the best EBVs from both the sib-tested and the progeny-tested groups of bulls. The situation is illustrated in Fig. 1. The distributions of EBVs for progeny tested bulls and for sib tested bulls have means m_1 and m_2 respectively, with standard deviations s_1 $(=r_1 h)$ and s_2 $(=r_2 h)$, respectively. As the bulls are in yearly test groups in a continuous testing programme, the number in each group should be the same. Normally a proportion (p_1^*) of the progeny-tested bulls is returned to the active commercial stud and their average merit $M_1 = i_1^* s_1$, where i_1^* is the mean of the proportion (p_1^*) selected from a normal distribution (i.e. the selection intensity). The alternative is to take bulls with the best EBVs from the two test groups, such that the total number of bulls used is the same. Operationally this can be done by finding a common threshold point T for the two distributions (1 and 2) such that

$$T = m_1 + x_1 s_1$$

$$T = m_1 + (m_2 - m_1) + x_2 s_2$$

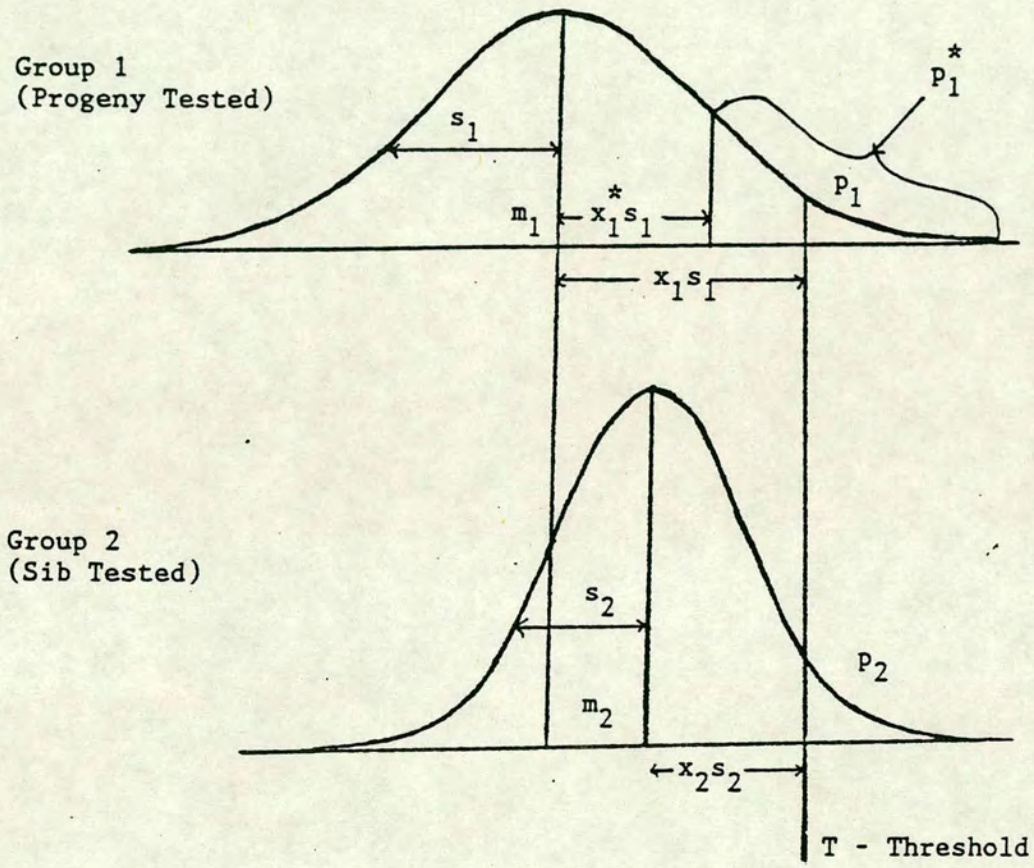
and

$$p_1^* = p_1 + p_2$$

where p_i is the proportion used from each distribution and x_i is the normal deviate corresponding to p_i. The threshold value T, for any particular case, can be found by trial and error using tables of the normal distribution. A computer program was written to do the calculations. The overall mean (M_2) of those used from the two

Figure 1.

Distributions of estimated breeding values and selection statistics



groups can then be calculated as

$$M_2 = \frac{p_1 i_1 s_1 + p_2((m_2 - m_1) + i_2 s_2)}{p_1 + p_2}$$

and the relative superiority (M_2/M_1) of the combined system evaluated.

For example, selecting the best 20% of progeny-tested sires gives $M_1 = i_1^* s_1 = i_1^* r_1 h = 1.40\ (0.88)\ (0.5) = 0.616$ SD units. With two groups of sires differing by 0.3 SD units ($m_2 - m_1$) and with $s_1 = r_1 h = 0.88\ (0.5) = 0.44$ and $s_2 = r_2 h = 0.5\ (0.5) = 0.25$, the threshold point T is 0.601 SD units, selecting $p_1 = 0.086$, ($T = 1.366\ (0.44)$) and $p_2 = 0.114$ ($T = 0.3 + 1.206\ (0.25)$). The genetic response using the two groups is

$$\frac{0.086(1.8248(0.44)) + 0.114(0.3 + 1.6918(0.25))}{0.086 + 0.114}$$

$= 0.758$ SD units

and the relative superiority is $M_2/M_1 = 0.758/0.616 = 1.23$ as shown in Table 1.

A range of genetic differences between the groups is used, representing different rates of genetic trend, or of selection in the breeding of that group of young bulls. Rates of genetic trend in bulls in the past have been estimated at about 0.05 SD units per year in North American populations, with current rates being higher at about 0.10 SD per year (Van Vleck et al., 1986). The rate of genetic change in the population possible by an efficient progeny testing system has been estimated at 0.126 SD units per year (Woolliams and Smith 1988). For a 2.5-year period between the sib

test and the progeny test, these trends correspond to genetic superiority of the sib test group of 0.125, 0.250 and 0.315 SD units, respectively. The population genetic trend includes the ineffective cow to cow selection pathway. With efficient selection of parents of bulls, the mean genetic superiority of sib-tested bulls over that of the progeny-tested bulls could be as high as 0.40 SD units.

Another variable to consider is the proportion of bulls normally used after progeny test for commercial use, and values of 0.05, 0.10 and 0.20 have been considered.

A standard progeny test with 50 effective daughters has been used, giving an accuracy of selection (correlation with true breeding value) of 0.88. Values for the accuracy of a sib test of 0.4, 0.5 and 0.6 have been used, corresponding to about 3, 7 and 19 full sisters, respectively. Information on sires and dams has not been added since it has already been used in breeding the young bull. However, there may be further records on the dam and there may be several half sibs bred by MOET from the same sire, and many more half sibs bred following the widespread use of the sire. All the information would be included in practice using best linear unbiased prediction (Henderson, 1984) to estimate breeding values, and this would add to the accuracy of the tests, but more to the sib test than the progeny test.

RESULTS

The results are presented in Table 1. The combined use of sib-tested bulls and of progeny-tested bulls increases the average merit of the bulls used. The relative genetic superiority of the combined scheme increases as the genetic difference between the sib and progeny test groups increases, as the accuracy of the sib test increases, and as the proportion of progeny-tested bulls normally

TABLE 1

Relative genetic superiority of semen from combined use of selected sib-tested bulls and progeny-tested bulls, relative to the use of progeny-tested bulls alone. The proportion of bulls in combined use which are progeny tested is also given (in parentheses).

Mean genetic superiority of sib-tested bulls over progeny-tested bulls* (SD units)	Proportion of progeny-tested bulls normally used								
	0.05			0.10			0.20		
	Accuracy of sib-test evaluation at 3 yr of age								
	0.4	0.5	0.6	0.4	0.5	0.6	0.4	0.5	0.6
0.075	1.00 (0.99)	1.01 (0.92)	1.03 (0.80)	1.01 (0.94)	1.02 (0.84)	1.06 (0.71)	1.03 (0.81)	1.07 (0.71)	1.13 (0.63)
0.150	1.00 (0.96)	1.02 (0.83)	1.05 (0.69)	1.01 (0.87)	1.04 (0.74)	1.09 (0.61)	1.06 (0.72)	1.11 (0.62)	1.11 (0.50)
0.225	1.01 (0.91)	1.03 (0.75)	1.08 (0.57)	1.03 (0.77)	1.07 (0.63)	1.13 (0.51)	1.10 (0.61)	1.17 (0.52)	1.20 (0.40)
0.300	1.02 (0.88)	1.06 (0.62)	1.12 (0.46)	1.06 (0.66)	1.12 (0.52)	1.19 (0.41)	1.16 (0.51)	1.23 (0.43)	1.31 (0.36)
0.375	1.04 (0.67)	1.10 (0.50)	1.17 (0.34)	1.10 (0.53)	1.17 (0.41)	1.25 (0.31)	1.22 (0.41)	1.30 (0.34)	1.39 (0.28)
0.450	1.07 (0.54)	1.14 (0.37)	1.23 (0.25)	1.15 (0.41)	1.23 (0.31)	1.32 (0.23)	1.30 (0.32)	1.39 (0.27)	1.48 (0.22)

* Genetic trend x years between groups
Accuracy of progeny test on 50 daughters = 0.88
Accuracy of sib test corresponds to 3, 7 and 19 full sibs, respectively

returned to widespread use increases. For current practice, with a difference of 0.25 SD (2.5 x 0.1 SD) between the sib and progeny test groups, and a proportion 0.2 progeny-tested bulls returned to commercial use, the relative superiority of the combined system with 3-7 full sibs tested ranges from 1.10 to 1.20. The proportion of progeny-tested bulls among the bulls used in the combined system is also given in Table 1, declining as the relative superiority of the combined system increases.

DISCUSSION

The results show that the combined system offers useful gains in the merit of bulls for commercial use. In practice, the number of full sisters produced by MOET in breeding a young bull for progeny testing may be few, and extra embryo flushes will be needed to get 5-10 full sisters for reasonable accuracy in selection. However, the extra gains from having 20 full sisters, rather than 10, are quite small.

The combined system is similar to increasing the size of the bull group available for selection, by having two groups to choose from rather than one. For example, selecting 10 out of 200 bulls rather than 10 out of 100 gives a relative superiority of 2.063/1.755, or 1.18. The advantage comes from having estimated breeding values on two groups, rather than from increasing the number of females tested. If instead of 10 full sibs, 10 extra daughters were used in the progeny test the accuracy of the progeny test would only be increased from 0.877 to 0.894, a ratio of 1.02.

Christensen and Liboriussen (1986) considered the proportion of progeny-tested sires that would be selected so that their mean would be equivalent to the mean of young MOET bred bulls. They found that a high proportion would be selected (i.e. low selection

intensity) unless the genetic trend and the age difference were both large. However, they considered the mean of the young MOET bulls, rather than sib tested selected MOET bulls.

The results have been presented to show the improvement in merit of commercial semen. The advantages of the combined system are much smaller in improving the rate of genetic change in the breeding population. This is because the bulls used in the elite breeding herds to breed both bulls (BB) and cows (BC), can be selected from the best 0.05 of the group tested (e.g. Woolliams and Smith 1988). The superiority of the combined system is then much lower, as shown in Table 1. There may be some gain in the cow to breed bull (CB) pathway, since in using MOET to produce young bulls for testing, full sibships of females of high genetic merit are also produced (McDaniel and Cassell, 1981). With 100 young bulls per year there may be some 500-1000 such females. These would be included in the large pool of females from which bull mothers would be selected in the next round, so adding to the genetic response in the CB pathway (Colleau, 1985, 1986, Christensen and Liboriussen, 1986).

An alternative breeding system would be to dispense with progeny testing and rely on sib testing alone. With 10 full sib sisters per bull, the annual genetic response rate would be similar to that from progeny testing and only a little higher with 20 full sibs per bull. However, the responses would be obtained (2.5 years) sooner, reducing the lag. But the main advantage of the combined system for commercial semen would then be lost, because there would be only one group to select from.

Several factors might reduce the extra merit from the combined scheme. There will be variation in the number of full sibs per bull and so in the accuracy of the full sib test. Selection on

full sibs produced by MOET may be affected by any maternal or cytoplasmic effects, and by dominance and epistatic variance affecting the trait being selected. Experimental investigation of these factors is needed, to measure their importance in practice and to take account of them in MOET nucleus schemes. Members of a full sib family might be spread over several herds to obtain a number of contemporaries and to avoid preferential treatments. The level of inbreeding would not be increased with the combined use of sib test and progeny test bulls, if the use of sib-tested bulls is limited to commercial use. There may be some uncertainty in industry about the use of sib tests since they will not be highly correlated with progeny test. If the accuracy of selection was 0.5 for the sib test and 0.88 for the progeny test, the expected correlation between the two tests would be only 0.44. However, if response rate rather than accuracy is stressed, the low correlation becomes secondary.

In genetic improvement it seems rational to use individuals with the highest estimated breeding values at the time of breeding to breed the next generation. Their use would be irrespective of their source, their age or the accuracy of evaluation. Risks from the lower accuracy of EBV in the sib test can be reduced by using several bulls rather than one in a herd, or by using several full sib bulls in a sibship team. EBVs may change if further information is added, so the individual selected for breeding may change over time. Continuous evaluation and selection should be used. The EBV on a bull at conception can be updated at birth and at mating age from additional information on the parents, with further updating as records on collateral relatives become available and as progeny records are obtained. This would require retention of more animals as potential breeders in case they are eventually selected, and an optimum policy needs to be derived. A computer simulation of the

different systems would be useful to quantify the gains in practice, with these and other factors included.

SUMMARY

Groups of sibs, sisters to bulls being bred for progeny testing, can be produced by multiple ovulation and embryo transfer (MOET). Sib tests are complete at 3 years of age and progeny tests when bulls are about 5.5-6 years of age. The merit of commercial semen could be increased by using the bulls with the highest estimated breeding values from both the sib test group and the progeny test group rather than only from the latter. With current selection rates (20%) among progeny-tested bulls for commercial use, current genetic trend (0.1 SD units per year) in bulls and with the equivalent of 3-7 full sisters per bull, the relative genetic superiority of semen from the combined groups could be from 1.10 to 1.20 times that from the progeny-tested group alone.

CHAPTER 3

THE VALUE OF DAUGHTERS OF BULL DAMS IN DAIRY CATTLE PROGENY TESTING SCHEMES

INTRODUCTION

In dairy cattle breeding, genetic progress is made along four pathways: selection of bulls to breed bulls (BB), selection of bulls to breed cows (BC), selection of cows to breed bulls (CB) and selection of cows to breed cows (CC). About 76% of the total genetic gain is made in selecting the parents of males (i.e. on the BB and CB pathways) and 24% in selecting the parents of females (Everett, 1984). However, in the absence of sexing, the matings of bull sires and bull dams will on average produce equal numbers of males and females. The daughters of bull dams (DBD) born have a higher genetic mean than the daughters of cow dams (DCD) born at the same time. With the scheme in steady state equilibrium, the difference in means (DBD–DCD) is

$$\frac{I_{BB} - \Delta GL_{BB} + I_{CB} - \Delta GL_{CB}}{2} - \frac{I_{CC} - \Delta GL_{CC} + I_{BC} - \Delta GL_{BC}}{2}$$

where ΔG, I and L represent the genetic gain per year, the genetic selection differential and the generation interval respectively. In a typical progeny testing scheme this difference may represent $3\Delta G$ to $4\Delta G$ (e.g. 3.4 ΔG in the example of Table 1).

The value of DBD has previously been underestimated because of the usual pooling of the DBD and the DCD populations into a single population of potential bull dams. The existence of DBD has

previously been ignored in calculations of genetic response, because their number is small. The contribution of the DBD to the CB pathway may be significant, especially when the number of selected bull dams is small due to the use of MOET (Multiple Ovulation and Embryo Transfer). Many authors (e.g. Cunningham, 1976), have shown that by using MOET on bull dams, more intense selection can be carried out on the CB pathway and hence response can be increased by up to 10%. A consequence of this strategy, which has not been examined, is that the DBD born are of very high genetic merit which may further raise the genetic response.

The genetic merit of selected bull dams is usually lower than expected. This is thought to be due, in part at least, to preferential treatment of high yielding cows (Van Vleck, 1977).

The aim of this study is to investigate the importance of the DBD in a progeny testing scheme, with or without using MOET on bull dams, and to study the effect of preferential treatment on the importance of DBD. The impact of DBD on the CC pathway is neglected here, because many cows have to be selected and so the contribution of DBD can only be small.

MATERIALS AND METHODS

To predict the steady state genetic gain of a progeny testing scheme all four selection pathways have to be included, although our interest is only in the CB pathway. Consider the following breeding plan shown in Table 1. Annually, 100 young bulls are progeny tested on 100 daughter records each. Without the use of MOET, about six bull dams are needed in practice to produce each young bull (Hinks, 1978). The generation interval for bulls is six years. The cow dams are assumed to be selected at random with respect to the breeding goal, with a generation interval of about

TABLE 1

Predicted genetic gain (ΔG) in a progeny testing scheme without the use of MOET and ignoring daughters of bulls dams (DBD)

Path way	Age class	Selected fraction (%)	Selection accuracy	Contribution* of age class (%)	Genetic[*1] selection differential (SD units)	Generation[*1] interval (years)
BB	6	2	0.933	100	1.13	6
BC	2	100	0.0	20	0.77	5.2
	6	5	0.933	80		
CB	4	1.3	0.5	54.1	0.74	4.6
	5	1.1	0.6	31.2		
	6	0.6	0.65	11.5		
	7	0.2	0.675	3.2		
CC	2-7	100	0.0	100	0.0	4

$\Delta G = (1.13+0.77+0.74)/(6+5.2+4.6+4)=0.133$ SD/year

* The contributions of the age classes sum to 100% within each pathway.

[*1] These mean values are weighted by the contributions of the age classes within a pathway.

four years. Some 50,000 heifers enter the cow population each year. Culling of cows is assumed to be independent of the breeding goal and is 30% annually of the total number. Thus for example there are 35,000 three year old cows. The total cow population amounts to 167,000 cows. Selection is for milk production, which is assumed to have an heritability of 0.25 and a repeatability between lactations of 0.4. The genetic correlation between lactations is one, unless stated otherwise.

Modern sire and cow evaluation methods make it possible to compare the estimated breeding values (EBVs) of animals of different ages. Thus the best cows can be selected irrespective of age. In the present breeding plan the bull dams are selected from age classes 4, 5, 6 and 7 (the age class number is the age at birth of their progeny), being selected on 1, 2 3 and 4 lactation records respectively. Each age class has a distribution of EBVs. The means of these distributions differ due to genetic progress (e.g. the mean of age class 2 is ΔG higher than the mean of age class 3) and the variances differ due to the amount of information that is available.

Ducrocq and Quaas (1988) described an algorithm to predict the fractions selected from each distribution if truncation selection is applied across several distributions. Because the differences in means between the distributions are determined by the genetic progress, the steady state genetic gain is calculated iteratively using this algorithm. If bull dams can also be selected from the DBD, there are four more distributions to select from i.e. the distributions of EBVs of the DBD of age classes 4, 5, 6 and 7.

Genetic progress is calculated both with and without DBD included for the following schemes. In each scheme the total number of young bulls and DBD produced is constant.

1. No MOET used on bull dams. Six hundred bull dams are selected with one offspring each.
2. One flush per bull dam. Two hundred bull dams are selected with three offspring per bull dam per year. This procedure is common practice in some AI organisations to increase the probability of producing a male calf. Only the female's own records are used for evaluation and information on full sibs is ignored.
3. Repeated use of MOET on bull dams. Sixty bull dams are selected with ten offspring per bull dam per year. Assuming there are five male and five female offspring, each DBD is thus evaluated on her own record and those of four full sisters. This scheme may be applied to sib test the young bulls (Smith and Ruane, 1987).
4. This is the same as scheme 3 except that preferential treatment of potential bull dams is considered.

The effects of preferential treatment are modelled in two ways in three different schemes (schemes 4a, 4b and 4c). In Scheme 4a it is assumed, that all the 'best' cows are treated preferentially, so that it is not possible to discriminate between the 'very best' and the 'best' cows. This situation is modelled by setting a limit on the maximum selection intensity possible within an age class. The maximum selection intensity is set to 2.421, which corresponds to 2% of females selected. For example, when the proportion of animals selected from age class 7 is 0.1% the genetic merit of the selected cows in this age class becomes $u_7 + (2.421)(r_7)(\sigma_G)$ instead of $u_7 + (3.367)(r_7)(\sigma_G)$ (where u_7, r_7 and σ_G are the mean of age class 7, the accuracy of selection of females in age class 7 and the genetic standard deviation of milk production).

In Scheme 4b it is assumed that the accuracy of bull dam

selection is not increased by including any records other than from the first lactation, as suggested by Van Vleck (1986). The reason for this is that cows seem to be treated evenly during the first lactation but preferentially thereafter (Murphy et al., 1982). This situation is modelled by at first assuming that the phenotypic variances and covariances are unaffected by preferential treatment. Secondly it is assumed, that the method of evaluation does not account for preferential treatment, i.e. the weighting factors for the EBVs are unchanged. These assumptions imply that the variances of the EBVs are not affected by preferential treatment. Thirdly, the genetic correlations between the first lactation and the second, third and fourth lactation record are assumed to be reduced to 0.67, 0.65 and 0.64 respectively. These correlations are chosen such that $r_4 = r_5 = r_6 = r_7$. The breeding goal is first lactation milk yield.

Scheme 4c is the same as Scheme 4b except that it is assumed that the DBD are also treated preferentially during the first lactation (based on their pedigree). It is assumed that the accuracies of selection of the DBD are reduced by 30%. The accuracies of selection of DCD are the same as in Scheme 4b.

It is assumed that the population is large enough to neglect the effects of reduced selection differentials due to finite population size and inbreeding. In addition, the reduction in variance due to selection is ignored. This effect is partly avoided by only selecting once on any information source. For example, DBD are selected on their own performance (and that of their contemporary full sibs) and not on the performance of their dam, because their dams were already selected on own performance. Similarly DBD are not selected on half sib records, because their sires were selected on progeny records.

RESULTS

Table 1 gives the contribution of the four pathways and of the different age classes within the pathways to the selection response of scheme 1. The steady state genetic response for this situation is 0.133 phenotypic standard deviations (SD) per year.

In Table 2 the effects of using MOET and including DBD on genetic gain are given. When DBD are ignored, the annual genetic gain can be increased from 0.133 to 0.143 SD units by selecting fewer bull dams and using MOET. This increase of 8% is in agreement with previous results (e.g. Cunningham (1976)). The response is further increased by including DBD in our calculations of genetic gain. Without MOET, this increase is 1.5%, with intense MOET (10 offspring per dam) it is increased by 7%. The influence of the DBD increases as the number of bull dams selected decreases. Thus combining these two features for scheme 3, response is increased by 13% (0.153/0.135) by selecting 60 bull dams to produce the young bulls needed instead of 600.

Table 2 also shows the impact that including DBD has when preferential treatment is present. In schemes 4a, 4b and 4c the genetic response is increased by 11, 8 and 2% respectively.

DISCUSSION

The genetic response predicted when including DBD in calculations for the CB pathway, in a progeny testing scheme where MOET is not used, is only slightly higher than if they are excluded (scheme 1, Table 2). However, through using MOET a smaller group of highly superior bull dams can be selected, that produce daughters of higher average genetic merit. In addition the breeding values of these daughters can be estimated with a higher accuracy because of the full sib information available. As a consequence, a greater

TABLE 2

The predicted genetic gain (ΔG) and the fraction of bull dams that are themselves daughters of bull dams (P_{DBD}) for schemes 1, 2, 3, 4a, 4b and 4c.

Scheme	DBD ignored ΔG (SD/yr)	DBD included	
		ΔG (SD/yr)	P_{DBD} (%)
1	0.133	0.135 (+1.5%)	14
2	0.138	0.141 (+2%)	30
3	0.143	0.153 (+7%)	80
4a	0.130	0.144 (+11%)	65
4b	0.138	0.149 (+8%)	74
4c	0.138	0.141 (+2%)	60

number of bull dams selected are themselves DBD and so they have a greater impact on genetic progress. For example, in scheme 3, 80% of the bull dams were DBD.

Apart from the generation interval of the bull dams, the progeny testing scheme approaches the MOET-hybrid schemes described by Colleau (1985), where all bull dams are DBD. If the young age classes are also included for selection, the generation intervals of the bull dams in the progeny testing and MOET-Hybrid schemes will be more alike. This also increases the genetic gain of the progeny testing scheme, since the number of selection candidates increases. Thus, using MOET on bull dams in a progeny testing scheme has a greater effect on genetic progress than previously considered. This should also lead to increased inbreeding rates due to the reduction of the effective population size, since the bulls and DBD are closely related.

The genetic merit of bull dams selected is equal to the genetic mean of the group from which they are selected, plus the genetic selection differential (u(DBD) + I(DBD) or u(DCD) + I(DCD) for DBD and DCD respectively). The genetic selection differentials, I(DBD) and I(DCD), are both reduced by preferential treatment. But I(DBD) is smaller than I(DCD), because the mean genetic level of the DBD (u(DBD)) is higher than that of the DCD (u(DCD)) and the truncation point is the same across these two distributions. Thus the absolute reduction of I(DBD) due to preferential treatment is smaller than that of I(DCD), if preferential treatment is applied equally to DCD and DBD (Schemes 4a and 4b). This implies that u(DBD) + I(DBD) is reduced by less than u(DCD) + I(DCD), which leads to an increased importance of DBD, when DBD and DCD receive equal preferential treatment. If greater preferential treatment is exercised among DBD due to their superior pedigrees (Scheme 4c), the

value of including DBD decreases substantially (i.e. from 7% in scheme 3 to 2% in scheme 4c).

Preferential treatment was modelled in three ways - the first limiting the selection intensity possible within an age class and the second and third limiting the accuracy of selection. When DBD are included in calculations, preferential treatment reduced response by 6, 3 and 8% respectively (0.144/0.153, 0.149/0.153 and 0.141/0.153 respectively). These calculations suggest that preferential treatment on the CB pathway cannot account for the large difference between the theoretical rates and the responses obtained in practice by progeny testing schemes. Factors such as the reduction in variance due to selection are likely to be far more important (Meyer and Smith, 1989).

This study has examined the impact of DBD on estimates of theoretical rates of response. In practice, DBD contribute to the realised response since they are evaluated and selected if their EBVs are high enough.

The impact of including DBD in calculations of the theoretical response to selection has been examined assuming that bull dams have an equal chance of producing progeny of either sex. If reliable embryo or semen sexing is used in progeny testing schemes the numbers of DBD may be reduced and hence their influence on genetic gain may become negligible. This should be taken into account when conventional progeny testing schemes are compared to breeding schemes which use embryo or semen sexing. In certain situations, for example if sib testing young bulls (Smith and Ruane, 1987), DBD may still be produced in sufficient numbers to have a considerable impact on genetic response.

SUMMARY

In dairy cattle progeny testing schemes, bull dams of high genetic merit are identified and bred to produce young bulls. Females will also be produced and they may themselves become bull dams. The impact of these daughters of bulls dams (DBD) on genetic gain has been underestimated in the past.

The predicted rate of genetic gain increased by 2%, when the DBD were included in the calculations for a conventional progeny testing scheme. When MOET (Multiple Ovulation and Embryo Transfer) was used on bull dams to produce 10 offspring per dam per year, this difference was 7%. When accounting for preferential treatment of bull dams by limiting the accuracy of selection or the intensity of selection, including DBD increased genetic gain by 2-11%.

CHAPTER 4

THE GENETIC RESPONSE POSSIBLE IN DAIRY CATTLE IMPROVEMENT BY SETTING UP A MULTIPLE OVULATION AND EMBRYO TRANSFER (MOET) NUCLEUS SCHEME

INTRODUCTION

Few alternative breeding strategies to rival the progeny testing of sires in dairy cattle breeding have been proposed in the past (Hinks, 1978). One which has received considerable attention in recent years was proposed by Nicholas (1979), using multiple ovulation and embryo transfer (MOET) within a single dairy herd as a means to increase response rates. This idea was elaborated by Nicholas and Smith (1983). They showed that the steady state rate of response of MOET nucleus schemes could be significantly superior to that of an efficient progeny testing scheme. The steady state response rate is calculated presuming that a breeding programme has been carried out for a sufficient length of time such that the population is improving at a constant rate. It could be argued that this is not the relevant comparison to make since progeny testing schemes are already in operation whereas MOET nucleus schemes are only being initiated now.

In dairy cattle breeding, the effect of a single round of selection on the genetic merit of animals in later generations is not constant until many years after selection. Hill (1974) proposed that the response from the selection of parents be calculated by multiplying the genetic superiority of parents by the proportion of their genes present in later generations (the gene flow method). The aim of this study is to use this method to evaluate the short and long term genetic response possible from establishing a MOET nucleus

herd using the best progeny tested bulls and bull dams and then selecting within the closed MOET breeding herd.

MATERIALS AND METHODS

The selection goal is economic merit, which is determined primarily by milk yield and so is taken to have a heritability value of 0.25 and a repeatability of 0.5. For simplicity, genetic gain is expressed in standard deviation units (σ_p).

a) Progeny Testing Scheme

A conventional progeny testing scheme in steady state equilibrium is described in Table 1. One hundred young bulls are progeny tested annually. The best 12 are chosen for use on the commercial herd after being evaluated on 50 effective daughters. The best four are selected as bull sires. Each selected bull is used for one year only. It is assumed that 1% of cows are selected to be bull dams after completing three full records, and that there is no effective selection of cows to breed cows.

Rendel and Robertson (1950) showed that the annual genetic gain (ΔG) of a breeding scheme in steady state equilibrium can be calculated from

$$\Delta G = \frac{I_{BB} + I_{BC} + I_{CB} + I_{CC}}{L_{BB} + L_{BC} + L_{CB} + L_{CC}} \quad \sigma_p$$

where I and L refer to the genetic superiorities and generation intervals of selected animals and B and C represent bulls and cows respectively. Thus the average genetic merit of all offspring born in year one, resulting from selection and mating at year zero, can be set to zero by subtracting $\Delta G(L_{BB} + L_{BC} + L_{CB} + L_{CC})$ from the

TABLE 1

Estimated genetic change in a conventional progeny testing scheme (in standard deviation units)

Pathway	Percent selected %	Selection intensity i	Accuracy of selection r	Heritability$^{1/2}$ h	Genetic superiority I(σ_p units) (irh)	Generation interval L(years)
Bull to bull (BB)	4	2.15	.88	.5	.94	6.75
Bull to cow (BC)	12	1.67	.88	.5	.73	6.28
Cow to bull (CB)	1	2.67	.65	.5	.86	6.25
Cow to cow (CC)	100	0	-	-	0	4.74

$$\Delta G = \frac{I_{BB} + I^{*}_{BC} + I_{CB} + I_{CC}}{L_{BB} + L^{*}_{BC} + L_{CB} + L_{CC}} \quad \text{(Rendel and Robertson, 1950)}$$

$$= .103\ \sigma_p$$

* 10% of commercial herd bred to young bulls

Thus $I_{BC} = (0.9)\ (.731) + (0.1)\ (0)$

$L_{BC} = (0.9)\ (6.75) + (0.1)\ (2)$

genetic superiorities of their parents. However, because of the higher genetic merit of bull parents over cow parents, there is a difference (D) at birth in the genetic merit of males and females. Thus the average merit of breeding males born is,

$$\frac{(I_{BB} - \Delta GL_{BB}) + (I_{CB} - \Delta GL_{CB})}{2} = 0.24 \ (= D/2)$$

The average merit of all females born is,

$$\frac{(I_{BC} - \Delta GL_{BC}) + (I_{CC} - \Delta GL_{CC})}{2} = -0.24(-D/2)$$

Thus the average merit of breeding males born at year one is D/2. These are mated to 10% of the commercial cow herd for progeny testing. The term commercial cow herd is used to define the 99% of cows that are not selected as bull dams. Thus, their main role is in yielding milk in their own lifetime and they are not used to breed males in the next generation. The average merit of all females born at year 1, which can be considered as the average merit of cows born in the commercial herd, is -D/2. With the scheme in a steady state, the average merit of breeding bulls born at year 20 over the offspring born in year one is,

$$D/2 + 19\Delta G = 2.19\ \sigma_p$$

The average merit of commercial cows born at year 20 is,

$$-D/2 + 19\Delta G = 1.72\ \sigma_p$$

b) MOET Nucleus Schemes

The two main schemes which propose using MOET to increase rates of genetic gain are the MOET nucleus schemes (Nicholas and Smith, 1983) and the MOET hybrid schemes (Colleau, 1985). These have been reviewed by Ruane (1988). In the MOET hybrid schemes, females are selected on first lactation performance while breeding males are progeny tested. In the MOET nucleus schemes, males are not progeny tested but instead are selected at an early age on family information in the same way that the females are. In this study, we have only investigated the genetic response from establishing a MOET nucleus scheme.

Nicholas and Smith (1983) examined two types of MOET nucleus schemes-adult and juvenile. In the adult scheme, animals are selected after the first lactation. Males are evaluated on their full sibs', half sibs' and dam's records and females are evaluated on the same information plus their own lactation record. In the juvenile scheme described here, animals are selected before first breeding using not only family information of the dam as proposed by Nicholas and Smith (1983) (i.e. records on the dam, her full sibs, her half sibs and her dam) but also of the sire (i.e. records on his full sibs, his half sibs and his dam). The generation intervals of the two schemes are 3.75 and 2 years respectively which are slightly longer than those used by Nicholas and Smith (1983).

In setting up the MOET nucleus herds, 4 bull sires and 64 bull dams are selected as nucleus founder animals. Since the number of nucleus founder males is equal to the number of bull sires normally selected in the progeny testing scheme, their genetic superiorities are equal. Although the number of nucleus founder females is much smaller than the number of bull dams normally used to produce young bulls for progeny testing, their genetic superiorities

are conservatively assumed to be equal. This is to allow for factors such as possible preferential treatment of top animals and avoiding selection of closely related cows.

Responses are calculated with 64 selected donors producing 4, 8 or 16 candidates for selection in the next generation. With 4 candidates per donor, the correlation of true with expected breeding values for juvenile animals (males or females), adult males and adult females is 0.42, 0.54 and 0.64 respectively. As the number of progeny per donor is raised to 16, this correlation increases by about 10%. Assuming a 50% survival rate of the embryo to selection age, the total number of embryos transferred and recipients needed is 512, 1024 and 2048 respectively. With a 50% sex ratio, the proportion of females selected as replacement donors is 1/2, 1/4 and 1/8 respectively. In order to reduce inbreeding, only one male per full sibship is eligible for selection. A mating ratio of 16 females per sire is used so the proportion of full sibships selected, from which one male is chosen randomly, is 4/64.

Selection intensities for MOET nucleus and progeny testing schemes are calculated under the assumptions of an infinite population size and unrelated candidates for selection. If the finite population size is accounted for, selection intensities would be reduced slightly. For example, in the adult scheme with 8 progeny per donor the selection intensities for males and females respectively would be reduced from 1.968 and 1.271 to 1.911 and 1.252. The corresponding reduction in annual response of all schemes would be quite small (about 2%) and of almost equal magnitude for the nucleus and progeny test schemes. Accounting for genetic relationships between candidates for selection is more problematic but would have a greater effect on the MOET nucleus than the progeny testing scheme.

As in the progeny testing scheme, 12 nucleus bulls are selected annually (the best from 64) for use on the commercial herd for one year. The structure of the cow commercial herd is taken from the British Milk Records survey 1981/1982 and is shown in Table 2. In evaluating the response from MOET nucleus schemes using Hill's (1974) method, the herd is split into yearly groups to make computation easier. The methods of setting up the two MOET nucleus systems are different and need to be considered separately.

1. Juvenile Scheme

Nucleus founder animals are selected as described at years zero and one. Selection of the resulting offspring before breeding is not possible since no milk records are produced in the MOET nucleus herd by that time. Since progeny tested sires are expected to have a higher genetic merit than unselected MOET nucleus males, they are bred to 64 unselected MOET nucleus females at years two and three. The offspring born (both males and female) can then be selected using the first lactation records of these females and progeny test data of the sires. From year four onwards the nucleus herd is closed and from year 6 onwards evaluation of candidates for selection is based on nucleus herd information only. This is shown in Appendix 1. Nucleus males are used on the commercial herd when fourteen months old for one year giving a generation interval of 2.42 years.

2. Adult Scheme

To establish the herd, four rounds of selection of nucleus founder males and females are needed at years zero, one, two and three. However at year three they are selected (to accommodate the gene flow method) to produce only 75% of the nucleus animals, the

TABLE 2

Age structure of the British Dairy Cow Commercial Herd (based on the National Milk Records 5 Year Survey 1981/1982)

Age when progeny born	Frequency (%)
2	11.80
3	23.76
4	22.60
5	11.06
6	10.28
7	7.83
8	5.37
9	3.21
10	1.94
11	1.16
12	0.58
13	0.26
14	0.10
15	0.05
	100.00

Thus commercial cows born in any year will receive 5.9% of their genes from 2 year old cows, 11.88% from 3 year old cows etc. The average age of cows at the birth of their daughters is 4.74 years.

remaining 25% being bred from within the nucleus. From year four onwards, nucleus stock are selected on MOET nucleus information to breed all nucleus replacements. Nucleus sires are also selected for use on the commercial herd for one year, with a generation interval of 4.08 years.

3. Calculation of Genetic Progress

This can be subdivided into two steps - the calculation of genetic progress from 1) the early rounds of selection when the nucleus herd is being established and 2) repeated selection within the nucleus once the herd is established.

Selection within the closed nucleus herd is carried out annually, without overlapping of sires or dams between years, and genetic gains were calculated using the GFLOW programme (Brascamp, 1978) of the Hill (1974) gene flow method. Genetic gains from the early rounds of selection were calculated using a modified version of this programme which accounted for changes in the population structure in the early rounds of selection when setting up the nucleus herd. These results were then added to those from repeated selection. The response at year t (r_t) from one early round of selection along a given selection pathway is calculated by

$$r_t = P_t \; r_{t-1} + EQ^{t-1}s$$

where the P,E and Q matrices describe respectively the movement of all genes in the whole population, along the given selection pathway and by ageing alone in the whole population (Hill, 1974). The vector s defines the genetic superiority of selected animals. A small example to illustrate the method is shown in Appendix 2.

For both MOET nucleus schemes it is assumed that the nucleus

founder males and females are of equal merit to the bull sires and bull dams from the progeny testing scheme. Taking the average genetic merit of all offspring born in the progeny testing scheme at year 1 as zero, then the genetic merit of nucleus founder sires at year 0 is $I_{BB} - L_{BB} \Delta G + D/2 = 0.49$ and of nucleus founder dams at year 0 is $I_{CB} - L_{CB} \Delta G - D/2 = -0.01$.

Since the progeny testing scheme is in steady state, the merit of nucleus founder stock used increases by ΔG each year. Thus for example the merit of nucleus founder sires selected at years one, two and three is $0.49 + \Delta G$, $0.49 + 2\Delta G$ and $0.49 + 3\Delta G$ respectively. Similarly, the merit of bulls used on the commercial herd at year 0 is $I_{BC} - L_{BC} \Delta G + D/2 = 0.25$ and of cows used to breed replacements at year 0 is $I_{CC} - L_{CC} \Delta G - D/2 = -0.72$.

In any commercial enterprise the timing of returns can be crucial to its success. The process of discounting allows us to discriminate between short and long term genetic gains so that the earlier the gains are accumulated, the greater the discounted response. An inflation-free discount rate of 5% per annum, which also allows for risk, is used (Bird and Mitchell, 1980). The returns from a national dairy cattle breeding programme can be seen as the increase in milk yield from the commercial herd cows due to selection. Thus the discounted genetic merit of the commercial herd was also calculated.

RESULTS

The expected genetic response of nucleus males and commercial cows born after 10, 20 and 30 years for 4, 8 and 16 progeny per donor is shown in Tables 3 and 4 for the adult and juvenile MOET nucleus schemes respectively. Results for 8 progeny per donor are also shown in Figures 1 and 2.

TABLE 3

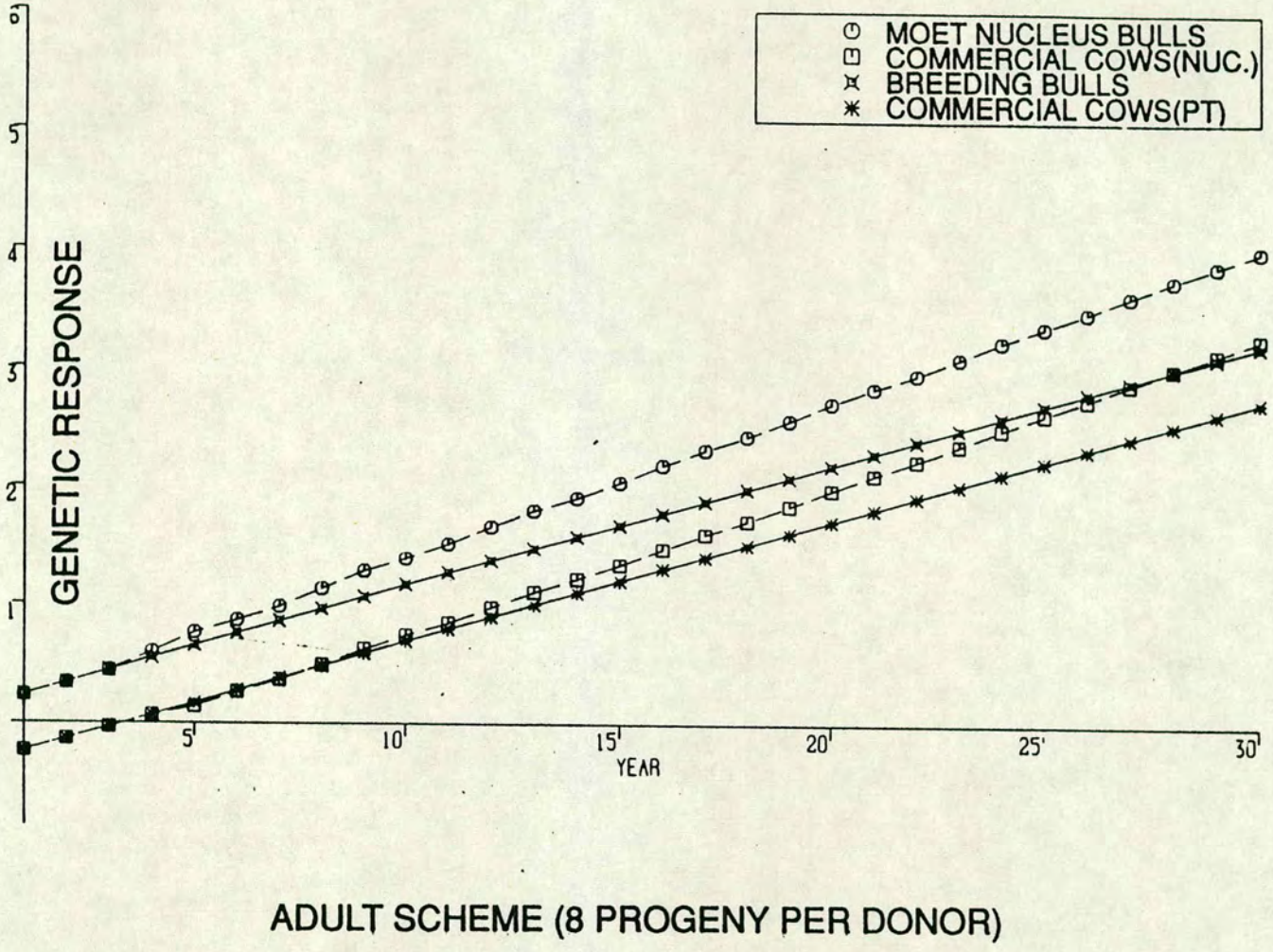
The expected genetic response (in standard deviation units) of newborn adult nucleus males and commercial females. The difference in genetic response compared to breeding males and commercial cows respectively born in the progeny testing scheme is shown in brackets

		Progeny per donor surviving to selection		
Animals	Year born	4	8	16
Nucleus males	10	1.18(.01)	1.38(.22)	1.56(.39)
	20	2.23(.04)	2.71(.52)	3.13(.94)
	30	3.27(.05)	4.02(.80)	4.65(1.43)
Commercial cows	10	0.67(-.02)	0.74(.05)	0.80(.11)
	20	1.69(-.02)	1.98(.27)	2.23(.51)
	30	2.73(-.01)	3.27(.53)	3.73(.99)

TABLE 4

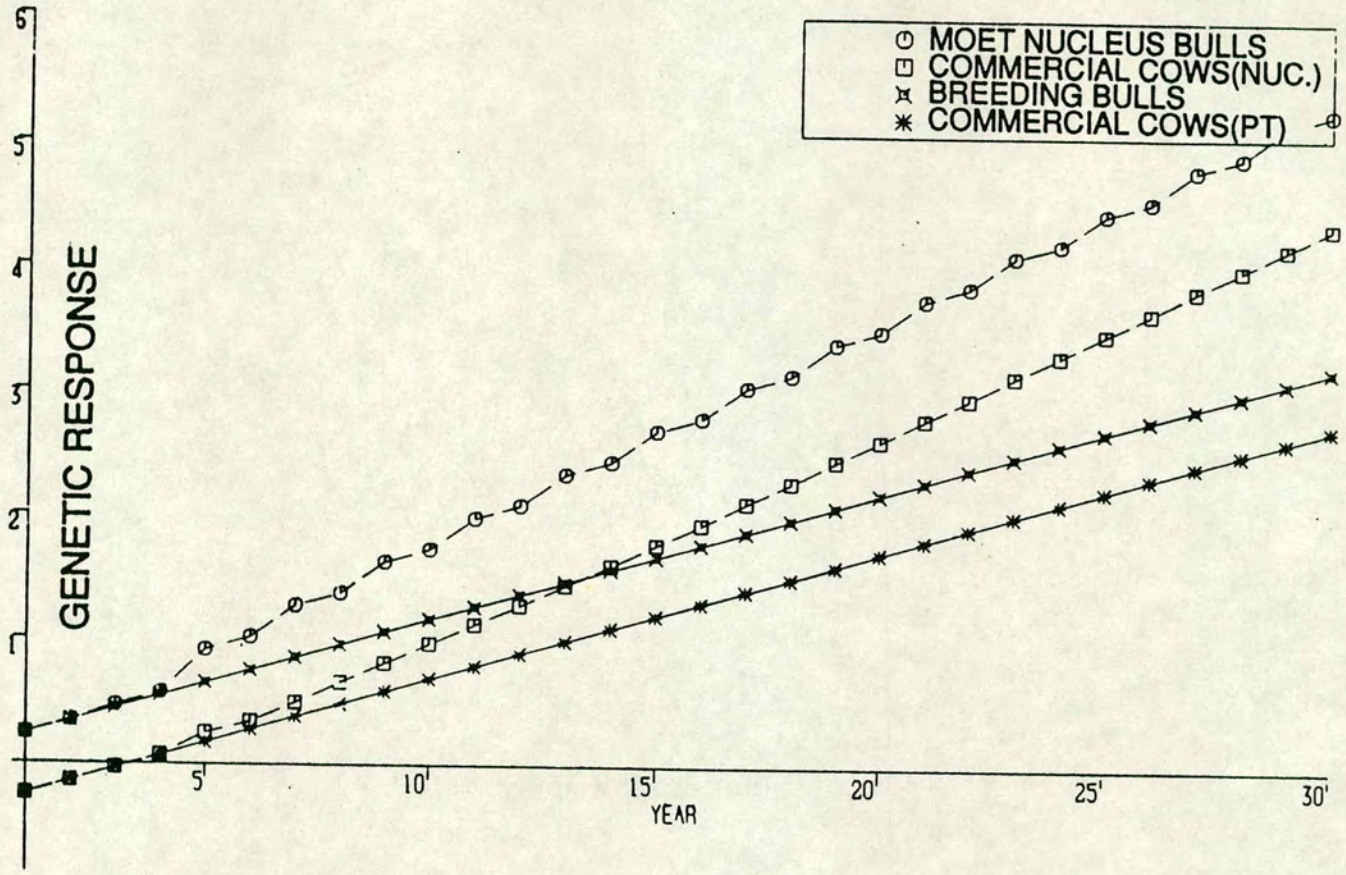
The expected genetic response (in phenotypic standard deviation units) of newborn juvenile nucleus males and commercial females. The difference in genetic response compared to breeding males and commercial cows respectively born in the progeny testing scheme is shown in brackets

		Progeny per donor surviving to selection		
Animals	Year born	4	8	16
Nucleus males	10	1.52(0.36)	1.73(0.57)	1.90(0.74)
	20	2.97(0.78)	3.51(1.31)	3.97(1.78)
	30	4.42(1.20)	5.29(2.07)	6.03(2.82)
Commercial cows	10	0.88(0.20)	0.97(0.28)	1.04(0.35)
	20	2.27(0.56)	2.62(0.91)	2.92(1.21)
	30	3.71(0.97)	4.37(1.63)	4.95(2.20)



ADULT SCHEME (8 PROGENY PER DONOR)

Fig. 1. Genetic response of animals born in a progeny testing (PT) and adult MOET nucleus scheme.



JUVENILE SCHEME (8 PROGENY PER DONOR)

Fig. 2. Genetic response of animals born in a progeny testing (PT) and juvenile MOET nucleus scheme.

The importance of ET success rates and herd management are shown by the significant increases in response achieved with higher numbers of progeny per donor. With 4, 8 and 16 progeny per donor the predicted superiority of juvenile nucleus bulls born at year 20 over breeding males born in the progeny testing scheme is 36, 60 and 81%. With the adult MOET nucleus scheme, the figures are 2, 24 and 43%. The commercial herd lags behind the nucleus herd in genetic merit. The corresponding figures for the commercial herd at year 20 are 33, 53, and 70% for the juvenile and -1, 16 and 30% for the adult MOET nucleus schemes. Although genetic gain increases with the number of progeny per donor, the costs of running the scheme also become more expensive. In deciding what the optimum size of the scheme should be, account should be taken of the extra costs needed as well as the greater returns possible from increasing the family size.

Further comparison between the schemes will be made with 8 progeny per donor. The gap between the predicted genetic merit of animals bred from the nucleus and progeny testing schemes increases with time, as shown by Figures 1 and 2. For the adult scheme, the average merit of nucleus bulls born in the first three years is the same as those breeding bulls born in the progeny testing scheme. The nucleus bulls born at year four are slightly superior and from then on they become progressively better. Commercial cows bred to nucleus sires exceed these bred to progeny tested sires from year 9 onwards. After that, the gap between them diverges.

For the juvenile nucleus scheme, response is far more substantial in the early years than with the adult scheme. By year 10, the genetic response of newborn potential breeding males is almost 50% higher in the MOET nucleus scheme than in the progeny testing scheme. Thus by year 15, the difference between them is

equivalent to about 10 years genetic gain of the progeny testing scheme. This increased genetic response is passed down to the commercial cow herd so that by year 15 the average genetic merit at birth of the commercial cows is higher than that of the progeny testing scheme breeding bulls at birth.

In a MOET nucleus scheme, the steady state response to selection depends only on two selection pathways, selection of sires to breed nucleus offspring and donors to breed nucleus offspring. The expected steady state rates of annual genetic change are given in Table 5. In setting up a nucleus scheme, genetic response in the nucleus herd fluctuates in the early years before stabilising at the steady state rate of response. In addition, it takes longer to stabilise in the commercial herd because of the time needed to disseminate the genetic progress from the nucleus to the commercial tier. This results in a genetic response of MOET nucleus bred animals which lags behind that expected if the scheme is in equilibrium from the start.

These time lags can be quantified by comparing the responses calculated up to year 10, from years 11 to 20 and from years 21 to 30 with those expected over the same three time periods if the nucleus schemes are in steady state equilibrium. For the juvenile scheme with 8 progeny per donor, the genetic gain of nucleus males and females is 0.11 σ_p (equivalent to 0.63 years steady state progress) lower in the first time period than the steady state but no difference in response exists for the two later periods since by then the scheme is in equilibrium. However, it takes longer to achieve steady state responses in the commercial herd. The responses of commercial cows bred to juvenile sires are 2.2 ΔG and 0.7 ΔG lower than the steady state responses over the first two time periods respectively but are equal for the third. Results are similar for

TABLE 5

Expected steady state annual genetic gain given in phenotypic standard deviation units. The expected difference in genetic response between animals born in a MOET nucleus and progeny testing scheme after 20 years is given in brackets

	Progeny per donor surviving to selection		
Scheme	4	8	16
Juvenile	0.145(0.84)	0.178(1.5)*	0.207(2.08)
Adult	0.104(0.03)	0.132(0.58)	0.155(1.04)

*1.5 = 20 (0.178 - 0.103)

the adult scheme. Genetic gain of adult nucleus males and females is about 0.3 ΔG lower than the steady state gains for the first period but does not differ thereafter. Commercial cows bred to these adult nucleus sires yield responses that are 1.6 ΔG and 0.5 ΔG lower over the first two time periods.

The genetic lag between nucleus animals, (nucleus males and females have the same average genetic merit), and commercial cows born in the same year increases with time until equilibrium is reached. The steady state genetic lags are given in Table 6. For comparison, the genetic lag between young breeding bulls and commercial cows born in the same year in the progeny testing scheme is $0.47\sigma_p$, which is equivalent to 4.6 years of improvement. The genetic lag in the MOET nucleus scheme is

$$\Delta G\ (L_{BC} + L_{CC}) - (I_{BC} + I_{CC})$$

where C refers to commercial cows. With the MOET nucleus schemes, the genetic lag is increased quite significantly due to the subdivision of the population into selected (nucleus herd) and non selected (commercial herd) levels.

The summed genetic merit of commercial cows born in the first 10 and 20 years of the MOET nucleus schemes, discounted to the present, is compared to that from commercial cows in the progeny test scheme. The results are given in Table 7. With 8 progeny per donor, discounted genetic returns from the juvenile scheme are much higher over the first 10 years compared to returns from the progeny testing and adult schemes which are roughly equal. When compared over 20 years, the juvenile scheme is still far superior while returns from the adult scheme are slightly higher than from the progeny testing scheme.

TABLE 6

Genetic lag in standard deviation units (with the equivalent number of years annual genetic gain of each scheme in brackets) between nucleus animals and commercial cows born in the same year

	Progeny per donor surviving to selection		
Scheme	4	8	16
Juvenile	0.74(5.1)	0.96(5.4)	1.15(5.6)
Adult	0.54(5.1)	0.75(5.7)	0.93(6.0)

TABLE 7

The summed discounted genetic response of commercial cows born in the first 10 or 20 years with a MOET nucleus scheme compared to those born over the same years in the progeny testing scheme (100). Discount rate is 5%

Years born	Juvenile scheme Progeny per donor			Adult scheme Progeny per donor		
	4	8	16	4	8	16
1–10	133%	143%	152%	92%	101%	109%
1–20	131%	147%	161%	97%	110%	121%

DISCUSSION

The results demonstrate that genetic response can be increased substantially within a short time by setting up a MOET nucleus scheme using the top animals from an efficient progeny test scheme. The larger the nucleus scheme established (in terms of the number of embryos transferred), the greater the predicted response.

The response of newborn nucleus animals is superior to that of newborn progeny test breeding bulls from early on and, as a consequence of the shorter generation intervals, this superiority is passed onto future generations of nucleus and commercial herd animals more quickly in the juvenile than in the adult scheme. Thus genetic response is more rapid both in the early and late years from the juvenile scheme.

Genetic gains achieved in practice are likely to be lower than those predicted here for both the progeny test and MOET nucleus schemes. The reasons for the observed gap between expected and realised genetic gains in progeny test schemes have been well discussed elsewhere (Van Vleck, 1977; Van Tassell and Van Vleck, 1987). The extensive use of family information combined with the small population size in MOET nucleus schemes should result in higher inbreeding rates (Burrows, 1984), lower selection intensities (Hill, 1977a) and greater variation in the response to selection due to genetic drift than expected. These problems are likely to be much worse in the juvenile than in the adult scheme (Ruane, 1988).

The largest response in the early years is expected to come from setting up a juvenile rather than an adult MOET nucleus scheme. This also has the additional advantage of requiring only two years of selection of nucleus founder females instead of four. A practical system may be to set up a juvenile nucleus scheme, run it for a given length of time and then open the herd to new genetic material. This

system should allow high genetic gains to be made in the early years as well as guarding against the problems previously referred to. However, due to the increased genetic lag of the commercial herd it may be more difficult to find commercial cows within the population of sufficiently high genetic merit for use in the nucleus herd. The trading of genetic material of high merit between different MOET nucleus schemes may be the preferred method of introducing novel genetic stock.

Another alternative would be to change from a juvenile to an adult scheme after a given length of time. This could be done quite simply by deferring selection until the first lactations of the female candidates are complete. Other strategies exist and should be considered such as the possibility that instead of selecting both sexes on parental pedigree from year four onwards in the juvenile scheme as described, females could be selected using their own performance with males selected on parental pedigree.

In this study schemes were compared chiefly under the assumption of four daughters and one son per donor surviving to selection. It should be possible to obtain such numbers in the adult scheme with a generation interval of 3.75 years. However, at present it may not be possible to achieve this family size within the two year generation interval described for the juvenile scheme since embryo recovery rates are lower in immature donors compared to mature donors (Gordon, 1983). To date, little emphasis has been placed on improving embryo recovery rates in young heifers and so considerable scope for improvement exists. The ability to produce large numbers of embryos for research purposes by methods such as in vitro fertilisation (e.g. Lu et al., 1987) should mean that current MOET success rates will be improved in the future.

Smith and Ruane (1987) examined the merits of using young

sires, bred by MOET and evaluated on full sister first lactation records, in addition to older progeny tested sires on the commercial herd. They showed that the genetic merit of commercial semen using the top animals from both groups could be increased by 10 to 20% in this manner. The question could be asked here whether it would be worthwhile to progeny test the young nucleus bulls and then select the top 12 bulls for commercial use from the young nucleus bulls evaluated on MOET nucleus information and the older nucleus animals evaluated on progeny test data. The answer seems to be no. With 4, 8 and 16 progeny per donor, the genetic merit of the 12 commercial bulls is highest when 10, 11 and 12 young juvenile nucleus bulls and 7, 8 and 9 young adult nucleus bulls are chosen respectively.

Thus further testing of MOET nucleus sires using progeny test information produces few sires of sufficiently high merit to be selected for use on the commercial herd, especially compared with young juvenile scheme sires. In addition, with a MOET nucleus breeding scheme, improvements on the bull to breed commercial cow pathway do not increase the annual rate of genetic gain. Thus for the adult scheme with four progeny per donor, when progeny testing of MOET nucleus bulls has most impact, the annual rate of genetic gain of commercial cows remains unchanged but their genetic merit compared to nucleus animals (the genetic lag) is reduced by 15%. Given the considerable costs of progeny testing it is unlikely that progeny testing nucleus bulls for use on the commercial herd would be worthwhile.

It may be useful to set up a nucleus breeding scheme in developing countries which lack the infrastructure necessary to maintain an efficient progeny testing scheme (Hinks, 1978; Land, 1986). Nucleus founder stock could be selected from foreign gene pools (if appropriate) and the resulting embryos imported to form the

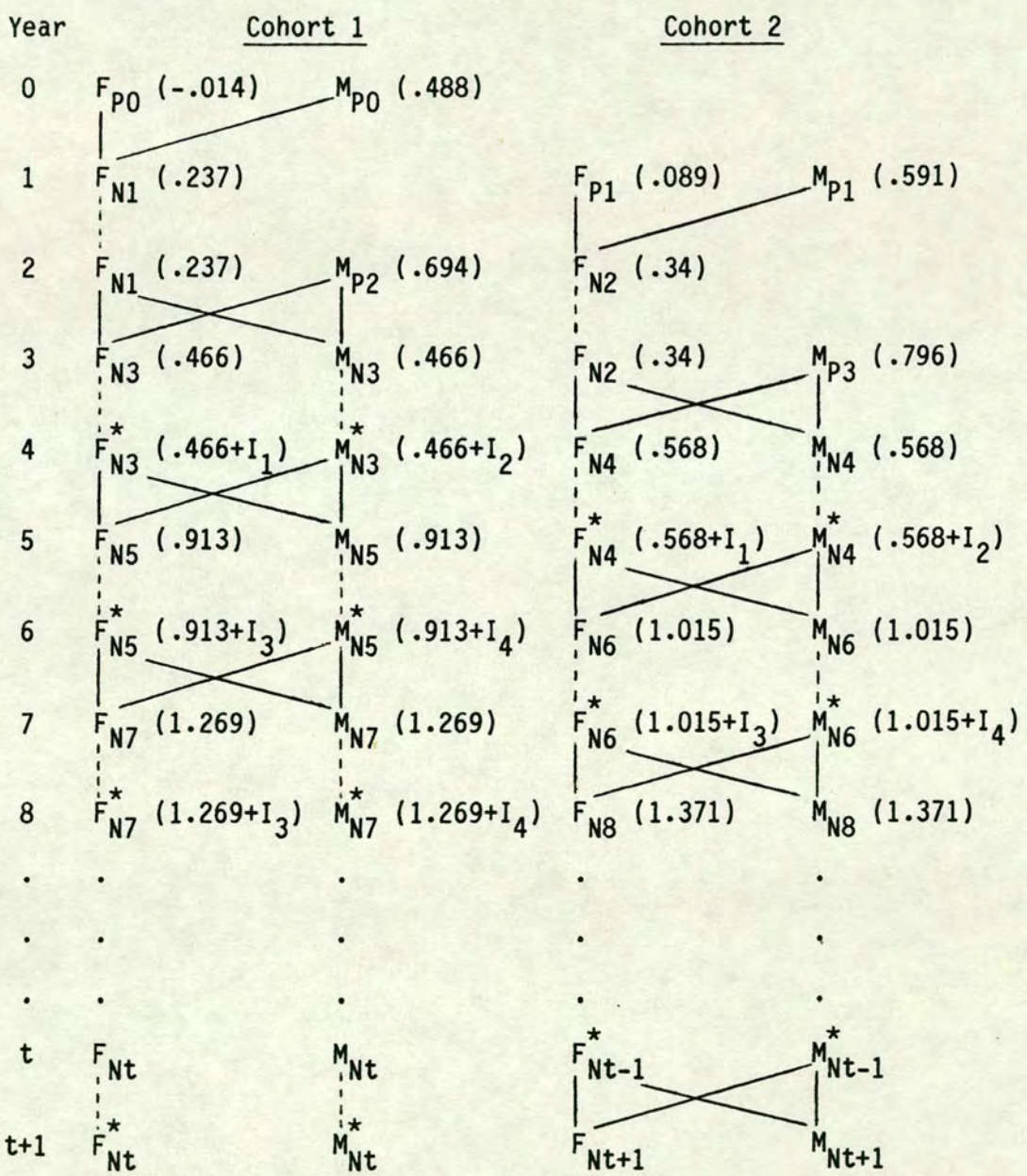
base population. Assuming no genotype-environment interaction, the expected genetic merit of bulls born at different years is as shown in Tables 3 and 4. The genetic merit of commercial cows born over time will depend on the population structure and the genetic lag.

SUMMARY

The genetic response in an efficient progeny testing scheme, improving at a constant annual rate of 0.103 phenotypic standard deviations, is compared to that possible from setting up a Multiple Ovulation and Embryo Transfer (MOET) nucleus scheme at a given year zero using bull parents from this scheme as nucleus herd founder animals. Two MOET nucleus schemes are described, juvenile, with selection before first breeding, and adult, with selection after first lactation. Four years of selection of bull sires are needed to set up the nucleus herds. Setting up the juvenile nucleus herd is less costly than the adult nucleus herd since only two years of selection of bull dams are needed instead of four. With 8 progeny per donor surviving to selection in the juvenile nucleus scheme, the average genetic response of nucleus bulls and commercial cows born at year 20 is 60 and 53% higher than the corresponding response of breeding males and commercial cows born in the same year if the progeny testing scheme is continued. With an adult nucleus scheme, responses are 24 and 16% higher. Short term gains are more substantial from the juvenile than from the adult nucleus scheme. The discounted genetic response of the commercial herd, summed over the first 10 years, is equivalent for the adult nucleus and progeny testing schemes but is over 40% higher for the juvenile nucleus scheme. When summed over the first 20 years, the juvenile scheme proves equally superior.

APPENDIX 1

Setting up the juvenile MOET nucleus scheme. M and F represent males and females; P and N represent animals from the progeny testing scheme and MOET nucleus scheme. The generation interval is two years. The genetic merit of animals is given in the brackets. I_1 and I_2 are the genetic superiorities of nucleus females and males used to breed nucleus offspring respectively, evaluated on nucleus records of the dam and her family and progeny test data of the sire. I_3 and I_4 are the genetic superiorities of nucleus females and males used to breed nucleus offspring respectively, evaluated using nucleus herd information on both the sire and the dam. These superiorities are calculated in appendix 2. The unbroken lines represent reproduction, the broken lines ageing. The asterisks refer to selected nucleus animals.



APPENDIX 2

An example to illustrate how the expected genetic response of newborn juvenile nucleus offspring is calculated (given in standard deviation units). Each donor produces 8 progeny as candidates for selection

Contribution to the Cumulative Genetic Response by Year

Year nucleus offspring born	Year of selection of parents										Cumulative genetic response
	0	1	2	3	4	5	6	7	8	9	
1	.237[1]										.237
2	0	.34[1]									.34
3	.119	0	.347								.466
4	0	.17	0	.398							.568
5	.119	0	.347	0	.447[2]						.913
6	0	.17	0	.398	0	.447[2]					1.015
7	.119	0	.347	0	.447	0	.356[3]				1.269
8	0	.17	0	.398	0	.447	0	.356			1.371
9	.119	0	.347	0	.447	0	.356	0	.356		1.624
10	0	.17	0	.398	0	.447	0	.356	0	.356	1.727

[1] Bull dams and bull sires are used. How these values are derived can be seen in Appendix 1 and the material and methods. Only half this genetic merit is passed on in subsequent generations because nucleus males are not used at years 2 and 3.

[2] $.447 = 1/2\ (I_2 + I_1)$ (see Appendix 1)

$= 1/2\ (i_m r_m h + i_f r_f h) = 1/2\ ((1.968)(0.5522)(0.5) + (1.271)(0.5522)\ (0.5))$

[3] $.356 = 1/2\ (I_4 + I_3)$ (see Appendix 1)

$= 1/2\ (i_m r_m h + i_f r_f h) = 1/2\ [(1.968)(0.4396)(0.5) + 1.271\ (0.4396)(0.5)]$

r_m and r_f represent the correlation of true with expected breeding values for males and females respectively and are calculated using selection index theory.

CHAPTER 5

MONTE CARLO SIMULATION OF AN ADULT MULTIPLE OVULATION AND EMBRYO TRANSFER (MOET) NUCLEUS BREEDING SCHEME IN DAIRY CATTLE WITH COMPARISONS OF SIMULATED AND PREDICTED RESPONSES TO SELECTION

INTRODUCTION

Multiple Ovulation and Embryo Transfer (MOET) is a reproductive technique enabling females to have increased family sizes. It has only been commercially available for cattle since the 1970's, and its use as a potential tool for the genetic improvement of dairy cattle in a nucleus herd was first outlined in detail by Nicholas and Smith (1983). They examined schemes over a broad range of mating ratios and family sizes and predicted that the rates of genetic gain in most of these MOET nucleus schemes would be superior to those achieved in conventional breeding programmes, which rely on evaluating sires by progeny testing.

Several assumptions were made in their predictions of response to selection. Among these, they assumed that the population size was large and consisted of unrelated candidates for selection and that the components of variance were unchanged by factors such as selection and inbreeding. These assumptions are likely to have overestimated the predicted response.

Nicholas and Smith (1983) described two types of MOET nucleus scheme, the juvenile scheme with selection preceding the first lactation and the adult scheme with selection following it. The aim of this study was to model the setting up and operation of an adult MOET nucleus scheme using Monte Carlo simulation and, where relevant, to compare simulated results with those from deterministic

formulae using the same assumptions made by Nicholas and Smith (1983) or with more realistic deterministic algorithms.

MATERIALS AND METHODS

A) Monte Carlo Simulation

(1) The Selection Scheme

The Monte Carlo simulation was of an adult nucleus scheme with discrete generations. Selection was for a single sex-limited trait. An infinitesimal genetic model (Bulmer, 1980) was assumed, implying that a large number of loci with small and additive effects control the trait under selection. It was also assumed that a closed nucleus herd of high genetic merit was established by intense selection of progeny tested sires and potential bull dams and a MOET selection regime was then followed. Six generations of selection were carried out within the nucleus herd. Each generation, animals were eligible for selection only once, after the first lactation record was completed. In practice, this would give a generation interval of about four years.

Selected females were kept in the nucleus for two further lactations to provide additional records for breeding value estimation. The genetic correlation between lactations was assumed to be one. The natural calves of these females were ignored and only offspring bred by MOET following selection were eligible for selection in the next generation. Unselected females had no further lactations.

The complete selection programme can be subdivided into three sections.

(i) Selection of founder animals at generation zero: It was assumed that 100 progeny tested sires and 6400 potential bull dams

were available for selection with accuracies of selection (i.e. the correlation between true breeding values (TBVs) and estimated breeding values (EBVs)) of 0.88 and 0.65 respectively. The TBVs were generated at random from a normal distribution with a mean of zero and a variance of 0.25. In the simulation the permanent and temporary environmental variances were assumed to be 0.25 and 0.5. Thus in the base generation, the phenotypic variance was 1.0 and the heritability and repeatability of the trait under selection were 0.25 and 0.5 respectively.

The candidates for selection were ranked according to their EBVs and then selected. The number of nucleus founder sires and dams selected was assumed to be equal to the number of sires and dams selected within the nucleus in subsequent generations. It was also assumed that the selected founders were unrelated. All matings were carried out at random under a hierarchical mating design.

The TBVs of their offspring, and the offspring born in subsequent generations, were derived using the formula

$$g_i = g_s/2 + g_D/2 + m_i$$

where g_i, g_s and g_D represent respectively the TBVs of an offspring, of its sire and of its dam. The term representing the effect of Mendelian sampling, m_i, was taken at random from a normal distribution with a mean of zero and variance equal to

$$(1 - (F_s + F_D)/2)\ \sigma^2_{go}/2$$

where F_s and F_D are the inbreeding coefficients of the sire and dam and σ^2_{go} represents the genetic variance in the base generation (i.e. 0.25). The parents' inbreeding coefficients were zero in

generations zero and one.

Since the selected trait was sex limited, only females had phenotypes. For the kth record of the ith individual measured in the jth herd-year, these were produced by

$$Y_{ijk} = g_i + p_i + b_j + t_{ijk}$$

where Y, g, p, b and t represent the full lactation record, TBV, permanent environmental effect, herd-year effect and temporary environmental effect respectively. The permanent and temporary environmental effects were chosen at random from normal distributions with means of zero and variances of 0.25 and 0.5 respectively. Each first lactation female was randomly assigned to one of four herds. These herd-year effects, athough treated as fixed in the mixed model evaluation procedures, were generated at random from a normal distribution with a mean of zero and a variance of 0.2. The inclusion of herd-year effects in the model did not affect the results.

(ii) Selection at generation one: Selection of both sexes was carried out once the daughters of the nucleus founders had a first lactation record. After generation zero only records on individuals born in the nucleus were used for evaluation, so that information on the nucleus founders was ignored. Females at generation one were evaluated using their own first record and those of their full and half sisters while males were selected solely on their full and half sister records. An animal model was used to derive Best Linear Unbiased Predictions (BLUP) of TBVs. The males and females with the highest EBVs were then selected and mated at random as before. Genotypes and phenotypes were generated as previously described.

(iii) Selection at generations two to six: Family sizes were the same and genotypes and phenotypes were generated as described. Selection was again based on EBVs, calculated using the animal model. As the scheme becomes established, more information accumulates for breeding value estimation. At generation two, information on nucleus animals born in the previous generation was available. Candidates for selection were evaluated using records of contemporaries, as before, with the addition of three dam records and records from aunts and half aunts. At generation three, grandparental records were included [redacted].

(2) Breeding Value Estimation

An individual animal model was used to derive the EBVs. The model was

$$y = Xb + Wp + Zg + e$$

where y is a nrec x 1 vector of lactation records

b is a nherd x 1 vector of herd-year fixed effects

p is a ndam x 1 vector of animal permanent environmental effects

g is a nind x 1 vector of animal additive genetic effects

e is a nrec x 1 vector of residual effects. For selected females this contains temporary environmental effects and for all other females it contains both temporary and permanent environmental effects.

X, W and Z are design matrices of sizes nrec x nherd, nrec x ndam and nrec x nind respectively.

and

1) nrec = number of lactation records generated within the nucleus.

2) nherd = number of herd-year effects.

3) ndam = number of females selected within the nucleus (each has three lactation records).

4) nind = number of males and females born in the nucleus.

$E(y) = Xb$

and

$$V\begin{bmatrix} p \\ g \\ e \end{bmatrix} = \begin{bmatrix} I\sigma_p^2 & 0 & 0 \\ 0 & A\sigma_g^2 & 0 \\ 0 & 0 & R\sigma_t^2 \end{bmatrix}$$

Note that the permanent environmental effects were only estimated for dams (i.e. females with more than one record). Thus R is a diagonal matrix with diagonal elements equal to 1 if the corresponding female is a dam or $(\sigma_t^2 + \sigma_p^2)/\sigma_t^2$ if not.

σ_t^2, σ_p^2 and σ_g^2 are the temporary environment, permanent environment and genetic variances respectively.

The mixed model equations were

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}W & X'R^{-1}Z \\ W'R^{-1}X & W'R^{-1}W + I\alpha_2 & W'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}W & Z'R^{-1}Z + A^{-1}\alpha_1 \end{bmatrix} \begin{bmatrix} b \\ p \\ g \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ W'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

where $\alpha_2 = \sigma_t^2/\sigma_p^2$ and $\alpha_1 = \sigma_t^2/\sigma_g^2$.

In the simulation, the mixed model equations were not implicitly set up in the matrix form described, as the "indirect approach" method of Schaeffer and Kennedy (1986) was used. It required the creation of two files. The first contained data relevant to each particular individual e.g. sex, phenotype, inbreeding coefficient of parents etc., while the second contained pedigree information. Combining the information from both files, estimates of b, p and g were derived using Gauss-Seidel iteration.

The rate of convergence was checked by dividing the sum of squares of differences in solutions between iterations by the sum of squares of the most recent solutions, as suggested by Schaeffer and Kennedy (1986). To speed up convergence, various relaxation factors were used. Solutions were considered to have stabilised when the convergence criterion was less than 10^{-8}.

(3) Breeding Programmes Simulated

Six different breeding programmes were examined and are described in Table 1. The number of dams selected was 16, 32 or 64 and, with each, four or eight sires were selected. Each dam produced four daughters and one son for selection. The number of sons per dam was restricted to one, so that only one male per full sib family was considered for selection. Thus, as the number of dams was increased, the number of embryos transferred, of recipients needed and of animals born were all increased. With 16, 32 and 64 dams, each simulation was replicated 600, 350 and 170 times respectively.

(4) Calculating Results from the Simulation

(i) Response to Selection

The expected response to selection per generation can be derived using

TABLE 1

Description of the six schemes simulated

	No. of sires selected					
	4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
No. of embryos transferred*	256	512	1024	256	512	1024
No. of dams mated per sire	4	8	16	2	4	8
No. of sons per dam	1	1	1	1	1	1
No. of sons per sire	4	8	16	2	4	8
No. of daughters per dam	4	4	4	4	4	4
No. of daughters per sire	16	32	64	8	16	32
Proportion of males selected	4/16	4/32	4/64	8/16	8/32	8/64
Proportion of females selected	16/64	32/128	64/256	16/64	32/128	64/256

*Assuming a 50% sex ratio and a 50% survival rate of embryos to selection.

$$\Delta G = (r_M \; i_M + r_F \; i_F) \; \sigma_g/2 \qquad [1]$$

where ΔG is the response to selection; σ_g is the genetic standard deviation; r_M and r_F represent the accuracies of selection for males and females while i_M and i_F represent selection intensities for males and females. These last five parameters are the components of response.

Genetic gain and each of the five components of genetic gain were calculated for each generation within a replicate and were then averaged over all replicates. The deterministic formulae used by Nicholas and Smith (1983) assumed that the MOET nucleus scheme was already established and in steady state equilibrium. To allow comparison with their results, simulated results from generations two to six (inclusive) were averaged within each replicate and then over all replicates.

In the simulation, the response to selection and the five components of response were calculated in the following way

a) ΔG : The response to selection at generation t was calculated by

$$\frac{\bar{g}_{S_t} + \bar{g}_{D_t}}{2} - \frac{\bar{g}_{M_t} + \bar{g}_{F_t}}{2}$$

where $\bar{g}_S$, $\bar{g}_D$, $\bar{g}_M$ and $\bar{g}_F$ represent the average TBVs of selected males, of selected females, of male candidates (including selected males) and of female candidates (including selected females) respectively.

This formula ignores the Mendelian sampling variance of the offspring bred by the selected parents. The magnitude of this extra source of variation was easily estimated and was included in the

results.

b) σ_g : Because hierarchical mating designs were used, the genetic variance, and hence the genetic standard deviation, were calculated separately for each sex using analysis of variance techniques. At the same time, the variance of EBVs and the covariance between TBVs and EBVs were also calculated in a similar fashion.

c) r_M and r_F : The accuracies of selection for both sexes were calculated using these variances and covariances.

d) i_M and i_F : These were calculated by dividing the selection differentials by the standard deviation of EBVs.

(ii) Inbreeding

Since the nucleus founders selected in the base generation were assumed to be unrelated, related individuals were first mated at generation one and so the first inbred individuals were born at generation two. Inbreeding coefficients were calculated using the relationship matrix and the rate of inbreeding was calculated for each generation using the formula.

$$\Delta F = (F_t - F_{t-1})/(1-F_{t-1}) \qquad \text{(Falconer, 1981)} \qquad [2]$$

where ΔF is the rate of inbreeding per generation and F_t and F_{t-1} are the average inbreeding coefficients of animals born at generations t and t-1 respectively.

B) Predicting results with simple deterministic formulae

Rates of genetic gain and of inbreeding for the six

simulated schemes were also calculated using the simple deterministic prediction formulae employed by Nicholas and Smith (1983).

(i) Response to Selection

The genetic variance was assumed to equal that in the base generation (i.e. 0.25). The accuracies of selection were calculated for both sexes using selection index theory. The indices included self (females only), full sib, half sib and dam information but ignored grandam records as they have little effect on accuracy. Selection intensities were calculated assuming the existence of a large population of unrelated candidates for selection.

(ii) Inbreeding

Predictions of inbreeding were based on the formula of Wright (1931)

$$\Delta F = 1/8M + 1/8F \qquad [3]$$

where M and F are the number of sires and dams respectively. This formula assumes random selection, random mating and a Poisson distribution of family sizes.

C) Predicting response to selection with more realistic deterministic formulae

By removing some of the assumptions made in the previous section, more realistic predictions of the response to selection were made for the six simulated schemes.

(1) Selection intensities were adjusted for the effect of having finite numbers of candidates available for selection. Extensive tables of these corrected values exist (e.g. Becker, 1975).

(2) Changes in genetic variance and in accuracies of selection over time were included. Wray (1989) recently described a deterministic method of estimating between and within family variances, accounting for inbreeding and selection, and of incorporating them into a pedigree selection index. The variance components were calculated and then used to set up matrices needed for the selection index each generation. Using this method, genetic variances and accuracies of selection for each generation were derived which were used, together with the selection intensities calculated, to predict the response to selection using equation [1].

Some parameters were needed to allow for the effects of selection and inbreeding on genetic variances. Since a pedigree index was not used in the base generation, the genetic variances following selection were calculated accounting for the accuracies and intensities of selection of the nucleus founders. For generation one onwards, the strength of the selection applied to the nucleus animals was represented by k (= i(i-x), where i was the intensity of selection and x the truncation point of the normal distribution and both were calculated accounting for finite numbers (see 1) above)). The value of k differed for males and females but was assumed constant for all generations. Inbreeding coefficients for each generation from the simulation were used.

The between sire ($\sigma^2_{s_t}$), between dam ($\sigma^2_{D_t}$) and within family variances ($\sigma^2_{W_t}$) calculated at generation t were

$$\sigma^2_{s_t} = (0.25\ \sigma^2_{g_{t-1}})\ (1-k_m r^2_{m_{t-1}})\ (1 + F_{t-1} - 2F_t)/(1-F_{t-1})$$

$$\sigma^2_{D_t} = (0.25\ \sigma^2_{g_{t-1}})\ (1-k_f r^2_{f_{t-1}})\ (1 + F_{t-1} - 2F_t)/(1-F_{t-1})$$

$$\sigma^2_{W_t} = 0.5\ \sigma^2_{g_o}\ (1-F_{t-1})$$

$$\sigma^2_{g_t} = \sigma^2_{s_t} + \sigma^2_{D_t} + \sigma^2_{W_t}$$

where $\sigma^2_{g_t}$ is the total genetic variance; t represents the generation number (t = 0 is the base generation); m and f represent males and females and r and F represent the accuracies of selection and the inbreeding coefficients of nucleus animals respectively.

RESULTS

(1) Response to Selection

(a) Simulation

The simulated response to selection and the five components of response averaged over generations two to six are presented in Table 2. Response varied from 0.2 - 0.3 phenotypic standard deviations per generation or 0.8 - 1.1% of the mean per annum.

Response to selection and the components of response for each generation are given in Tables 3 and 4. Because the effect of time on the five components was similar for all six schemes, only one scheme was examined in detail.

As the number of dams, and hence the size of the scheme, was increased, the overall responses increased. This was associated with increases in the accuracies of selection and the male selection intensities, while the genetic standard deviation and the female selection intensities remained relatively constant. With more dams selected, a greater number of animals were available for selection, thus allowing more intense selection of males and providing a greater amount of information for evaluating selection candidates.

With the number of dams constant, the female selection intensities and the genetic standard deviation were slightly higher and the male selection intensities were lower when eight sires were selected instead of four. The effect of sire number on the male selection intensities was greatest when the numbers of dams, and

TABLE 2

Simulated genetic response in phenotypic standard deviation units, and the five components of response averaged over generations two to six inclusive. Results are presented ± standard errors.

	No. of sires selected					
	4			8		
	no. of dams selected			no. of dams selected		
	16	32	64	16	32	64
σ_g	0.422 ±0.001	0.420 ±0.001	0.421 ±0.002	0.443 ±0.001	0.437 ±0.001	0.432 ±0.001
r_M	0.369 ±0.005	0.401 ±0.005	0.445 ±0.005	0.380 ±0.005	0.408 ±0.005	0.433 ±0.005
i_M	1.155 ±0.002	1.456 ±0.004	1.675 ±0.008	0.761 ±0.001	1.215 ±0.002	1.552 ±0.005
r_F	0.517 ±0.003	0.535 ±0.003	0.561 ±0.003	0.533 ±0.003	0.546 ±0.003	0.557 ±0.003
i_F	1.191 ±0.001	1.199 ±0.002	1.197 ±0.002	1.223 ±0.001	1.233 ±0.002	1.237 ±0.002
ΔG	0.225 ±0.003	0.260 ±0.003	0.301 ±0.004	0.210 ±0.002	0.261 ±0.003	0.296 ±0.004
	(0.84%)*	(0.98%)	(1.13%)	(0.79%)	(0.98%)	(1.11%)

*% Genetic gain per annum with a 15% coefficient of variation and an average generation interval of four years.

TABLE 3

Simulated response to selection for generations one to six. ΔG is the average response from generations two to six. Results are presented ± standard deviation of response.

Generation number	No. of sires selected: 4 — no. of dams selected: 16	4 — 32	4 — 64	8 — 16	8 — 32	8 — 64
1	0.198 ±0.128*	0.226 ±0.135	0.254 ±0.123	0.164 ±0.096	0.210 ±0.098	0.239 ±0.098
2	0.245 ±0.145	0.283 ±0.139	0.327 ±0.140	0.211 ±0.104	0.273 ±0.106	0.320 ±0.099
3	0.241 ±0.130	0.277 ±0.146	0.323 ±0.126	0.220 ±0.106	0.271 ±0.108	0.309 ±0.098
4	0.223 ±0.146	0.262 ±0.133	0.291 ±0.127	0.206 ±0.108	0.263 ±0.102	0.302 ±0.101
5	0.217 ±0.130	0.255 ±0.118	0.288 ±0.115	0.210 ±0.103	0.251 ±0.100	0.279 ±0.101
6	0.199 ±0.133	0.226 ±0.123	0.275 ±0.117	0.206 ±0.103	0.246 ±0.106	0.270 ±0.093
ΔG	0.225 ±0.062	0.260 ±0.060	0.301 ±0.057	0.210 ±0.049	0.261 ±0.050	0.296 ±0.047

* The standard error is (standard deviation)/ $\sqrt{\text{no. of replicates}}$. With 16, 32 and 64 dams selected, the $\sqrt{\text{no. of replicates}}$ is 24.5, 18.7 and 13.0 respectively.

TABLE 4

The five components of response over generations one to six for the scheme with four sires and 32 dams selected. Results are given ± standard errors.

Generation	σ_g	r_M	i_M	r_F	i_F
1	0.430 ±0.001	0.294 ±0.011	1.478 ±0.010	0.502 ±0.005	1.221 ±0.003
2	0.447 ±0.002	0.397 ±0.011	1.454 ±0.010	0.542 ±0.006	1.203 ±0.003
3	0.439 ±0.002	0.413 ±0.011	1.454 ±0.010	0.553 ±0.006	1.200 ±0.004
4	0.422 ±0.002	0.412 ±0.011	1.463 ±0.010	0.540 ±0.007	1.200 ±0.004
5	0.402 ±0.002	0.397 ±0.011	1.451 ±0.009	0.531 ±0.007	1.194 ±0.004
6	0.385 ±0.002	0.390 ±0.011	1.456 ±0.010	0.508 ±0.007	1.197 ±0.004

hence the number of male candidates, was lowest. The net result was that although selecting four bulls instead of eight yielded higher genetic gains with 16 dams, sire number had no effect on genetic gain with 32 or 64 dams.

Response to selection varied considerably over generations one to six. The response from the first round of selection of nucleus animals (generation one) was 12-22% lower than the mean response over the following five generations. This was due to both lower accuracies of selection, especially for males, caused by the lack of ancestral information and, more importantly, to the large reductions in between family variances resulting from accurate and intense selection of founder animals in the previous generation. This affected the accuracies of selection for males more than for females, due to the total dependance of males on pedigree information.

For all six schemes, response was highest at generations two or three and declined thereafter. The decline in response over time was a consequence of gradual reductions in the genetic variance and in the accuracies of selection due both to selection and to the accumulation of inbreeding. When four sires and 16 or 32 dams were selected, the response to selection at generation six was as low as that in generation one. By comparison, with eight sires and 16 dams selected, the response from generations two to six was very similar, and remained within the narrow range of 0.206 - 0.220.

Table 3 also shows the influence that the selection strategy had on the variation in response. The number of sires selected was the most important factor, and the standard deviation of response was highest for all generations when four sires were selected. With a constant number of sires selected, the number of dams had relatively little effect. In general, greater variation in response was found

in schemes with more inbreeding (see Table 9), as was expected (Hill, 1977b).

(b) Simple deterministic formulae

The response to selection and the components of response were substantially overestimated by the simple deterministic model, as shown in Table 5. The predicted rates of genetic gain were 40-67% higher than responses from simulation. The predictions deviated most from simulated results when few sires were selected.

There was wide variation in the extent to which the components of response differed between simulated values and deterministic predictions. Over the range of schemes examined, the components of response were overestimated by 3 to 42%. When the five components were ranked by the agreement of predicted and simulated results, the same order was found for all six schemes. The selection intensities for females and males respectively were predicted most accurately with the simple deterministic model, while the predictions of the genetic standard deviation and the accuracies of selection for females and males respectively were the least successful.

The predicted selection intensities for both sexes were derived assuming that a large number of unrelated candidates were available for selection. The female selection intensities predicted were closer to the simulated values due to the relatively large number of female candidates and the low selection pressure applied (25%). By comparison, the number of male candidates was small and the selection pressure ranged from 50% up to 6%. The selection intensity deviated most from simulation when the number of sire families was small and the selection pressure on males was high, as predicted by Hill (1976).

TABLE 5

Predictions of genetic gain and the five components of genetic gain from simple deterministic formulae, assuming base generation variances and large population sizes. The percentage differences between these predictions and the simulated values (Table 2) are given in brackets

	No. of sires selected					
	4			8		
	no. of dams selected			no. of dams selected		
	16	32	64	16	32	64
σ_g	0.500 (18%)*	0.500 (19%)	0.500 (19%)	0.500 (13%)	0.500 (14%)	0.500 (16%)
r_M *1	0.523 (42%)	0.550 (37%)	0.573 (29%)	0.494 (30%)	0.523 (28%)	0.550 (27%)
i_M	1.271 (10%)	1.647 (13%)	1.968 (17%)	0.798 (5%)	1.271 (5%)	1.647 (6%)
r_F *2	0.636 (23%)	0.653 (22%)	0.667 (19%)	0.619 (16%)	0.636 (16%)	0.653 (17%)
i_F	1.271 (7%)	1.271 (6%)	1.271 (6%)	1.271 (4%)	1.271 (3%)	1.271 (3%)
ΔG	0.368 (63%)	0.434 (67%)	0.494 (64%)	0.295 (40%)	0.368 (41%)	0.434 (47%)

*Calculated by (σ_g Predicted/σ_g Simulated - 1) x 100

*1 Each male is evaluated using a single record from four full sisters and 4(x-1) half sisters and three records from the dam, where x is the number of dams mated to each sire.

*2 Each female is evaluated using her own record, single records from three full sisters and 4(x-1) half sisters and three records from her dam.

The predictions of the genetic standard deviation and the accuracies of selection were substantially overestimated because it was assumed that the genetic variance in the population was equal to that in the base generation. In the simulation it was considerably lower, due to the effect of selection on between family genetic variances (Bulmer, 1971) and the effect of inbreeding on the between and within family variances.

(c) More realistic deterministic formulae

By comparison, the predictions of response with deterministic formulae accounting for changes in genetic variances and for the effect of finite numbers on selection intensities agreed very well with simulated responses. Results are shown in Table 6. Although individual components of response were up to 5% lower and 14% higher than simulation, the predicted responses were within 4% of the simulated responses for all six schemes.

The deterministic algorithms underestimated slightly the accuracies of selection and the genetic standard deviation and overestimated the intensities of selection. Accuracies of selection may have been higher than predicted because an animal model with BLUP of breeding values was used instead of a selection index. Intensities of selection were lower than predicted because the EBVs of the candidates for selection were correlated (Hill, 1976). The selection intensities may also have been affected by departures from normality.

Although the deterministic algorithms predicted the selection responses with considerable accuracy, the benefits of selecting fewer sires were slightly overestimated. The predicted selection responses with four sires selected were up to 3% higher than simulated responses but were up to 4% lower with eight sires

TABLE 6

Predictions of genetic gain and the five components of genetic gain from more realistic deterministic formulae. Selection intensities were calculated accounting for the finite population size. The method of Wray (1989) was adopted to account for the effects of inbreeding and selection on genetic variances and on the accuracies of selection. Inbreeding coefficients from the simulation were used in these predictions. The predicted values were calculated for generations two to six (inclusive) and then averaged. The percentage differences between these predictions and the simulated values (Table 2) are given in brackets.

	No. of sires selected					
	4			8		
	no. of dams selected			no. of dams selected		
	16	32	64	16	32	64
σ_g	0.414 (-2%)	0.413 (-2%)	0.413 (-2%)	0.437 (-1%)	0.433 (-1%)	0.429 (-1%)
r_M	0.369 (0%)	0.397 (-1%)	0.424 (-5%)	0.366 (-3%)	0.387 (-5%)	0.411 (-5%)
i_M	1.201 (4%)	1.583 (9%)	1.911 (14%)	0.760 (0%)	1.235 (2%)	1.614 (4%)
r_F	0.520 (0%)	0.535 (0%)	0.551 (-2%)	0.529 (-1%)	0.538 (-1%)	0.550 (-1%)
i_F	1.252 (5%)	1.261 (5%)	1.265 (6%)	1.252 (2%)	1.261 (2%)	1.265 (2%)
ΔG	0.226 (0%)	0.269 (3%)	0.311 (3%)	0.205 (-2%)	0.250 (-4%)	0.292 (-1%)

selected. Consequently, a 10, 8 and 7% increase in response was predicted when selecting four instead of eight sires with 16, 32 and 64 dams respectively, whereas the simulated increases were only 7, 0 and 2%.

To distinguish between the effects of selection and inbreeding on the efficiency of the predictors of response, the inbreeding coefficients were set to zero for all generations in the algorithms so that the impact of inbreeding on the predicted response was ignored. Results are shown in Table 7.

Substantial improvements in deterministic predictions of response were achieved when the effects of selection were accounted for. The genetic standard deviation and the accuracies of selection predicted were 0-11% higher than simulated results compared to 13-42% higher when selection was ignored (Table 5).

Combined with the small improvement in predicting selection intensities by adjusting for finite numbers, predictions of response accounting for selection overestimated the simulated response by 6-23% compared to 40-67% using simple deterministic formulae. The overestimation of response was greater with four sires selected (21-23%) than with eight sires (6-9%). Thus, accounting for selection substantially narrowed the gap between predicted and simulated responses and including the simulated inbreeding coefficients in the algorithms effectively closed the gap.

The inbreeding coefficients used were simulated values calculated using pedigree information. In practice, these values would not be available and estimates would be needed. To examine the effect this would have on the predictions, inbreeding coefficients calculated by

$$F_t = 1 - (1 - \Delta F)^t \qquad \text{(Falconer, 1981)} \qquad [4]$$

TABLE 7

The genetic standard deviation and the accuracies of selection predicted by deterministic algorithms which account for selection but ignore inbreeding. These values were calculated for generations two to six (inclusive) and averaged. Genetic gain was calculated using these three components of response and the selection intensities adjusted for finite numbers (as shown in Table 6). The percentage difference between these predictions and the simulated values (Table 2) are given in brackets.

	No. of sires selected					
	4			8		
	no. of dams selected			no. of dams selected		
	16	32	64	16	32	64
σ_g	0.458 (8%)	0.455 (8%)	0.453 (7%)	0.461 (4%)	0.458 (5%)	0.455 (5%)
r_M	0.409 (11%)	0.433 (8%)	0.454 (2%)	0.388 (2%)	0.409 (0%)	0.432 (0%)
r_F	0.561 (8%)	0.574 (7%)	0.585 (4%)	0.551 (3%)	0.561 (3%)	0.573 (3%)
ΔG	0.273 (21%)	0.321 (23%)	0.364 (21%)	0.227 (8%)	0.278 (6%)	0.324 (9%)

where ΔF is estimated from the simplistic equation [3], were used in the deterministic algorithms. The results are given in Table 8.

The simple equations for predicting inbreeding underestimated the true inbreeding coefficients at each generation. As a result, the influence of inbreeding on the genetic variances and on the accuracies of selection was underestimated. Consequently, the predicted responses overestimated the simulated responses by 11-14% with four sires selected and by 2-5% with eight sires. Nevertheless, these results were an improvement compared with predictions made ignoring inbreeding.

(2) Inbreeding

The average inbreeding coefficients of animals born at different generations from the simulation are shown in Table 9. The number of sires selected had a dramatic effect on inbreeding. Inbreeding was far higher when four sires were selected than with eight sires. As an illustration, animals born at generation seven, about 25 years after the nucleus founders were selected, were 37-39% and 23-26% inbred with four and eight sires selected respectively.

As the number of dams increased, it was expected that inbreeding would be reduced because of the increased number of selection candidates etc. However, in the schemes studied, increasing the number of dams reduced inbreeding when four sires were selected but increased it with eight sires.

This result was brought about by changes in sire family sizes. The number of progeny per sire was directly proportional to the number of dams (see Table 1). As the sires' family size increased, greater numbers of progeny per sire were selected due to the high intra class correlations of EBVs of relatives, (see Table

TABLE 8

The genetic standard deviation and accuracies of selection predicted by deterministic algorithms which account for selection and inbreeding. The inbreeding coefficients used were derived from simplistic formulae and so underestimated the simulated inbreeding values. These three components of response were calculated for generations two to six (inclusive) and averaged. Genetic gain was calculated using these components and the selection intensities adjusted for finite numbers (as shown in Table 6). The percentage difference between these predictions and the simulated values (Table 2) are given in brackets.

	No. of sires selected					
	4			8		
	no. of dams selected			no. of dams selected		
	16	32	64	16	32	64
σ_g	0.435 (3%)	0.435 (4%)	0.434 (3%)	0.447 (1%)	0.447 (2%)	0.445 (3%)
r_M	0.390 (6%)	0.417 (4%)	0.441 (-1%)	0.376 (-1%)	0.399 (-2%)	0.425 (-2%)
r_F	0.541 (5%)	0.557 (4%)	0.570 (2%)	0.539 (1%)	0.551 (1%)	0.565 (1%)
ΔG	0.249 (11%)	0.296 (14%)	0.339 (13%)	0.215 (2%)	0.265 (2%)	0.312 (5%)

TABLE 9

Inbreeding coefficients (in %) of animals born in the nucleus. Results are expressed ± standard errors

Generation	No. of sires selected: 4 — no. of dams selected: 16	32	64	No. of sires selected: 8 — no. of dams selected: 16	32	64
2	7.54 ± 0.12	6.84 ± 0.12	6.33 ± 0.14	3.81 ± 0.08	4.08 ± 0.07	3.91 ± 0.09
3	14.51 ± 0.15	14.09 ± 0.17	13.39 ± 0.22	7.78 ± 0.10	8.10 ± 0.10	8.68 ± 0.16
4	21.48 ± 0.20	20.93 ± 0.22	19.96 ± 0.29	11.65 ± 0.12	12.56 ± 0.14	13.07 ± 0.22
5	27.90 ± 0.23	27.39 ± 0.25	26.04 ± 0.34	15.62 ± 0.14	16.53 ± 0.17	17.47 ± 0.24
6	33.89 ± 0.25	33.26 ± 0.29	31.73 ± 0.37	19.63 ± 0.16	21.04 ± 0.19	21.78 ± 0.29
7	39.31 ± 0.26	38.47 ± 0.31	37.26 ± 0.39	23.27 ± 0.17	25.08 ± 0.20	25.79 ± 0.31

10). These correlations reveal the extent of co-selection of relatives. With a value of one, EBVs of family members are identical and all will be selected together.

Inbreeding rates are determined by the number of selected offspring that each individual produces. Because of the hierarchical mating structure and the restriction of one son per dam, the different mating designs used gave rise to different rates of inbreeding. Thus when eight sires were selected, they could be bred by a minimum of four sires when 16 dams were selected and a minimum of one sire with 64 dams selected. By comparison, when four sires were selected, it was possible in all three schemes for a single sire to have bred all animals selected.

Using equation [2], the rate of inbreeding (ΔF) was calculated for each generation and these results are presented in Table 11. For a given scheme, the inbreeding rate was not constant over all generations. Inbreeding rates were lowest in the early generations. In five of the six schemes, the inbreeding rates were lowest, sometimes substantially, at generation two. This was due to the low intra class correlations of EBVs of family members at generation one, resulting from poor accuracy of evaluation of the candidates for selection. The intra class correlations of EBVs of male half sibs, of female half sibs and of female full sibs were 7-20%, 34-46% and 17-23% lower respectively at generation one than at generations two to six and so both the probabilities of selecting full and half sibs and the inbreeding rates were reduced compared to later generations.

In Table 11, the inbreeding rates averaged over generations two to six were compared to predictions from the simplistic equation [3]. Simulated inbreeding rates were 1.8-2.7 times higher than predicted.

TABLE 10

Intra class correlations of EBVs of male half sibs (mhsibs), of female half sibs (fhsibs) and of female full sibs (ffsibs). The (1) represents generation one and (2) represents the average for generations two to six (inclusive). Results are expressed ± standard errors.

Intra class correlations		No. of sires selected: 4, no. of dams selected: 16	4, 32	4, 64	8, 16	8, 32	8, 64
mhsibs	(1)	0.457 ±0.014	0.513 ±0.016	0.543 ±0.021	0.504 ±0.014	0.544 ±0.014	0.613 ±0.016
mhsibs	(2)	0.571 ±0.005	0.611 ±0.005	0.656 ±0.006	0.590 ±0.004	0.622 ±0.004	0.660 ±0.004
fhsibs	(1)	0.212 ±0.010	0.243 ±0.012	0.266 ±0.016	0.219 ±0.010	0.249 ±0.010	0.293 ±0.012
fhsibs	(2)	0.383 ±0.005	0.410 ±0.005	0.446 ±0.006	0.403 ±0.004	0.421 ±0.004	0.442 ±0.005
ffsibs	(1)	0.545 ±0.007	0.569 ±0.008	0.600 ±0.010	0.551 ±0.007	0.574 ±0.007	0.614 ±0.008
ffsibs	(2)	0.705 ±0.003	0.722 ±0.003	0.738 ±0.004	0.715 ±0.002	0.728 ±0.002	0.738 ±0.003

TABLE 11

Inbreeding rates per generation. Results are expressed as percentages ± standard errors. ΔF represents the average inbreeding rates for generations two to six (inclusive)

	No. of sires selected					
	4			8		
Generation	no. of dams selected			no. of dams selected		
	16	32	64	16	32	64
2	7.54 ±0.12	6.84 ±0.12	6.33 ±0.14	3.81 ±0.08	4.08 ±0.07	3.91 ±0.09
3	7.50 ±0.15	7.78 ±0.15	7.54 ±0.19	4.09 ±0.13	4.18 ±0.11	4.97 ±0.14
4	8.14 ±0.18	7.95 ±0.19	7.59 ±0.23	4.16 ±0.14	4.83 ±0.14	4.80 ±0.16
5	8.16 ±0.20	8.17 ±0.20	7.62 ±0.22	4.46 ±0.15	4.53 ±0.14	5.05 ±0.18
6	8.32 ±0.20	8.12 ±0.21	7.71 ±0.22	4.71 ±0.14	5.38 ±0.16	5.24 ±0.19
7	8.16 ±0.19	7.83 ±0.21	8.11 ±0.24	4.50 ±0.15	5.10 ±0.16	5.11 ±0.20
ΔF	7.93 +0.07 (203%)*	7.77 +0.08 (221)	7.36 +0.10 (222)	4.25 +0.04 (181)	4.60 +0.05 (236)	4.79 +0.07 (272)

*Inbreeding rate expressed as a percentage of predictions from equation [3].

DISCUSSION

While most of the emphasis in this study was placed on comparing average rates of genetic gain of MOET nucleus schemes once they were fully operational (i.e. generations two to six), responses in the first two generations were also of interest. The cumulative selection responses from all seven rounds of selection are presented in Table 12.

It is noteworthy that whereas the rates of response in the nucleus increased as the schemes became bigger, the smaller schemes had the highest genetic lift in the base generation. The initial superiority of the smaller schemes affected the cumulative responses so that the advantages of selecting more dams were less pronounced in the early generations and the benefits of selecting fewer sires were enhanced.

The response from the first round of selection of nucleus animals was substantially lower than the average response over the following five generations. This was due to lower accuracies of selection (especially for males) resulting from less available information and the substantial reductions in between family genetic variances due to selecting the nucleus founders. For this reason, the success or failure of MOET nucleus schemes in practice, should not be judged too readily.

The decline in response in later generations (as well as the continuous accumulation of inbreeding) indicates that it would be inappropriate to operate small closed MOET nucleus schemes for long periods of time. For long term genetic response, larger schemes or open nucleus schemes would be needed.

This study has shown that the rates of genetic gain predicted by simple deterministic formulae assuming the existence of large population sizes and base generation genetic variances,

TABLE 12

Cumulative genetic response to selection (in phenotypic standard deviations) for generations zero to six (inclusive). The genetic mean of the candidates for selection at generation zero was zero.

Generation	No. of sires selected: 4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
0	0.970	0.932	0.899	0.908	0.872	0.833
1	1.167	1.157	1.153	1.073	1.083	1.072
2	1.413	1.440	1.480	1.284	1.355	1.392
3	1.654	1.717	1.803	1.503	1.626	1.701
4	1.877	1.979	2.093	1.709	1.889	2.003
5	2.094	2.234	2.382	1.919	2.140	2.282
6	2.294	2.459	2.656	2.124	2.386	2.552

seriously overestimated likely responses to selection. Predictions were least accurate with few sires and so genetic gains were overestimated by 63-67% with four sires selected and by 40-47% with eight sires.

The most erroneous assumption made was that the genetic variances were equal to those in the base generation. This assumption led to substantial overestimates of both the accuracies of selection and the genetic standard deviation. By comparison, the assumption of large population sizes had less effect as the simulated selection intensities were relatively close to the deterministic predictions.

The number of sires selected had a crucial influence on the simulated results. Contrary to simplistic deterministic predictions, selecting four sires instead of eight involved no increase in response, except with 16 dams selected. Inbreeding and the variance of response to selection were substantially higher when four sires were selected. These results show clearly the disadvantages of selecting too small a number of sires.

When comparing results from schemes of equal size, the differences between simulated and predicted responses (assuming large population sizes and base generation variances) were greater in this study than in two other adult nucleus scheme simulation studies. In addition, the responses found by Juga and Maki-Tanila (1987) were higher than those described in this study, while the responses of Jansen and Schlote (1987) were lower.

The study of Juga and Maki-Tanila (1987) ignored the effect of inbreeding on genotypes and so overestimated the genetic variance in the population and the response to selection. By setting the inbreeding coefficients to zero in schemes of equal size and comparing the responses with those from schemes accounting for

inbreeding, the overestimation of response was found to be about 10%. Meuwissen (1989a) used a deterministic model to predict quite accurately (i.e. within 7%) the genetic gain expected in two of the three schemes simulated by Juga and Maki-Tanila (1987). The model accounted for the reduction in genetic variance due to selection (but not due to inbreeding) and for the effects of finite numbers and the family structure on the intensities of selection.

The simulation results from this study and that of Juga and Maki-Tanila (1987) differed in one other way. They estimated the accuracies of selection for both sexes from the diagonal elements of the inverted coefficient matrix and found that they agreed closely with expectations from selection index theory using base generation variances. It is possible that the small number of replicates used in their study (10) may explain this discrepancy.

Simulated responses were lowest in the study of Jansen and Schlote (1987). The reduced responses were a consequence of evaluating the candidates for selection with less accuracy. Males and females were selected solely on full sib family means and their own first lactation records respectively.

The deterministic algorithms accounting for the effects of selection and inbreeding on genetic variances and accuracies of selection were developed by Wray (1989) for large pig nucleus breeding schemes. In the present study, despite having much smaller population sizes and more intense selection for a sex-limited trait, the deterministic algorithms were efficient predictors of the simulated responses.

The development of accurate deterministic predictions of response will be useful for optimising breeding schemes in small populations. Compared to simulation studies of such schemes, they require little computation and are less time consuming. However

these algorithms are only appropriate for populations with discrete generations and would require expansion to deal with overlapping generations.

Since the deterministic algorithms accounting for selection and inbreeding were efficient predictors of response for the six simulated schemes, responses were calculated for a wide range of alternative schemes and these are presented in Table 13. The inbreeding coefficients used in the algorithms were derived from equation [4] and the inbreeding rates were assumed to be twice the values predicted by equation [3].

The schemes varied considerably in size so that the smallest schemes required about 250 recipients, and the largest, 8000. Responses ranged from 0.6 to 1.6% per annum. The benefits of increasing the size of the schemes diminished as the schemes got bigger. Thus the increase in response from replacing 32 dams (500 recipients) with 128 dams (2000 recipients) was greater than that resulting from the selection of 512 dams (8000 recipients) instead of 128 dams.

The inbreeding coefficients used in the deterministic algorithms had a considerable effect on the responses predicted. For schemes with high rates of inbreeding (e.g. with four sires), underestimating the rate of inbreeding resulted in over-optimistic predictions of response (Tables 7 and 8). Methods to predict inbreeding in selected populations (Woolliams, 1989; Wray and Thompson, 1990) should prove useful in overcoming this problem. For schemes with relatively low rates of inbreeding (e.g. with eight sires), predicted responses were less influenced by the inbreeding coefficients used.

The simulated rates of inbreeding ranged from 1 to 2% per year and depended primarily on the number of sires selected. The

TABLE 13

Predictions of genetic gain for a wide range of schemes with deterministic algorithms accounting for the effects of selection and inbreeding on genetic variances and accuracies of selection and of finite numbers on selection intensities. Each dam had four daughters and one son. Genetic gain per annum with a 15% coefficient of variation and a four year generation interval is given in brackets.

Number of sires	Number of dams					
	16*	32	64	128	256	512
2	0.222 (0.83%)	0.264 (0.99%)	0.300 (1.12%)	0.331 (1.24%)	0.356 (1.34%)	0.385 (1.44%)
4	0.226 (0.85%)	0.273 (1.02%)	0.315 (1.18%)	0.352 (1.32%)	0.384 (1.44%)	0.415 (1.56%)
6	0.215 (0.81%)	0.264 (0.99%)	0.309 (1.16%)	0.349 (1.31%)	0.384 (1.44%)	0.417 (1.56%)
8	0.203 (0.76%)	0.253 (0.95%)	0.300 (1.12%)	0.342 (1.28%)	0.379 (1.42%)	0.414 (1.55%)
10	0.191 (0.72%)	0.243 (0.91%)	0.291 (1.09%)	0.335 (1.26%)	0.373 (1.40%)	0.410 (1.54%)
12	0.179 (0.67%)	0.234 (0.88%)	0.283 (1.06%)	0.328 (1.23%)	0.368 (1.38%)	0.405 (1.52%)
16	0.151 (0.57%)	0.218 (0.82%)	0.268 (1.00%)	0.314 (1.18%)	0.357 (1.34%)	0.395 (1.48%)
20		0.202 (0.76%)	0.255 (0.96%)	0.303 (1.14%)	0.346 (1.30%)	0.384 (1.44%)

*Assuming a 50% sex ratio and a 50% survival rate of embryos to selection, the number of embryo transfers needed for each scheme is 16 x (number of dams).

formula of Wright (1931) for predicting inbreeding rates in populations with random selection was inappropriate for these breeding schemes and substantially underestimated the simulated rates.

SUMMARY

Six generations of selection in a closed adult multiple ovulation and embryo transfer (MOET) nucleus breeding scheme with discrete generations in dairy cattle were modelled using Monte Carlo simulation. The six schemes simulated had 16, 32 or 64 dams and four or eight sires selected with a hierarchical mating design and four daughters and one son per dam. Selection was for a single trait with a heritability of 0.25 and a repeatability of 0.5 in the base generation. Response to selection ranged from 0.2-0.3 phenotypic standard deviations per generation or 0.8-1.1% per year. Selecting eight sires instead of four resulted in no loss in response, except with 16 dams, and brought about substantial reductions both in inbreeding and in the variance of response. Simple predictions of genetic gain, assuming infinite population sizes and base generation variances, overestimated simulated responses by 40-47% with eight sires and by 63-67% with four sires selected. More realistic predictions of genetic gain, accounting for the effect of finite population sizes on selection intensities and the effects of inbreeding and selection on genetic variances and accuracies of selection, were within 4% of the simulated responses. Simulated inbreeding rates were 4.2-4.8% and 7.4-7.9% per generation with eight and four sires selected respectively. These inbreeding rates were 1.8-2.7 times higher than predicted by simple formulae, assuming random selection.

CHAPTER 6

THE EFFECT OF ALTERNATIVE MATING DESIGNS AND SELECTION STRATEGIES ON ADULT MULTIPLE OVULATION AND EMBRYO TRANSFER (MOET) NUCLEUS SCHEMES IN DAIRY CATTLE

INTRODUCTION

The results of the previous chapter showed that the adult MOET nucleus schemes as described by Nicholas and Smith (1983) are likely to yield substantially lower rates of genetic progress and far higher rates of inbreeding than originally predicted.

However, the schemes proposed by Nicholas and Smith (1983) were of a specific design. They assumed a hierarchical mating design with each sire mated at random to a constant number of dams and each dam mated to only one sire. Each mating produced a fixed number of daughters and a single son as candidates for selection. The number of sons eligible for selection per dam was restricted to one in order to reduce inbreeding by preventing the automatic coselection of male full sibs. This would occur since males are evaluated on pedigree information only and so all full sibs have the same estimated breeding value (EBV).

The aim of this study was to examine the implications of using alternative mating designs and selection strategies in adult MOET nucleus schemes. Four alternatives were investigated. The first was the use of assortative mating instead of random mating. The introduction of a positive correlation between the EBVs of mated individuals was expected to result in an increase in between family genetic variances but at a cost of increased inbreeding rates (McBride and Robertson, 1963).

The second alternative examined was the use of more than one male from a selected sibship. By doing so the number of males selected was increased without reducing the selection pressure. Nicholas and Smith (1983) suggested that this strategy would reduce inbreeding but made no attempt to quantify the possible benefits.

The third alternative examined was the use of factorial mating designs, where each dam is mated to more than one sire. As pointed out by Woolliams (1989), with this arrangement the number of sire x dam mating combinations is increased compared to the hierarchical design. With one son per mating eligible for selection, he predicted that higher rates of response would be achieved, due to the increased number of male candidates, without increasing inbreeding.

Finally, the benefits possible from combining the use of more than one male from a selected sibship with factorial mating designs were investigated.

MATERIALS AND METHODS

Description of simulation

The assumptions contained in these simulations were the same as in the previous chapter.

(1) Assortative Mating

Once males and females were selected, they were either mated at random with respect to their EBVs or, alternatively, the males with the highest EBVs were mated to the highest ranking females and the lowest ranking males to the lowest ranking females (i.e. positive assortative mating). Six different breeding schemes were examined. Four or eight sires were mated to 16, 32 or 64 dams in a hierarchical mating design and with four daughters and one son eligible for

selection from each mating. The results from schemes using random mating were the same as those presented in the previous chapter. Schemes with 16, 32 and 64 dams selected were replicated 600, 350 and 170 times respectively.

(2) Using full brothers from selected sibships (sibship schemes)

Since the EBV of each male was identical to that of his full brothers, allowing more than one male per sibship to be eligible for selection had no effect on the selection pressure applied to males, provided the number of selected sibships was constant. To keep the selection pressure constant (at one in four or one in eight respectively), the number of sires selected increased in proportion to the number of males per sibship eligible for selection. Eight breeding schemes were examined and are described in Table 1.

The number of males per sibship eligible for selection was set to 1, 2, 3 or 4 while the number of female full sibs was four in all cases. Thirty two dams and four or eight sibships were selected. With 1, 2 and 4 males per sibship, each sire was mated to an equal number of dams in a hierarchical mating pattern. With three males per sibship, some sires, chosen at random, were mated to an additional dam. The results with one male per sibship were the same as those presented in the previous chapter.

The number of founder sires selected to set up the nucleus in the base generation was assumed to equal the number of male sibships selected within the nucleus in subsequent generations. Thirty two dams were selected in all generations and each scheme was replicated 350 times.

(3) Factorial mating designs (factorial schemes)

The technique of multiple ovulation and embryo transfer

TABLE 1

Description of schemes permitting the selection of full brothers (sibship schemes). Thirty two dams were selected in each scheme.

	No. of male sibships selected							
	4				8			
	No. of sons per dam eligible for selection				No. of sons per dam eligible for selection			
	1	2	3	4	1	2	3	4
No. of sires selected	4	8	12	16	8	16	24	32
No. of dams mated per sire	8	4	2.67*[1]	2	4	2	1.33*[2]	1
No. of sons per sire	8	8	8*[1]	8	4	4	4*[2]	4
Total no. of male candidates	32	64	96	128	32	64	96	128
No. of daughters per dam	4	4	4	4	4	4	4	4
No. of daughters per sire	32	16	10.67*[1]	8	16	8	5.33*[2]	4
Proportion of males selected	4/32	8/64	12/96	16/128	8/32	16/64	24/96	32/128
Proportion of females selected	32/128	32/128	32/128	32/128	32/128	32/128	32/128	32/128

*[1] Eight sires were mated to three dams and four sires to two dams.
*[2] Sixteen sires were mated to one dam and eight sires to two dams.

involves flushing a small number of fertilised eggs from the donor at repeated time intervals, usually 6-8 weeks. Because a different sire can be used at each flush, this opens up the possibility of utilising factorial mating designs. Compared to hierarchical mating designs, this means that a given donor is mated to more than one sire and that a given sire is mated to an increased number of donors. The total number of different mating pairs increases, while the number of offspring per mating decreases.

In this study the number of sires mated to each donor was set to 1, 2, 3 or 4 and the impact of these designs was studied when either four or eight sires were mated with 32 donors. All schemes were replicated 350 times. The eight schemes are described in Table 2.

One sire per donor represents the hierarchical mating design and the results are the same as shown in the previous chapter. As assumed by Nicholas and Smith (1983), only one male per full sibship was eligible for selection. With 1, 2, 3 and 4 sires per donor, the number of matings i.e. the number of sibships, was 32, 64, 96 and 128 respectively. In all cases, the number of daughters per donor was four. Factorial designs were used in each generation, including the base generation.

By replacing hierarchical with factorial mating designs, the population structure and the genetic relationships among individuals were changed. Maternal as well as paternal half sibs were generated. In addition, the number of full sisters was reduced, each being replaced by one maternal and one paternal half sib. For example, with eight sires and 32 dams selected, each male had four full sisters and 12 paternal half sisters in the hierarchical situation. By comparison, when each dam was mated to two sires, each male had two full sisters and 14 paternal and two maternal half

TABLE 2

Description of schemes utilising factorial mating designs (factorial schemes). Thirty two dams were selected in each scheme.

	No. of sires selected							
	4				8			
	No. of sires mated per dam				No. of sires mated per dam			
	1	2	3	4	1	2	3	4
No. of dams mated per sire	8	16	24	32	4	8	12	16
No. of sons per dam	1	2	3	4	1	2	3	4
No. of sons per sire	8	16	24	32	4	8	12	16
Total no. of male candidates	32	64	96	128	32	64	96	128
No. of daughters per dam	4	4	4	4	4	4	4	4
No. of daughters per sire	32	32	32	32	16	16	16	16
Proportion of males selected	4/32	4/64	4/96	4/128	8/32	8/64	8/96	8/128
Proportion of females selected	32/128	32/128	32/128	32/128	32/128	32/128	32/128	32/128

sisters. Furthermore with one son per mating the number of males was increased so that each individual had more half brothers.

The factorial designs were arranged so that the number of different combinations of sires mated to each donor was maximised, thus making the population as heterogeneous as possible. For a given number of sires selected (n) and a given number of sires mated to each donor (r), the total number of different combinations of sires per donor possible can be derived by

$$\binom{n}{r} = \frac{n(n-1)\ (n-2)\ \ldots\ (n-r+1)}{1.2.3\ldots.\ (r-1).r}$$

With n = 4 there are 4, 6, 4 and 1 different sire combinations for r = 1, 2, 3 and 4 respectively. With n = 8 there are 8, 28, 56 and 70 combinations for r = 1, 2, 3 and 4. Because the number of donors, and hence the number of different combinations possible, was 32, four of the six designs had at least one complete set of sire combinations. With eight sires selected and each donor mated to three or four sires, a cyclic design (John et al., 1972, p.37) and an incomplete block design (Cochran and Cox, 1957, p.473) were used respectively.

As described in the previous chapter, the five components of response were calculated using the variances of the distributions of TBVs and EBVs and the covariance between TBVs and EBVs, estimated using analysis of variance techniques assuming a hierarchical population structure. With factorial mating designs in use, the assumption of a hierarchical structure resulted in a negligible overestimation of these (co) variance values.

(4) Factorial mating designs with selection of male sibs (Factorial sibship schemes)

In the factorial mating designs just outlined, one male per mating was eligible for selection so that full sib males would not be selected. An alternative proposal would be to allow more than one male per sibship to be selected while selecting a constant number of sibships. With this strategy, the selection pressure would be unchanged and, since a greater number of males would be selected, inbreeding should be reduced.

With fixed resources the number of males eligible for selection per sibship is limited when factorial mating designs are used, since the increased number of matings is achieved by reducing the number of offspring per mating. Let us assume that each donor has four flushes, with one son and one daughter surviving to selection from each. If the donor is mated to the same sire at all four flushes (i.e. hierarchical mating) then four female full sibs and, depending on any restrictions placed, up to four male full sibs are eligible for selection. In contrast, if four different sires are used at each flush then each sibship contains just one daughter and one son. With these limitations, it is only when each donor is mated to two sires (two flushes per sire), resulting in sibships of two males and two females, that more than one male can be selected from each sibship.

For this reason, the combination of selecting sibships of males with factorial mating designs was investigated with each donor mated to two sires and with two sons and two daughters per mating eligible for selection. The number of male sibships selected was 4 or 8, with 16, 32 or 64 donors selected. The schemes were replicated 600, 350 and 170 times with 16, 32 and 64 donors selected and they are described in Table 3. In addition, to allow comparison

with the effects of sibship selection and of factorial designs independently, results for these six schemes were also derived with two males and four females per sibship and a hierarchical mating design (sibship scheme) and with one male and two females per sibship and two sires per donor in a factorial mating design (factorial scheme).

For the three schemes with four sibships selected, four sires were selected in the base generation and mated in a hierarchical design (for the sake of simplicity), to the 16, 32 or 64 base generation founder dams. Each mating resulted in two sons and four daughters. Because the number of matings and sibships was halved, the male selection intensities were lower in generation one than in subsequent generations. For generations one to six, eight sires (i.e. four sibships of two males each) were selected. With 32 and 64 donors, all 28 pairwise combinations of the eight sires were possible and so were used. With 16 donors all combinations were not possible, so an incomplete block cyclic design (John et al., 1972) was used.

For the three schemes with eight sibships selected, eight sires were selected in the base generation and mated in a hierarchical design to the 16, 32 or 64 donors. For all other generations, 16 sires (i.e. eight sibships of two males each) were selected and mated to 32 or 64 donors using a cyclic design (John et al., 1972) and to 16 donors with a partially balanced incomplete block design (Cochran and Cox, 1957).

TABLE 3

Description of schemes permitting the selection of full brothers and utilising factorial mating designs (factorial sibship schemes). Each dam was mated to two sires and there were two sons and two daughters per sibship

	No. of male sibships selected					
	4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
No. of sires selected	8	8	8	16	16	16
No. of dams mated per sire	4	8	16	2	4	8
No. of sons per dam	4	4	4	4	4	4
No. of sons per sire	8	16	32	4	8	16
Total no. of male candidates	64	128	256	64	128	256
No. of daughters per dam	4	4	4	4	4	4
No. of daughters per sire	8	16	32	4	8	16
Proportion of males selected	8/64	8/128	8/256	16/64	16/128	16/256
Proportion of females selected	16/64	32/128	64/256	16/64	32/128	64/256

RESULTS

(1) Assortative Mating

The response to selection, the components of response and the between and within family genetic variances, averaged over generations two to six are shown in Table 4. Compared to random mating, assortative mating increased genetic gain by up to 5% in five of the six schemes simulated and reduced response by 5% in the sixth scheme.

Assortative mating increased the genetic variance between sire families by between 7-24% and reduced the genetic variance between dams (within sires) by about 10%, since there was a greater genetic uniformity in the groups of dams mated to each sire. Because selection lessens the impact of assortative mating by reducing variances between families (e.g. Tallis and Leppard, 1987), assortative mating was most useful when selection pressures were low, i.e. with eight sires selected instead of four and with a small number of dams selected (since this reduced the number of male candidates).

An examination of the five components of response reveals that the male accuracies of selection were most affected by assortative mating. Since males were evaluated using pedigree information only, the accuracies of selection of males were influenced more by changes in the between family variances than the female accuracies of selection. Because each female had a complete lactation record, they were less dependent on pedigree information than males.

The selection responses achieved at each generation are given in Table 5. Compared to random mating, assortative mating was, in general, most beneficial in the early generations. For four of the six schemes, the differences in response were greatest at

TABLE 4

The genetic response, the five components of response and the between sire (σ_s^2), between dam (within sires) (σ_D^2) and within family (σ_w^2) genetic variances when assortative mating is used. Results were averaged over generations two to six (inclusive). The standard errors ranged from 0.001 to 0.008. The percentage difference between these results and those under random mating are given in brackets

	No. of sires selected					
	4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
σ_s^2	0.044 (11.6%)*	0.043 (19.6%)	0.040 (7.4%)	0.056 (24.5%)	0.051 (23.5%)	0.044 (15.9%)
σ_D^2	0.030 (-9.9%)	0.031 (-7.0%)	0.030 (-9.2%)	0.033 (-12.7%)	0.033 (-9.3%)	0.032 (-8.6%)
σ_w^2	0.101 (-4.8%)	0.105 (-1.0%)	0.105 (-1.6%)	0.108 (-5.3%)	0.108 (-4.4%)	0.110 (-2.9%)
σ_g	0.418 (-1.1%)	0.422 (1.1%)	0.420 (-0.6%)	0.443 (0.0%)	0.438 (0.4%)	0.431 (0.0%)
r_M	0.396 (7.5%)	0.416 (3.6%)	0.427 (-4.1%)	0.422 (11.3%)	0.438 (7.4%)	0.442 (2.0%)
i_M	1.151 (-0.4%)	1.421 (-2.4%)	1.634 (-2.5%)	0.760 (-0.1%)	1.215 (0.0%)	1.553 (0.0%)
r_F	0.524 (1.3%)	0.544 (1.7%)	0.555 (-1.1%)	0.549 (3.2%)	0.561 (2.7%)	0.565 (1.6%)
i_F	1.185 (-0.5%)	1.191 (-0.6%)	1.198 (0.0%)	1.223 (0.0%)	1.229 (-0.3%)	1.235 (-0.2%)
ΔG	0.232 (2.8%)	0.264 (1.4%)	0.286 (-4.9%)	0.222 (5.4%)	0.272 (4.5%)	0.299 (1.2%)

*calculated by ((σ_s^2 under assortative mating/σ_s^2 under random mating) - 1) x 100

TABLE 5

Response to selection with assortative mating for generations one to six. ΔG is the average response from generations two to six. Results are presented ± standard deviation of response. The percentage difference between these results and those under random mating are given in brackets

	No. of sires selected					
	4			8		
	No. of dams selected			No. of dams selected		
Generation number	16	32	64	16	32	64
1	0.212 +0.129* (7.0%)	0.246 +0.130 (8.8%)	0.251 +0.136 (−1.2%)	0.191 +0.096 (16.2%)	0.225 +0.101 (6.8%)	0.260 +0.110 (8.7%)
2	0.257 +0.150 (4.6%)	0.296 +0.142 (4.7%)	0.305 +0.147 (−6.7%)	0.227 +0.111 (7.5%)	0.294 +0.113 (7.9%)	0.330 +0.123 (3.2%)
3	0.242 +0.146 (0.6%)	0.279 +0.148 (0.9%)	0.316 +0.132 (−2.2%)	0.231 +0.111 (5.4%)	0.283 +0.111 (4.6%)	0.312 +0.107 (0.9%)
4	0.237 +0.146 (6.0%)	0.264 +0.133 (0.6%)	0.292 +0.123 (0.5%)	0.231 +0.112 (12.3%)	0.272 +0.116 (3.6%)	0.292 +0.110 (−3.4%)
5	0.215 +0.142 (−0.8%)	0.246 +0.132 (−3.3%)	0.268 +0.130 (−7.1%)	0.218 +0.113 (4.0%)	0.263 +0.112 (4.6%)	0.282 +0.105 (1.1%)
6	0.207 +0.132 (3.8%)	0.235 +0.122 (4.1%)	0.249 +0.117 (−9.5%)	0.201 +0.106 (−2.2%)	0.250 +0.107 (1.4%)	0.282 +0.111 (4.3%)
ΔG	0.232 +0.066 (2.8%)	0.264 +0.061 (1.4%)	0.286 +0.057 (−4.9%)	0.222 +0.055 (5.4%)	0.272 +0.055 (4.5%)	0.299 +0.051 (1.2%)

*The standard error is the standard deviation divided by 24.5, 18.7 and 13.0 with 16, 32 and 64 dams selected respectively.

generation one.

Table 6 shows that inbreeding rates were higher when selected individuals were mated assortatively instead of at random. The faster accumulation of inbreeding under assortative mating led to more substantial reductions in the between and within family genetic variances. Because of this, the differences in response due to using assortative instead of random mating were smaller in later generations.

With assortative mating, family members were more alike with respect to the trait under selection. The intra class correlations of EBVs of male half sibs, of female half sibs and of female full sibs are shown in Table 6. Assortative mating resulted in higher intra class correlations of EBVs of male half sibs (by 10 to 24%) and of female half sibs (by 8 to 27%), due to the increased variance of EBVs between sires. The increase for full sib females was more moderate (-1 to 6%).

Since assortative mating had the greatest effect on variances with a large number of sires and a small number of dams selected, the intra class correlations followed the same pattern. Thus the intra class correlations were increased most with eight sires and 16 dams, and changed least with four sires and 64 dams.

Since selection was based on EBVs, the increased intra class correlations resulted in 10-24% (with four sires) and 26-49% (with eight sires) higher rates of inbreeding. The increased rates of inbreeding were responsible for the greater variation in response found with assortative mating (see Table 5) than with random mating.

(2) Sibship schemes

The response to selection, the components of response and the rates of inbreeding averaged over generations two to six are

TABLE 6

Intra-class correlations of EBVs of male half sibs (mhsibs), of female half sibs (fhsibs) of female full sibs (ffsibs) and rates of inbreeding (expressed in % per generation) with assortative mating (± standard errors). The percentage changes in these values compared to random mating are shown in brackets. All results were calculated for generations two to six and averaged

	No. of sires selected					
	4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
Intra class correlations						
a) mhsibs	0.674 ±0.005 (18.1)	0.706 ±0.005 (15.5)	0.720 ±0.007 (9.7)	0.730 ±0.004 (23.7)	0.753 ±0.004 (21.0)	0.767 ±0.004 (16.2)
b) fhsibs	0.458 ±0.005 (19.7)	0.477 ±0.006 (16.1)	0.481 ±0.008 (8.0)	0.513 ±0.005 (27.1)	0.525 ±0.005 (24.9)	0.522 ±0.006 (18.1)
c) ffsibs	0.729 ±0.003 (3.4)	0.733 ±0.003 (1.6)	0.734 ±0.004 (−0.7)	0.755 ±0.003 (5.6)	0.759 ±0.003 (4.2)	0.755 ±0.003 (2.3)
ΔF	9.86 +0.10 (24.2)	8.64 +0.10 (11.2)	8.06 ±0.13 (9.5)	6.19 +0.08 (45.9)	6.86 +0.12 (49.1)	6.02 +0.13 (25.6)

shown in Table 7. The results show that using full brothers from selected sibships reduced the rates of inbreeding substantially without adversely affecting response.

The rates of inbreeding were highest with only one son per dam eligible for selection. When full brothers were selected, the inbreeding rates were reduced by 26-34% and by 24-31% with four and eight sibships selected respectively.

Sibship selection produced distinct changes in each of the five components of response. The genetic standard deviation was increased by selecting more sires and by the subsequent reduction in inbreeding. The subdivision of the population into smaller groups, and the break up of large discrete sire family units by selecting more sires, affected the accuracies and intensities of selection. By using more than one male from a selected sibship, the accuracies of selection for both sexes were reduced because half sib records were replaced by an equal number from first cousins.

For example, with eight sibships selected, each male candidate had four sisters and 12 half sisters when one male per sibship was eligible per selection. However, when four males per sibship were eligible for selection, each male had four sisters (as before) and 12 female first cousins but no half sisters. Thus, as more sires were selected, the accuracies of selection declined.

The subdivision of the population structure into smaller units reduced the impact of the family structure on the male and female intensities of selection (Hill, 1976). In addition, by selecting more sires the effect of finite numbers was diminished so that the male selection intensities were further increased.

The resulting increases in the intensities of selection were considerably greater when four sibships were selected. For this reason, the genetic gain achieved when using more than one male

TABLE 7

The genetic response, the five components of response and the rates of inbreeding in sibship selection schemes. Results were averaged over generations two to six (inclusive) and are presented ± standard errors. Thirty two dams were selected in each scheme

	No. of male sibships selected							
	4				8			
	No. of sons per dam eligible for selection				No. of sons per dam eligible for selection			
	1	2	3	4	1	2	3	4
σ_g	0.420 ±0.001	0.429 ±0.001	0.429 ±0.001	0.431 ±0.001	0.437 ±0.001	0.442 ±0.001	0.442 ±0.001	0.443 ±0.001
r_M	0.401 ±0.005	0.395 ±0.003	0.380 ±0.004	0.375 ±0.003	0.408 ±0.005	0.391 ±0.004	0.384 ±0.003	0.378 ±0.003
i_M	1.456 ±0.004	1.547 ±0.004	1.568 ±0.005	1.582 ±0.004	1.215 ±0.002	1.243 ±0.002	1.244 ±0.002	1.250 ±0.002
r_F	0.535 ±0.003	0.536 ±0.002	0.527 ±0.002	0.527 ±0.003	0.546 ±0.003	0.541 ±0.002	0.536 ±0.002	0.535 ±0.002
i_F	1.199 ±0.002	1.234 ±0.001	1.240 ±0.001	1.249 ±0.001	1.233 ±0.002	1.250 ±0.001	1.251 ±0.001	1.256 ±0.001
ΔG	0.260 ±0.003	0.277 ±0.003	0.268 ±0.003	0.270 ±0.003	0.261 ±0.003	0.258 ±0.002	0.254 ±0.002	0.254 ±0.002
ΔF	7.77 ±0.08	5.71 ±0.07	5.25 ±0.06	5.13 ±0.07	4.60 ±0.05	3.50 ±0.04	3.19 ±0.03	3.42 ±0.04

instead of a single male from a selected sibship, was increased when four sibships were selected but reduced when eight sibships were selected.

When four or eight sibships were selected, genetic gain was higher with two males per sibship eligible for selection than with three or four males. This was due to the reduction in the accuracies of selection exceeding the increases in selection intensities and the genetic standard deviation, as the number of males per sibship was increased.

The selection responses over generations one to six are shown in Table 8. Because of the higher inbreeding rates, response was considerably more variable with one son per dam eligible for selection. The decline in response from generations two to six was also greater. By comparison, the decline in response with four sons per dam was quite small.

(3) Factorial schemes

The response to selection, the components of response and the rates of inbreeding averaged over generations two to six are shown in Table 9. As the number of sires mated to each donor increased, the total number of matings and the number of male candidates increased, since it was assumed that one son per mating was produced. As a consequence, genetic gain was increased by up to 13% as the number of sires mated to each donor was raised from one to four. Woolliams (1989), using deterministic methods, predicted increases of a similar magnitude for comparable schemes, although the responses he predicted were over 50% higher than simulated results because the effects of selection and inbreeding on genetic variances were ignored.

The benefits of having a greater number of males candidates

TABLE 8

Response to selection for generations one to six in sibship selection schemes. ΔG is the average response from generations two to six. Results are presented ± standard deviation of response. Thirty two dams were selected in each scheme

Generation Number	No. of male sibships selected: 4 — No. of sons per dam eligible for selection: 1	2	3	4	No. of male sibships selected: 8 — No. of sons per dam eligible for selection: 1	2	3	4
1	0.226 ±0.135	0.234 *±0.116	0.226 0.100	0.224 ±0.104	0.210 ±0.098	0.205 ±0.085	0.208 ±0.080	0.207 ±0.080
2	0.283 ±0.139	0.292 ±0.118	0.272 ±0.097	0.270 ±0.102	0.273 ±0.106	0.251 ±0.093	0.254 ±0.083	0.250 ±0.080
3	0.277 ±0.146	0.286 ±0.113	0.278 ±0.104	0.279 ±0.104	0.271 ±0.108	0.272 ±0.091	0.262 ±0.093	0.259 ±0.082
4	0.262 ±0.133	0.284 ±0.121	0.270 ±0.103	0.277 ±0.097	0.263 ±0.102	0.263 ±0.090	0.261 ±0.085	0.252 ±0.084
5	0.255 ±0.118	0.268 ±0.114	0.265 ±0.110	0.262 ±0.118	0.251 ±0.100	0.251 ±0.084	0.255 ±0.085	0.254 ±0.084
6	0.226 ±0.123	0.256 ±0.107	0.254 ±0.102	0.260 ±0.104	0.246 ±0.106	0.255 ±0.091	0.241 ±0.082	0.254 ±0.085
ΔG	0.260 ±0.060	0.277 ±0.049	0.268 ±0.050	0.270 ±0.047	0.261 ±0.050	0.258 ±0.040	0.254 ±0.043	0.254 ±0.040

*The standard error is the standard deviation divided by 18.7.

TABLE 9

The genetic response, the five components of response and the rates of inbreeding with factorial mating designs. Results were averaged over generations two to six (inclusive) and are presented ± standard errors. Thirty two dams were selected in each scheme

	No. of sires selected							
	4				8			
	No. of sires mated per dam				No. of sires mated per dam			
	1	2	3	4	1	2	3	4
σ_g	0.420 ±0.001	0.420 ±0.001	0.420 ±0.001	0.421 ±0.001	0.437 ±0.001	0.435 ±0.001	0.433 ±0.001	0.433 ±0.001
r_M	0.401 ±0.005	0.388 ±0.004	0.394 ±0.004	0.395 ±0.004	0.408 ±0.005	0.387 ±0.004	0.383 ±0.003	0.378 ±0.003
i_M	1.456 ±0.004	1.713 ±0.005	1.847 ±0.006	1.932 ±0.006	1.215 ±0.002	1.565 ±0.004	1.738 ±0.004	1.848 ±0.005
r_F	0.535 ±0.003	0.530 ±0.003	0.530 ±0.003	0.533 ±0.003	0.546 ±0.003	0.533 ±0.002	0.531 ±0.002	0.527 ±0.002
i_F	1.199 ±0.002	1.207 ±0.001	1.207 ±0.001	1.206 ±0.001	1.233 ±0.002	1.236 ±0.001	1.239 ±0.001	1.239 ±0.001
ΔG	0.260 ±0.003 (0.391)*	0.270 ±0.003 (0.425)*	0.286 ±0.003	0.294 ±0.003 (0.448)*	0.261 ±0.003	0.275 ±0.003	0.288 ±0.003	0.292 ±0.003
ΔF	7.77 ±0.08 (6.63)*	7.47 ±0.06 (6.58)*	7.71 ±0.06	7.65 ±0.05 (6.75)*	4.60 ±0.05	4.95 ±0.05	5.14 ±0.05	5.23 ±0.05

*Predictions from Woolliams (1989), with four sires and 36 dams selected

were demonstrated by the substantial increases in male selection intensities achieved. By comparison, the other four components of response were little affected. The accuracies of selection were reduced slightly, probably resulting from smaller between sire variances, following more intense selection (Bulmer, 1971).

With four sires selected, inbreeding was only marginally lower with factorial mating designs. Inbreeding was relatively constant with factorial designs compared to the hierarchical design because the increased probability of coselecting half sibs was balanced by the reduced probability of coselecting full sibs. Woolliams (1989) similarily found little change in inbreeding for comparable schemes.

With eight sires selected the picture was slightly different. Inbreeding rates increased (up to 14%) as more sires were mated to each donor. With hierarchical mating designs, the number of sons per sire eligible for selection was restricted so that the males selected were bred by at least two sires. With factorial mating designs, this restriction was removed and consequently individual sires were able to have a greater number of sons selected, thus increasing the inbreeding rates.

The selection responses achieved over generations one to six are shown in Table 10. Almost without exception, the response at each generation increased steadily as the number of sires mated to each dam was increased. Because the factorial schemes had little impact on inbreeding, the standard deviations of response were virtually unaffected by the mating design.

(4) Factorial sibship schemes

The response to selection, the components of response and the rates of inbreeding averaged over generations two to six are

TABLE 10

Response to selection for generations one to six with factorial mating design schemes. ΔG is the average response from generations two to six. Results are presented ± standard deviation of response. Thirty two dams were selected in each scheme

	No. of sires selected							
	4				8			
	No. of sires mated per dam				No. of sires mated per dam			
Generation Number	1	2	3	4	1	2	3	4
1	0.226 ±0.135*	0.239 ±0.129	0.233 ±0.126	0.250 ±0.130	0.210 ±0.098	0.224 ±0.104	0.223 ±0.100	0.234 ±0.103
2	0.283 ±0.139	0.285 ±0.141	0.304 ±0.145	0.310 ±0.138	0.273 ±0.106	0.291 ±0.109	0.296 ±0.111	0.303 ±0.115
3	0.277 ±0.146	0.285 ±0.132	0.296 ±0.136	0.313 ±0.141	0.271 ±0.108	0.277 ±0.119	0.301 ±0.120	0.309 ±0.115
4	0.262 ±0.133	0.275 ±0.137	0.302 ±0.131	0.307 ±0.136	0.263 ±0.102	0.269 ±0.104	0.291 ±0.110	0.294 ±0.120
5	0.255 ±0.118	0.262 ±0.134	0.267 ±0.137	0.276 ±0.129	0.251 ±0.100	0.276 ±0.107	0.283 ±0.111	0.285 ±0.104
6	0.226 ±0.123	0.245 ±0.122	0.259 ±0.126	0.264 ±0.128	0.246 ±0.106	0.262 ±0.102	0.271 ±0.110	0.270 ±0.106
ΔG	0.260 ±0.060	0.270 ±0.062	0.286 ±0.062	0.294 ±0.059	0.261 ±0.050	0.275 ±0.051	0.288 ±0.053	0.292 ±0.052

*The standard error is the standard deviation divided by 18.7.

shown in Table 11. Compared to schemes using hierarchical mating designs and with one son selected per dam (i.e. hierarchical schemes), responses were 5-14% higher and, apart from one scheme, rates of inbreeding were 13-30% lower.

The increased responses were due mainly to substantial increases in the male selection intensities (23-64%) resulting from both the presence of more sire families, thus reducing the effects of the population structure (Hill, 1976) and, more importantly, the increased numbers of male candidates. Because full brothers were used in the factorial sibship schemes, some (up to all) half sib records were replaced with information on first cousins. Consequently, the accuracies of selection were reduced by 1-10%.

The selection responses over generations one to six are shown in Table 12. As the schemes increased in size with more dams selected, responses increased and, due to the larger effective population sizes, the standard deviation of response decreased. Compared to the hierarchical scheme, the highest responses were generally achieved slightly later (in generation three instead of in generation two) and the decline in response over time was less extreme.

Table 13 summarises the mean responses achieved by the hierarchical and factorial sibship schemes. In addition, to disentangle the effects of the mating design and the use of full brothers, results of factorial (two sires per dam) and sibship (two males per sibship eligible for selection) schemes are also presented.

The factorial schemes yielded rates of response 2-13% higher than the hierarchical schemes. When the use of two males per selected sibship was combined with factorial mating (factorial sibship schemes), additional genetic gains were achieved only with four sibships selected. In this situation, the benefits of using

TABLE 11

The genetic response, the five components of response and the rates of inbreeding with factorial sibship schemes. Each dam was mated to two sires and two males and two females per sibship were eligible for selection. Results were averaged over generations two to six (inclusive). The standard errors were similar in size to those in previous tables. The figures in brackets represent percentage changes compared to the standard Nicholas and Smith (1983) design i.e. hierarchical mating design with one son per dam

	No. of male sibships selected					
	4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
σ_g	0.426 (0.9%)*	0.430 (2.6%)	0.429 (1.8%)	0.437 (-1.2%)	0.442 (1.1%)	0.441 (2.2%)
r_M	0.346 (-6.2%)	0.384 (-4.4%)	0.413 (-7.3%)	0.339 (-10.5%)	0.366 (-10.4%)	0.393 (-9.3%)
i_M	1.554 (34.5%)	1.823 (25.2%)	2.055 (22.7%)	1.244 (63.5%)	1.605 (32.1%)	1.905 (22.7%)
r_F	0.504 (-2.6%)	0.528 (-1.4%)	0.549 (-2.1%)	0.493 (-7.4%)	0.525 (-4.0%)	0.544 (-2.3%)
i_F	1.234 (3.6%)	1.235 (3.0%)	1.238 (3.4%)	1.278 (4.5%)	1.253 (1.6%)	1.256 (1.6%)
ΔG	0.250 (10.9%)	0.296 (13.6%)	0.326 (8.5%)	0.231 (9.7%)	0.275 (5.5%)	0.314 (6.2%)
ΔF	6.79 (-14.4%)	5.77 (-25.8%)	5.44 (-26.0%)	4.81 (13.4%)	3.80 (-17.4%)	3.33 (-30.4%)

*((σ_g factorial sibship/σ_g hierarchical) - 1) x 100 = 0.9

TABLE 12

Response to selection for generations one to six with factorial sibship schemes. ΔG is the average response from generations two to six. Results are presented $\pm$ standard deviation of response

Generation Number	No. of male sibships selected: 4 — No. of dams selected: 16	32	64	No. of male sibships selected: 8 — No. of dams selected: 16	32	64
1	0.199 $\pm$0.116*	0.220 $\pm$0.108	0.251 $\pm$0.100	0.172 $\pm$0.086	0.201 $\pm$0.086	0.247 $\pm$0.084
2	0.270 $\pm$0.134	0.303 $\pm$0.122	0.331 $\pm$0.114	0.236 $\pm$0.102	0.274 $\pm$0.093	0.324 $\pm$0.085
3	0.265 $\pm$0.128	0.317 $\pm$0.137	0.342 $\pm$0.117	0.243 $\pm$0.103	0.282 $\pm$0.101	0.328 $\pm$0.094
4	0.253 $\pm$0.129	0.305 $\pm$0.119	0.332 $\pm$0.117	0.234 $\pm$0.105	0.277 $\pm$0.097	0.319 $\pm$0.097
5	0.236 $\pm$0.127	0.290 $\pm$0.117	0.309 $\pm$0.115	0.225 $\pm$0.100	0.270 $\pm$0.099	0.306 $\pm$0.088
6	0.225 $\pm$0.124	0.264 $\pm$0.116	0.317 $\pm$0.112	0.217 $\pm$0.098	0.272 $\pm$0.092	0.295 $\pm$0.090
ΔG	0.250 $\pm$0.061	0.296 $\pm$0.055	0.326 $\pm$0.055	0.231 $\pm$0.048	0.275 $\pm$0.046	0.314 $\pm$0.043

*The standard error is the standard deviation divided by 24.5, 18.7 and 13.0 with 16, 32 and 64 dams selected respectively.

TABLE 13

Rates of response averaged over generations two to six (inclusive) with hierarchical schemes, sibship schemes (two sons per sibship), factorial schemes (two sires per dam) and factorial sibship schemes (two sires per dam and two sons per sibship eligible for selection). Results are presented ± standard errors

Scheme	No. of male sibships selected					
	4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
Hierarchical	0.225 ±0.003	0.260 ±0.003	0.301 ±0.004	0.210 ±0.002	0.261 ±0.003	0.296 ±0.004
Sibship	0.229 ±0.002	0.277 ±0.003	0.300 ±0.004	0.204 ±0.002	0.258 ±0.002	0.304 ±0.003
Factorial	0.244 ±0.003	0.270 ±0.003	0.308 ±0.005	0.237 ±0.002	0.275 ±0.003	0.319 ±0.003
Factorial sibship	0.250 ±0.002	0.296 ±0.003	0.326 ±0.004	0.231 ±0.002	0.275 ±0.002	0.314 ±0.003

TABLE 14

Rates of inbreeding, expressed as % per generation ± standard errors with hierarchical schemes, sibship schemes (two sons per dam), factorial schemes (two sires mated to each dam) and factorial sibship schemes (two sires per dam and two sons per sibship eligible for selection). Inbreeding rates were averaged over generations two to six (inclusive)

	No. of male sibships selected					
	4			8		
Scheme	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
Hierarchical	7.93 ±0.07	7.77 ±0.08	7.36 ±0.10	4.25 ±0.04	4.60 ±0.05	4.79 ±0.07
Sibship	6.66 ±0.07	5.71 ±0.07	5.31 ±0.08	3.90 ±0.03	3.50 ±0.04	3.18 ±0.06
Factorial	7.94 ±0.06	7.47 ±0.06	7.42 ±0.09	5.13 ±0.04	4.95 ±0.05	5.10 ±0.06
Factorial sibship	6.79 ±0.06	5.77 ±0.06	5.44 ±0.08	4.81 ±0.04	3.80 ±0.04	3.33 ±0.05

more sires (e.g. by increasing the male selection intensities) outweighed the losses of family information.

Table 14 summarises the rates of inbreeding for the four alternative breeding scheme designs. The results varied, depending on whether four or eight sibships were selected. With four sibships selected, inbreeding in the factorial and hierarchical schemes accumulated at a similar rate. By using two males instead of one from each selected sibship, the inbreeding rates were substantially reduced and were approximately equal in the sibship and factorial sibship schemes.

With eight sibships selected, inbreeding rates increased as more dams were selected in the hierarchical schemes because of the restrictions placed on the sires' family size by the mating structure. These restrictions were greatest with 16 dams. The factorial schemes increased the number of sons per sire and so produced higher inbreeding rates. The sibship schemes reduced the inbreeding rates by 8% (16 dams) to 34% (64 dams). Thus, the factorial sibship schemes had higher inbreeding rates with 16 dams than the hierarchical schemes and inbreeding decreased as the number of dams increased.

DISCUSSION

While the theoretial studies of Baker (1973) and Smith and Hammond (1987) concluded that assortative mating would always increase the genetic variance and yield higher rates of genetic progress than random mating, neither study accounted for the effects of inbreeding on the genetic variance and hence on response. When the effects of inbreeding were accounted for in this study, assortative mating was seen to be of little value as a means of increasing response.

In the schemes studied here, the rates of inbreeding were 10-50% higher with assortative mating than with random mating. Because of this, the total genetic variance over the time period examined was equal for both mating strategies. The increased response achieved with assortative mating in five of the six schemes was therefore not due to increasing the total genetic variance. Rather it was a consequence of the higher accuracies of selection resulting from changes in the between sire, between dam and within family variances.

Assortative mating had the biggest impact on response in the early generations, especially at generation one. For this reason, assortative mating of nucleus founder animals may prove useful in reducing the drop in response expected at generation one.

Since selection acts against assortative mating by reducing variances between families, assortative mating was most useful when selection pressures are low. Nevertheless, the genetic gains achieved were quite small when compared to the substantial increases found in the rates of inbreeding and so the strategy of assortative mating may be of limited use in small herds of dairy cattle.

It is widely recognised that the problem of inbreeding, caused by selecting small numbers of sires and dams from a finite pool of candidates using overlapping family information, is of the utmost importance in MOET nucleus breeding programmes. For this reason any practical method of minimising the problem should be evaluated. Sibship schemes offer some possibilities here.

Unless embryo or semen sexing is available and in use, equal numbers of sons and daughters are expected on average from each donor. By allowing more than one male from a selected sibship to be used as a sire, inbreeding should be reduced due to the increased numbers of sires used without suffering a loss in selection pressure.

Simulation results showed this to be true. With 32 donors, inbreeding rates per generation were reduced by about 25-30% with 2, 3 or 4 sons per donor eligible for selection. Similar reductions in inbreeding in juvenile MOET nucleus schemes were found by Toro and Silio (1989). The trend between inbreeding rates and the number of sons eligible for selection was not linear. The reduction in inbreeding from having two sons per donor eligible for selection instead of one son was far superior to having four sons per donor instead of two. Thus little effort is required to make substantial reductions in inbreeding.

The effect of selecting more than one male per sibship on genetic response was relatively small and depended on the balance between the intensities and accuracies of selection. By increasing the number of sires and thus replacing half sib information with records from first cousins, the selection intensities were increased but the accuracies of selection were reduced. Because of the balance between these two forces, the genetic response was increased by 4-6% and reduced by 1-3% with four and eight sibships selected respectively and genetic gain was higher with two sons per donor eligible for selection than with three or four.

Full sib males have identical EBVs for dairy traits when evaluated using pedigree information. Consequently the number of males used from a selected sibship does not affect the selection pressure applied. However, if it was possible to discriminate and select between full sibs for dairy traits using physiological indicators (Woolliams and Smith, 1988) or for other economically important traits, such as beef traits (Ruane, 1988) the use of full brothers to reduce inbreeding would reduce the selection pressure on males.

In such circumstances, it may still be desirable to select

full brothers because of the reduction in inbreeding rates possible and the disadvantages of selecting too few sires. In these cases, it would seem advisable to use two males from a selected sibship. If the number of males per sibship was greater than two, within sibship selection would still be possible and the advantages of sibship selection would be obtained.

Nicholas and Smith (1983) suggested that embryo sexing would be useful in MOET nucleus schemes because, with one son per dam eligible for selection, the number of male embryos needed would be reduced considerably. Any selection strategy involving the use of male full sibs, whether for within family selection or for sibship selection, would rule out this possibility.

Woolliams (1989) predicted that factorial mating designs in MOET nucleus schemes, with one male per sibship eligible for selection, would increase response without affecting inbreeding. His predictions were based on schemes with four sires and 36 donors. The simulation results presented here for four sires and 32 donors support his conclusions, despite the higher inbreeding rates and the substantially lower rates of response found. The benefits of factorial mating designs in juvenile MOET nucleus schemes have also been shown by Toro and Silio (1989).

As the number of sires mated to each dam was increased from one to four, thus moving from a hierarchical to a complete factorial design, response to selection was increased stepwise by up to 13% due solely to increases in the male selection intensities. For these four schemes the rate of inbreeding was restricted to 7.5-7.8% per generation and was highest when one sire was mated to each dam (the hierarchical design).

The results with eight sires and 32 donors suggest that the conclusions of Woolliams (1989) are not universal. In this case,

the increase in response was accompanied by a corresponding increase in inbreeding. Response to selection was increased by up to 12% while inbreeding was raised by 14% as the number of sires mated to each dam was raised from one to four.

The increase in inbreeding under factorial mating designs with eight sires selected was probably a consequence of relaxing the restrictions on family sizes inherent in the hierarchical design. With 32 donors selected, all the selected males must be bred by at least two sires since each sire has only four sons eligible for selection. Once factorial designs are used, all selected males could be bred by a single sire.

The increased responses achieved with factorial mating were brought about by changes in the male intensities of selection. Because of this, the advantages of using factorial mating designs depend on the proportion of males selected. The additional responses achieved by using factorial instead of hierarchical designs should be greater in schemes with a high proportion of males selected (i.e. low selection intensities) than in schemes with a low proportion selected. The results in Table 13 confirm this. Of the six schemes studied, the benefits of factorial mating were highest with eight sires and 16 dams (50% of males selected) and lowest with four sires and 64 dams (6% of males selected).

Factorial mating designs depend on the potential of each donor to produce embryos fertilised by more than one sire. Unless the semen of different bulls is mixed, the number of sires mated to each dam is limited by the number of flushes per dam. Since the time between each flush is about two months, some factorial designs may result in slightly longer generation intervals, depending on the number of sires mated to each donor and the family size per donor required.

In general, selecting sibships of males was a successful strategy for reducing inbreeding while factorial mating designs were successful in increasing response. Factorial sibship schemes, which use both strategies, combined together these two advantages. For the six breeding programmes examined, factorial sibship schemes yielded 5-14% higher genetic gains and, with one exception, 18-30% lower rates of inbreeding than schemes with hierarchical mating designs.

The factorial sibship schemes outlined required each dam to be mated to two sires with two sons and two daughters eligible for selection from each mating. The number of flushes required and hence the generation interval achieved should be equal to that in the hierarchical mating designs described, where each donor produced four daughters and up to four sons from a single sire. Unless the number of flushes was increased, however, it would not be possible to select between males within a sibship, if such a strategy was required. In addition, if embryo sexing was available, it would present no advantages to the factorial sibship schemes.

The original proposals by Nicholas and Smith (1983) for the use of MOET in a closed dairy cattle herd were based on a hierarchical mating design. This study has shown that these breeding schemes may be substantially improved by altering the mating structure. Using more than one male from a selected sibship reduces the inbreeding rate while factorial mating designs increase the response to selection. Factorial sibship schemes, which combine both strategies, reduce inbreeding and increase response.

SUMMARY

The impact of four different mating designs and selection strategies on rates of response and of inbreeding was investigated

with Monte Carlo simulation of a closed adult MOET nucleus scheme. The use of assortative mating was investigated with 16, 32 or 64 dams and four or eight sires selected. Although response was increased by up to 5% in five of the six schemes, it was more variable and inbreeding rates were 10-50% higher compared to random mating. Compared to having one male per sibship eligible for selection, using two to four males from a selected sibship reduced inbreeding by 26-34% and by 24-31% with 32 dams and four or eight sires selected respectively. Response was increased by 4-6% and reduced by 1-3% with four and eight sires selected. With 32 dams selected, employing factorial instead of hierarchical mating designs increased response by up to 13% with no increase in inbreeding when four sires were selected but with an increase in inbreeding of up to 14% with eight sires. Combining the selection of full brothers with factorial mating designs (i.e. factorial sibship schemes) allied the advantages of both. These schemes yielded higher genetic gains (5-14%) in all six schemes and lower inbreeding rates (14-30%) in five of the six schemes examined compared to hierarchical mating designs with one male per sibship eligible for selection.

CHAPTER 7

THE EFFECT OF DIFFERENT FAMILY SIZES AND VARIATION IN EMBRYO NUMBERS, IN SEX RATIOS AND IN SURVIVAL RATES ON ADULT MULTIPLE OVULATION AND EMBRYO TRANSFER (MOET) NUCLEUS BREEDING SCHEMES IN DAIRY CATTLE

INTRODUCTION

This chapter investigates the implications of removing some of the assumptions previously held concerning family sizes. Firstly, in the hierarchical schemes examined in chapter 5, each dam had four daughters and one son eligible for selection. In this study, alternative family sizes were permitted. Secondly, family sizes per dam were no longer assumed to be constant. The importance of variation in the number of progeny and in sex ratios between families was examined in both hierarchical and factorial mating schemes.

In the hierarchical schemes described in chapter 5, each dam produced four daughters and four sons, but at most one son was selected. These schemes followed Nicholas and Smith (1983), who suggested that only one son per dam should be eligible for selection to prevent inbreeding becoming unacceptably high. In this study, the number of sons per dam eligible for selection was increased up to four to determine whether this restriction was necessary. It should be noted that this situation differs from the sibship schemes described in the previous chapter, in which the increase in the number of sons per dam was accompanied by an increase in the number of males selected so that the proportion of males selected was constant.

With four daughters per dam eligible for selection, the

female replacement rate was fixed at 25%. To examine the impact of altering the replacement rate, each dam was allowed two, four or eight daughters. Whereas the decision to use more than one son per dam would not involve any extra time or cost, increasing the number of daughters would be achieved by flushing the dam for a longer time period and thus extending the generation interval. Where resources for testing animals are limited, the practical problem of whether to select many dams with small family sizes or fewer dams with greater family sizes is one of importance.

With the exception of Jansen and Schlote (1987), studies of MOET nucleus breeding programmes have assumed that all selected cows have offspring and that they contribute equal numbers of offspring for selection. In practice, considerable variation in the number of progeny per family and in sex ratios within families will exist due to variable success of current MOET methods and to chance.

The MOET techniques are now standard and involve treating cows with hormones to induce multiple ovulation of eggs. The egg donors are then inseminated and the fertilised eggs are recovered from the uterus in a process called flushing. The eggs are transferred to recipient cows either directly or after a period of storage at low temperatures. The process can be repeated about every six weeks (Woolliams and Wilmut, 1989).

The variation in family sizes due to the use of MOET stems from several sources. The greatest source is variability in the number of eggs recovered per flush, where the number of eggs recovered can range from 0-33 (Hahn, 1989) and 0-40 (Woolliams and Wilmut, 1989). Pregnancy rates per embryo transferred will also vary, depending on factors such as the quality of the embryos, the synchrony between donors and recipients and the skill of the individuals involved (Seidel, 1984).

MOET techniques apart, variation in family sizes between families will also exist due to skewed sex ratios arising by chance and to animals dying prior to selection. The influence of all these sources of variation on MOET nucleus breeding programmes, using hierarchical or factorial mating designs, was examined in this study.

With a maximum of one male per sibship eligible for selection, variation in family sizes will tend to reduce the total number of male candidates. Relative to hierarchical schemes, factorial mating designs increase the number of sire x dam mating combinations but reduce the family size per combination.

Because the probability of failing to produce a single male per sibship will be higher with smaller families, variation in family sizes is expected to have a greater influence of the number of male candidates and the male selection intensities in factorial schemes than in hierarchical schemes. Similarly, the influence should be greater in factorial schemes using four sires instead of two sires per dam.

MATERIALS AND METHODS

The computer simulation model of an adult MOET nucleus scheme with discrete generations, as described in Chapter 5, was used.

(1) Altering the family size in hierarchical schemes

(a) Number of sons per dam

The eight schemes examined are described in Table 1. The number of dams and of daughters per dam were kept constant at 32 and four respectively. The number of sires selected was four or eight and the number of sons per dam eligible for selection was 1, 2, 3 or 4. The schemes with one son per dam are the same as described in Chapter 5. All schemes were replicated 350 times.

TABLE 1

Description of hierarchical schemes with more than one son per dam eligible for selection. Thirty two dams were selected. Assuming a 50% sex ratio and a 50% survival rate of embryos to selection, this would require 512 embryos. Each dam had four daughters and the proportion of females selected was 32/128

	No. of sires selected							
	4				8			
	Number of sons per dam				Number of sons per dam			
	1	2	3	4	1	2	3	4
No. of dams mated per sire	8	8	8	8	4	4	4	4
No. of sons per sire	8	16	24	32	4	8	12	16
Total no. of males	32	64	96	128	32	64	96	128
Proportion of males selected	4/32	4/64	4/96	4/128	8/32	8/64	8/96	8/128

(b) Number of daughters per dam

In Chapter 5, six schemes were examined. Four or eight sires and 16, 32 or 64 dams were selected with four daughters and one son per dam. In this study, the same six sire x dam mating combinations were used with two additional family sizes, two daughters and one son or eight daughters and one son per dam. These schemes are described in Tables 2 and 3 respectively. Schemes with 16, 32 and 64 dams were replicated 600, 350 and 170 times.

(2) Allowing for variation in embryo numbers, sex ratios and survival rates in MOET nucleus schemes

(a) Hierarchical mating designs

Nine schemes were examined with eight sires and 32 dams selected in each. These are described in Table 4. Four practical factors were included in the simulation.

(i) Some females may not produce eggs. Three situations were modelled. In the first, all selected females produced eggs. In the second and third situations, 8 and 16 (i.e. 25% and 50%) respectively of the selected females, chosen at random from the top 32, produced no eggs. These were replaced by 8 and 16 of the next highest ranking females respectively, all of whom produced eggs. Thus eggs were recovered from 32 of the top ranking 32, 40 and 48 cows respectively.

(ii) The number of eggs from the 32 donor females may vary. This was modelled by picking the number of eggs recovered per donor from a normal distribution with a mean of 16 and with variances of either 0, 16 or 64.

Such a situation could arise if it is assumed that on average 16 eggs are recovered from four flushes, with four eggs per flush, and that there is no covariance between egg numbers in

TABLE 2

Description of hierarchical schemes with two daughters and one son per dam

	No. of sires selected					
	4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
No. of embryos transferred*	128	256	512	128	256	512
No. of dams mated per sire	4	8	16	2	4	8
No. of sons per dam	1	1	1	1	1	1
No. of sons per sire	4	8	16	2	4	8
No. of daughters per dam	2	2	2	2	2	2
No. of daughters per sire	8	16	32	4	8	16
Proportion of males selected	4/16	4/32	4/64	8/16	8/32	8/64
Proportion of females selected	16/32	32/64	64/128	16/32	32/64	64/128

*Assuming a 50% sex ratio and a 50% survival rate of embryos to selection

TABLE 3

Description of hierarchical schemes with eight daughters and one son per dam

	No. of sires selected					
	4			8		
	No. of dams selected			No. of dams selected		
	16	32	64	16	32	64
No. of embryos transferred*	512	1024	2048	512	1024	2048
No. of dams mated per sire	4	8	16	2	4	8
No. of sons per dam	1	1	1	1	1	1
No. of sons per sire	4	8	16	2	4	8
No. of daughters per dam	8	8	8	8	8	8
No. of daughters per sire	32	64	128	16	32	64
Proportion of males selected	4/16	4/32	4/64	8/16	8/32	8/64
Proportion of females selected	16/128	32/256	64/512	16/128	32/256	64/512

*Assuming a 50% sex ratio and a 50% survival rate of embryos to selection

TABLE 4

Description of hierarchical MOET nucleus schemes allowing for variation in biological factors. Eight sires were selected and embryos were recovered from 32 of the top 32, 40 or 48 females ranked for milk production. Each sire was mated to four dams and, on average, 512 embryos were transferred. The mean number of eggs per donor was 16.

	Variance of egg no. per donor								
	0			16			64		
	No. top females flushed			No. top females flushed			No. top females flushed		
	32	40	48	32	40	48	32	40	48
Average no. of males*	31.68 ± 0.55	31.67 ±0.57	31.69 ±0.56	31.36 ±0.78	31.37 ±0.79	31.41 ±0.76	29.57 ±1.50	29.59 ±1.48	29.53 ±1.50
Average no. of females*	128.27 ±9.81	127.67 ±9.49	127.52 ±9.58	128.31 ±11.41	127.76 ±11.20	128.17 ±11.44	127.87 ±14.55	128.05 ±14.42	127.82 ±14.31
Average no. of sons per dam	0.99	0.99	0.99	0.98	0.98	0.98	0.92	0.92	0.92
Average no. of sons per sire	3.96	3.96	3.96	3.92	3.92	3.92	3.70	3.70	3.69
Average no. of daughters per dam	4.01	3.99	3.99	4.01	3.99	4.01	4.00	4.00	3.99
Average no. of daughters per sire	16.03	15.96	15.94	16.04	15.97	16.02	15.98	16.01	15.98
Proportion of males selected	8/31.7	8/31.7	8/31.7	8/31.4	8/31.4	8/31.4	8/29.6	8/29.6	8/29.5
Proportion of females selected	32/128.3	40/127.7	48/127.5	32/128.3	40/127.8	48/128.2	32/127.9	40/128	48/127.8

*Simulation values presented ± average standard deviation at any generation

different flushes (i.e. zero repeatability). Then these variances reflect the situations (a) when there is no variance in egg numbers; (b) when the mean number of eggs per flush equals the variance of egg numbers per flush and (c) when the mean equals the standard deviation respectively.

With a variance of 64, 1.96% of flushes were expected to give negative numbers of eggs. To prevent this, simulated values less than zero were set to zero and simulated values greater than 32 were set to 32.

(iii) Each egg recovered may not develop into a candidate for selection and was assumed to have a 50% probability of not doing so. This figure accounts for failure to develop to term within the recipient cow as well as for failure to survive to selection once born. The probability of producing any given number of candidates from a given number of eggs can be derived from binomial distribution theory.

(iv) Each animal born may be male or female. A 50% probability of either sex was assumed. The sex ratios will vary according to binomial distribution theory.

To allow comparison with the original schemes proposed by Nicholas and Smith (1983), only one son per dam was considered to be eligible for selection. Because of this, the average number of male candidates was less than 32. For example, with no variance in egg numbers but with variation in survival rates and sex ratios, 1% (= 0.75^{16}) of sibships were expected to yield no males and so the average number of males expected was 31.68. There were no such restrictions on females and 128 females were expected in all situations.

As the number of embryos per donor became more variable, fewer males were available for selection and a greater proportion of

males were selected. In addition, as more selected cows failed to produce embryos, the proportion of females selected was increased.

Each scheme was replicated 350 times. The scheme with eight of the top 32 cows yielding no eggs is shown in Figure 1 as an example.

(b) Factorial mating designs

To limit the number of permutations, it was assumed that all selected females produced eggs. The effects of deviations from this assumption, which were investigated for hierarchical mating designs (see a(i)) would be similar for factorial mating designs. Six schemes were examined, and these are described in Table 5. Again, eight sires and 32 donors were selected so that comparisons could be made with hierarchical schemes. The schemes were replicated 350 times and it was again assumed that no full brothers were eligible for selection.

Two factorial mating designs were examined. Two or four sires were mated to each donor in a complete and partially balanced incomplete block design respectively, as previously described.

The three practical factors included in the simulation (which are equivalent to a(ii), a(iii) and a(iv)) were

(i) The number of eggs recovered per donor may vary. It was assumed that every donor was flushed four times and that the number of eggs per flush was chosen at random from a normal distribution with a mean of 4 and a variance of 0, 4 or 16 (i.e. no variance, mean equal to the variance and mean equal to the standard deviation respectively). A repeatability of zero between flushes was again assumed.

To prevent negative values and to keep the mean at four, the minimum and maximum numbers of eggs per flush were set to zero and

Figure 1. Model of the practical factors causing variation in family sizes with hierarchical mating designs. In this particular scheme, 8 of the top ranking 32 females produced no eggs. The number of eggs from each donor was chosen at random from a normal distribution with a mean of 16 and a variance of 0, 16 or 64. A 50% sex ratio and a 50% survival rate of embryos to selection was assumed.

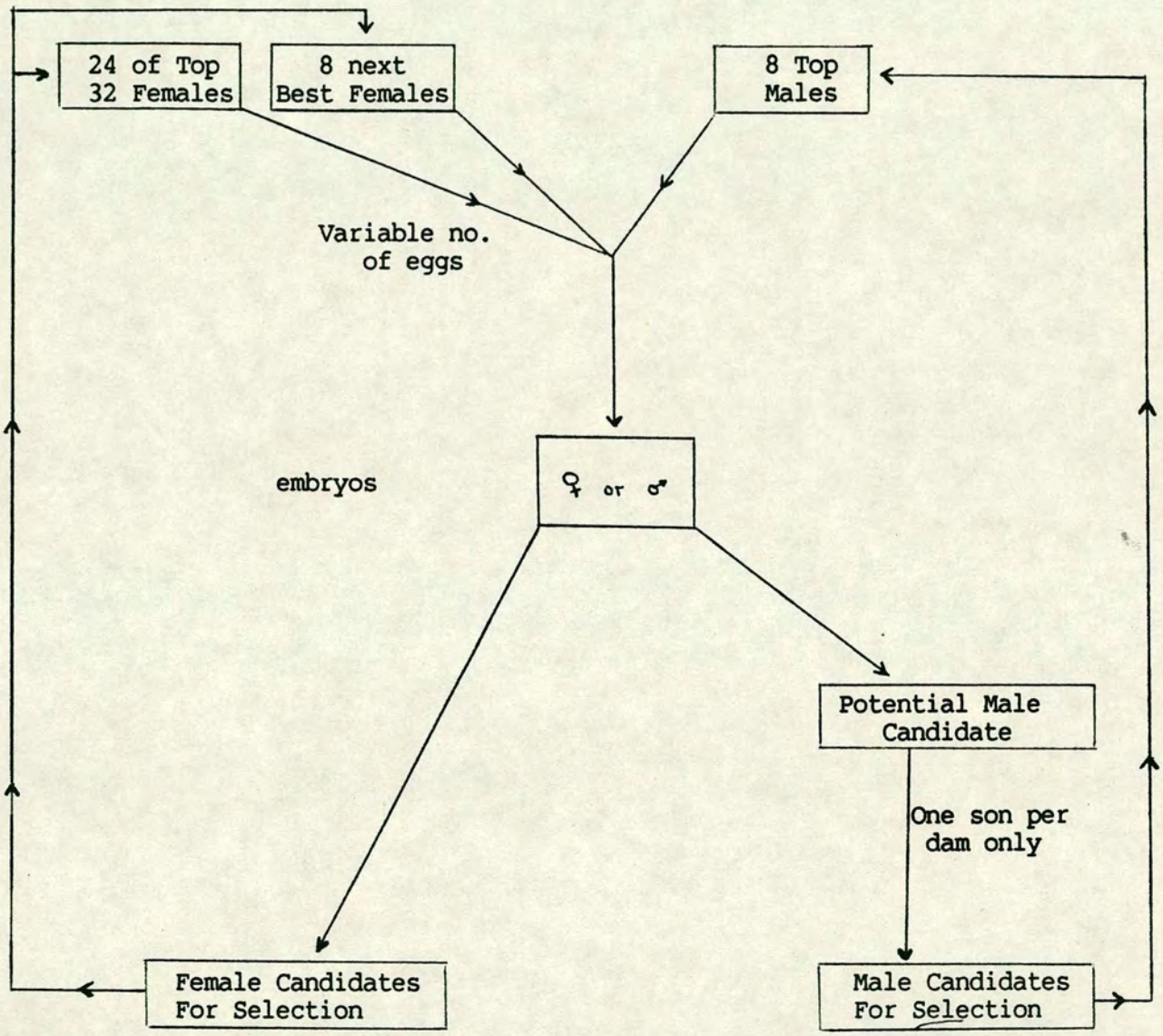


TABLE 5

Description of factorial MOET nucleus schemes allowing for variation due to biological factors. Eight sires and 32 donors were selected in each scheme. On average, 512 embryos were transferred. The mean number of eggs per flush was four

	No. of sires mated to each dam					
	2			4		
	Variance of egg no. per flush			Variance of egg no. per flush		
	0	4	16	0	4	16
No. dams mated to each sire	8	8	8	16	16	16
Average no. of males*	57.56 ±2.46	55.26 ±2.72	51.87 ±3.22	87.40 ±5.41	80.82 ±5.26	72.19 ±5.68
Average no. of females*	127.91 ±9.68	128.20 ±11.51	127.88 ±12.22	127.91 ±9.68	128.20 ±11.51	127.88 ±12.22
Average no. of sons per dam	1.80	1.73	1.62	2.73	2.53	2.26
Average no. of sons per sire	7.20	6.91	6.48	10.92	10.10	9.02
Average no. of daughters per dam	4.00	4.01	4.00	4.00	4.01	4.00
Average no. of daughters per sire	15.99	16.03	15.98	15.99	16.03	15.98
Proportion of males selected	8/57.6	8/55.3	8/51.9	8/87.4	8/80.8	8/72.2
Proportion of females selected	32/127.9	32/128.2	32/127.9	32/127.9	32/128.2	32/127.9

*Simulated values presented ± average standard deviation at any generation

eight. With variances of 4 and 16, an expected average of 2.4% and 26.1% of flushes respectively would have produced values outside these limits if no restrictions were used.

When every donor was mated to two sires, semen from each of the two sires was used at two flushes and each sire was mated to eight different donors. When every donor was mated to four sires, semen from each of the four sires was used for one flush per dam only. Each sire was mated to 16 donors.

(ii) Each egg recovered may not develop into a candidate for selection. As in the hierarchical design schemes, a 50% probability of survival to selection was assumed.

(iii) Each animal born may be male or female. As in the hierarchical design schemes, a 50% probability of either sex was assumed.

RESULTS

(1) Altering the family size in hierarchical schemes

(a) Number of sons per dam

The genetic response, the components of response and the rates of inbreeding averaged over generations two to six are shown in Table 6.

The number of male candidates was directly proportional to the number of sons per dam eligible for selection. By allowing more than one son per dam to be selected, the response to selection was increased by up to 5% and 8% with four and eight sires selected respectively.

Response and the number of sons per dam were not linearly related. With four sires selected, genetic gain increased as the number of sons eligible for selection was raised from one to three. On the other hand, using four sons per dam (and hence selecting one

TABLE 6

The effect of the number of sons per dam eligible for selection on genetic gain, the components of genetic gain and inbreeding rates. Results were averaged over generations two to six (inclusive) and are presented ± standard errors. Thirty two dams were selected in each scheme

	No. of sires selected							
	4				8			
	Number of sons per dam				Number of sons per dam			
	1	2	3	4	1	2	3	4
σ_g	0.420 ±0.001	0.414 ±0.001	0.413 ±0.001	0.403 ±0.001	0.437 ±0.001	0.427 ±0.001	0.424 ±0.001	0.420 ±0.001
r_M	0.401 ±0.005	0.391 ±0.005	0.393 ±0.004	0.370 ±0.004	0.408 ±0.005	0.394 ±0.004	0.386 ±0.004	0.378 ±0.004
i_M	1.456 ±0.004	1.677 ±0.007	1.756 ±0.008	1.877 ±0.009	1.215 ±0.002	1.549 ±0.005	1.685 ±0.006	1.794 ±0.007
r_F	0.535 ±0.003	0.530 ±0.003	0.527 ±0.003	0.511 ±0.003	0.546 ±0.003	0.536 ±0.003	0.529 ±0.003	0.524 ±0.003
i_F	1.199 ±0.002	1.200 ±0.002	1.200 ±0.002	1.207 ±0.001	1.233 ±0.001	1.234 ±0.001	1.232 ±0.001	1.235 ±0.002
ΔG	0.260 ±0.003	0.264 ±0.003	0.273 ±0.003	0.266 ±0.003	0.261 ±0.003	0.274 ±0.003	0.279 ±0.003	0.282 ±0.003
ΔF	7.77 ±0.08	8.53 ±0.09	8.81 ±0.08	9.44 ±0.08	4.60 ±0.05	6.05 ±0.07	6.53 ±0.08	7.16 ±0.09

sibship of four brothers) achieved lower rates of response than using three sons per dam, despite the further increase in the number of male candidates. With eight sires selected, response increased as the number of sons eligible for selection increased, but by progressively decreasing amounts.

The components of response show that as the number of sons per dam increased, the genetic standard deviation and the accuracies of selection declined. This was a consequence of both the reduction in between sire variances following selection and higher rates of inbreeding.

The male selection intensities increased as more males were available for selection. However, because of the highly correlated EBVs among the candidates (Hill, 1976), the effect of increasing the number of males was less than expected if the family structure was ignored.

For example, by selecting 4/128 instead of 4/32 and 8/128 instead of 8/32 males, the intensities of selection (accounting for finite numbers) were expected to increase from 1.58 to 2.20 (39%) and from 1.24 to 1.94 (57%) respectively. Instead, the simulated increases were from 1.46 to 1.88 (29%) and from 1.21 to 1.79 (48%).

Inbreeding rates were highest as the number of sons per dam, and hence the number of full brothers selected, increased. Because of the high rates of inbreeding present with four sires selected and with one son per dam eligible for selection, selecting full brothers had considerably less impact on inbreeding compared with selecting eight sires. As a result, the inbreeding rate with four sons instead of one son per dam eligible for selection was 21 and 56% higher when four and eight sires were selected respectively.

The responses achieved over generations one to six are presented in Table 7. Because of the higher inbreeding rates,

TABLE 7

The effect of the number of sons per dam eligible for selection on genetic gain over generations one to six. Thirty two dams were selected. The response in each generation is expressed ± standard deviation of response. The standard error is standard deviation/18.7.

	No. of sires selected							
	4				8			
	Number of sons per dam				Number of sons per dam			
Generation Number	1	2	3	4	1	2	3	4
1	0.226 ±0.135	0.247 ±0.130	0.241 ±0.145	0.235 ±0.155	0.210 ±0.098	0.233 ±0.109	0.243 ±0.112	0.244 ±0.125
2	0.283 ±0.139	0.299 ±0.139	0.302 ±0.149	0.294 ±0.153	0.273 ±0.106	0.294 ±0.122	0.299 ±0.134	0.302 ±0.129
3	0.277 ±0.146	0.288 ±0.147	0.293 ±0.146	0.294 ±0.143	0.271 ±0.108	0.291 ±0.119	0.297 ±0.117	0.309 ±0.130
4	0.262 ±0.133	0.255 ±0.136	0.269 ±0.138	0.265 ±0.138	0.263 ±0.102	0.260 ±0.116	0.279 ±0.117	0.276 ±0.125
5	0.255 ±0.118	0.252 ±0.126	0.251 ±0.135	0.249 ±0.141	0.251 ±0.100	0.267 ±0.111	0.269 ±0.117	0.272 ±0.118
6	0.226 ±0.123	0.227 ±0.126	0.252 ±0.129	0.229 ±0.141	0.246 ±0.106	0.257 ±0.113	0.250 ±0.113	0.251 ±0.117

greater variation in response was found as the number of brothers selected increased.

(b) Number of daughters per dam

For both financial and practical reasons, the number of first lactation cows recorded and eligible for selection in MOET nucleus schemes is likely to be limited. These cows could be bred by many dams with small family sizes or fewer dams with larger families.

The results are presented with this in mind. The genetic response and the components of response averaged over generations two to six, are given in Tables 8 and 9 with four and eight sires selected respectively. Rates of inbreeding and of response for all 18 schemes are summarised in Table 10.

Three general observations can be made concerning the rates of response achieved. Firstly, as expected, responses were higher with more first lactation cows available for selection. They ranged from 0.64 - 1.25% per year with four sires and from 0.56 - 1.32% with eight sires selected.

Secondly, with a constant number of sires selected and cows recorded, responses were in general higher with few dams selected and large family sizes. Despite the increased number of dams, responses with two daughters per dam were substantially lower than with four or eight daughters per dam, which tended to be similar in magnitude.

Thirdly, with a constant number of cows recorded, selecting four instead of eight sires only increased response when the schemes were small. Indeed, for the largest scheme, selecting four instead of eight sires yielded a 5.2% lower rate of response.

These observations can be explained by referring to the components of response. By selecting more dams, each with one son,

TABLE 8

The effect of the number of daughters per dam on response and the components of response. Four sires were selected in each scheme. Results were averaged over generations two to six (inclusive) and are presented ± standard errors. The numbers in brackets are the number of dams x number of daughters per dam. The proportion of males and females selected was 4/(number of dams) and 1/(number of daughters per dam) respectively

	Number of first lactation females recorded								
	32 (16x2)	64 (16x4)	64 (32x2)	128 (16x8)	128 (32x4)	128 (64x2)	256 (32x8)	256 (64x4)	512 (64x8)
σ_g	0.433 ±0.001	0.422 ±0.001	0.434 ±0.001	0.411 ±0.001	0.420 ±0.001	0.429 ±0.001	0.412 ±0.001	0.421 ±0.002	0.413 ±0.001
r_M	0.341 ±0.005	0.369 ±0.005	0.374 ±0.005	0.410 ±0.005	0.401 ±0.005	0.403 ±0.006	0.438 ±0.005	0.445 ±0.005	0.457 ±0.006
i_M	1.174 ±0.002	1.155 ±0.002	1.487 ±0.004	1.156 ±0.002	1.456 ±0.004	1.732 ±0.008	1.448 ±0.005	1.675 ±0.008	1.670 ±0.007
r_F	0.496 ±0.004	0.517 ±0.003	0.521 ±0.003	0.537 ±0.002	0.535 ±0.003	0.542 ±0.004	0.559 ±0.003	0.561 ±0.003	0.571 ±0.003
i_F	0.755 ±0.001	1.191 ±0.001	0.759 ±0.001	1.515 ±0.003	1.199 ±0.002	0.760 ±0.001	1.527 ±0.003	1.197 ±0.002	1.527 ±0.004
ΔG	0.170 ±0.002 (0.64%)*	0.225 ±0.003 (0.84)	0.207 ±0.003 (0.78)	0.269 ±0.002 (1.01)	0.260 ±0.003 (0.98)	0.231 ±0.004 (0.87)	0.308 ±0.003 (1.16)	0.301 ±0.004 (1.13)	0.334 ±0.004 (1.25)

*% Genetic gain per annum with a 15% coefficient of variation and an average generation interval of four years

TABLE 9

The effect of the number of daughters per dam on response and the components of response. Eight sires were selected in each scheme. Results were averaged over generations two to six (inclusive) and are presented ± standard errors. The numbers in brackets are the number of dams x number of daughters per dam. The proportion of males and females selected was 8/(number of dams) and 1/(number of daughters per dam) respectively

	No. of first lactation females recorded								
	32 (16x2)	64 (16x4)	64 (32x2)	128 (16x8)	128 (32x4)	128 (64x2)	256 (32x8)	256 (64x4)	512 (64x8)
σ_g	0.451 ±0.001	0.443 ±0.001	0.449 ±0.001	0.432 ±0.001	0.437 ±0.001	0.441 ±0.001	0.428 ±0.001	0.432 ±0.001	0.425 ±0.001
r_M	0.345 ±0.005	0.380 ±0.005	0.370 ±0.005	0.417 ±0.004	0.408 ±0.005	0.392 ±0.005	0.446 ±0.004	0.433 ±0.005	0.467 ±0.005
i_M	0.764 ±0.001	0.761 ±0.001	1.225 ±0.002	0.762 ±0.001	1.215 ±0.002	1.577 ±0.005	1.211 ±0.002	1.552 ±0.005	1.556 ±0.006
r_F	0.506 ±0.003	0.533 ±0.003	0.527 ±0.003	0.551 ±0.002	0.546 ±0.003	0.544 ±0.003	0.569 ±0.002	0.557 ±0.003	0.579 ±0.003
i_F	0.771 ±0.001	1.223 ±0.001	0.777 ±0.001	1.565 ±0.003	1.233 ±0.002	0.778 ±0.001	1.578 ±0.003	1.237 ±0.002	1.590 ±0.003
ΔG	0.149 ±0.002 (0.56%)*	0.210 ±0.002 (0.79)	0.197 ±0.002 (0.74)	0.258 ±0.002 (0.97)	0.261 ±0.003 (0.98)	0.231 ±0.004 (0.87)	0.307 ±0.003 (1.15)	0.296 ±0.004 (1.11)	0.353 ±0.004 (1.32)

*% genetic gain per annum with a 15% coefficient of variation and an average generation interval of four years

TABLE 10

The effect of number of daughters per dam on inbreeding and response rates. Results were averaged over generations two to six (inclusive) and are presented ± standard errors. The numbers in brackets are the number of dams x the number of daughters per dam.

	Number of first lactation females recorded								
No. of sires	32 (16x2)	64 (16x4)	64 (32x2)	128 (16x8)	128 (32x4)	128 (64x2)	256 (32x8)	256 (64x4)	512 (64x8)
ΔF									
4	6.29 ±0.05	7.93 ±0.07	6.06 ±0.05	9.30 ±0.08	7.77 ±0.08	6.16 ±0.08	8.92 ±0.10	7.36 ±0.10	8.54 ±0.12
8	3.24 ±0.02	4.25 ±0.04	3.39 ±0.03	4.94 ±0.05	4.60 ±0.05	3.63 ±0.05	5.64 ±0.07	4.79 ±0.07	5.85 ±0.09
ΔG									
4	0.170 ±0.002	0.225 ±0.003	0.207 ±0.003	0.269 ±0.002	0.260 ±0.003	0.231 ±0.004	0.308 ±0.003	0.301 ±0.004	0.334 ±0.004
8	0.149 ±0.002	0.210 ±0.002	0.197 ±0.002	0.258 ±0.002	0.261 ±0.003	0.231 ±0.004	0.307 ±0.003	0.296 ±0.004	0.353 ±0.004

more males were available for selection and the male selection intensities were increased. On the other hand, increasing the number of daughters per dam raised the female selection intensities. Because females were evaluated more accurately than males, changes in the female selection intensities had a greater impact on genetic gain. For this reason, increasing the number of daughters per dam at the expense of reducing the number of dams yielded higher responses in most situations.

With few dams selected, the number of males eligible for selection was reduced. In this situation, selecting four rather than eight sires had a substantial impact on the male intensities of selection. With many dams selected, the impact was quite small.

The rates of inbreeding shown in Table 10 vary from 3% to 9% per generation. Inbreeding rates with four sires were 46-94% higher than with eight sires selected. With a constant number of first lactation cows recorded, inbreeding rates were increased as the number of dams decreased.

The considerable impact of selection on inbreeding was apparent by observing the higher rates of inbreeding for all six sire x dam combinations when the family size was increased, thus allowing more intense selection of females. Inbreeding rates were increased by 39-66% as the number of daughters per dam was raised from two to eight.

The response to selection over generations one to six are shown in Tables 11 (four sires) and 12 (eight sires). With the number of first lactation cows constant, response at generation one was substantially higher when few dams were selected and family sizes were large.

Because of the intense and accurate selection of the nucleus founders at generation zero, the between family genetic variances and

TABLE 11

The effect of the number of daughters per dam on genetic gain over generations one to six. Four sires were selected in each scheme. Response is expressed ± standard deviation of response. The standard error is the standard deviation divided by 24.5, 18.7 and 13.0 with 16, 32 and 64 dams respectively. The numbers in brackets are the number of dams x the number of daughters per dam. The proportion of males and females selected is 4/(number of dams) and 1/(number of daughters per dam) respectively

	Number of first lactation females recorded								
Generation number	32 (16x2)	64 (16x4)	64 (32x2)	128 (16x8)	128 (32x4)	128 (64x2)	256 (32x8)	256 (64x4)	512 (64x8)
1	0.123 ±0.127	0.198 ±0.128	0.149 ±0.131	0.264 ±0.133	0.226 ±0.135	0.165 ±0.116	0.286 ±0.131	0.254 ±0.123	0.322 ±0.132
2	0.172 ±0.134	0.245 ±0.145	0.218 ±0.125	0.298 ±0.147	0.283 ±0.139	0.234 ±0.125	0.326 ±0.134	0.327 ±0.140	0.267 ±0.137
3	0.186 ±0.129	0.241 ±0.130	0.215 ±0.126	0.289 ±0.146	0.277 ±0.146	0.244 ±0.122	0.324 ±0.143	0.323 ±0.126	0.357 ±0.140
4	0.179 ±0.122	0.223 ±0.146	0.216 ±0.130	0.272 ±0.136	0.262 ±0.133	0.239 ±0.115	0.311 ±0.146	0.291 ±0.127	0.344 ±0.127
5	0.160 ±0.128	0.217 ±0.130	0.198 ±0.123	0.251 ±0.128	0.255 ±0.118	0.220 ±0.108	0.298 ±0.132	0.288 ±0.115	0.314 ±0.106
6	0.154 ±0.122	0.199 ±0.133	0.188 ±0.117	0.237 ±0.135	0.226 ±0.123	0.220 ±0.108	0.282 ±0.121	0.275 ±0.117	0.290 ±0.113

TABLE 12

The effect of number of daughters per dam on genetic gain over generations one to six. Eight sires were selected in each scheme. Response is expressed ± standard deviation of response. The standard error is the standard deviation divided by 24.5, 18.7 and 13.0 with 16, 32 and 64 dams respectively. The numbers in brackets are the number of dams x the number of daughters per dam. The proportion of males and females selected is 8/(number of dams) and 1/(number of daughters per dam) respectively.

	Number of first lactation females recorded								
Generation number	32 (16x2)	64 (16x4)	64 (32x2)	128 (16x8)	128 (32x4)	128 (64x2)	256 (32x8)	256 (64x4)	512 (64x8)
1	0.106 ±0.094	0.164 ±0.096	0.133 ±0.094	0.231 ±0.098	0.210 ±0.098	0.160 ±0.094	0.280 ±0.099	0.239 ±0.098	0.320 ±0.105
2	0.144 ±0.100	0.211 ±0.104	0.188 ±0.102	0.268 ±0.110	0.273 ±0.106	0.230 ±0.101	0.325 ±0.105	0.320 ±0.099	0.379 ±0.106
3	0.155 ±0.098	0.220 ±0.106	0.200 ±0.100	0.265 ±0.109	0.271 ±0.108	0.239 ±0.099	0.314 ±0.108	0.309 ±0.098	0.365 ±0.110
4	0.156 ±0.096	0.206 ±0.108	0.204 ±0.095	0.258 ±0.109	0.263 ±0.102	0.233 ±0.096	0.305 ±0.113	0.302 ±0.101	0.358 ±0.107
5	0.144 ±0.098	0.210 ±0.103	0.203 ±0.101	0.255 ±0.103	0.251 ±0.100	0.228 ±0.091	0.311 ±0.104	0.279 ±0.101	0.337 ±0.108
6	0.145 ±0.097	0.206 ±0.103	0.188 ±0.092	0.246 ±0.101	0.246 ±0.106	0.226 ±0.098	0.279 ±0.103	0.270 ±0.093	0.325 ±0.094

consequently the male accuracies of selection at generation one were reduced considerably compared with later generations. The female accuracies of selection were relatively unaffected because each female had a single record and was not evaluated solely on pedigree information. In this situation, increasing the female selection intensities (by producing more daughters per dam) yielded higher rates of response than increasing the male selection intensities (by increasing the number of dams).

Response was more variable in schemes with higher inbreeding rates. Thus, the standard deviation of response was substantially higher when four rather than eight sires were selected. With the numbers of cows recorded constant, it was also higher when few dams were selected.

(2) Allowing for variation in embryo numbers, sex ratios and survival rates in MOET nucleus schemes

(a) Hierarchical mating designs

The genetic response, the components of response and the rates of inbreeding, averaged over generations two to six, are shown in Table 13. Compared with designs assuming that all selected cows have families of equal size, variation in embryo numbers, in sex ratios and in survival rates in hierarchical MOET nucleus schemes reduced genetic gain by 2-15%.

Removing the assumptions of fixed sex ratios and survival rates resulted in a 2% drop in response. Including variation in the number of eggs recovered per donor reduced response by up to 4%. However, it was the first source of variation, the number of selected cows that yielded no eggs, which had the greatest impact on response. When the 32 donors were among the top ranking 48 cows, response was 9-13% lower than when all the top 32 cows produced eggs.

TABLE 13

The effect of variation due to biological factors in hierarchical MOET nucleus schemes on response to selection, the components of response and the rates of inbreeding. Eight sires were selected and embryos were recovered from 32 of the top 32, 40 or 48 females ranked for milk production that were flushed. Each embryo recovered had a 50% probability of being male or female and a 50% probability of surviving to be eligible for selection. The mean number of embryos per donor was 16. The standard errors were between 0.001-0.005 for the mean and components of response and about 0.05 for the inbreeding rates. The figures in brackets represent the percentage change compared to the scheme with fixed family sizes (Chapter 5). The results were averaged over generations two to six (inclusive)

	Variance of egg no. per donor								
	0			16			64		
	No. top females flushed			No. top females flushed			No. top females flushed		
	32	40	48	32	40	48	32	40	48
σ_g	0.437 (0.0)	0.439 (0.4)	0.440 (0.6)	0.435 (-0.4)	0.438 (0.3)	0.439 (0.4)	0.436 (-0.1)	0.437 (-0.1)	0.439 (0.5)
r_M	0.405 (-0.7)	0.402 (-1.5)	0.404 (-1.1)	0.390 (-4.3)	0.405 (-0.7)	0.401 (-1.7)	0.399 (-2.3)	0.405 (-0.8)	0.396 (-3.0)
i_M	1.206 (-0.7)	1.207 (-0.6)	1.211 (-0.3)	1.199 (-1.3)	1.204 (-0.9)	1.206 (-0.7)	1.167 (-3.9)	1.168 (-3.8)	1.167 (-3.9)
r_F	0.547 (0.2)	0.550 (0.7)	0.555 (1.6)	0.546 (0.0)	0.551 (1.0)	0.548 (0.4)	0.554 (1.4)	0.550 (0.7)	0.549 (0.6)
i_F	1.227 (-0.5)	1.097 (-11.1)	0.978 (-20.7)	1.224 (-0.7)	1.094 (-11.3)	0.978 (-20.7)	1.220 (-1.0)	1.089 (-11.7)	0.972 (-21.2)
ΔG	0.256 (-1.9%)	0.239 (-8.3)	0.229 (-12.3)	0.249 (-4.3)	0.241 (-7.5)	0.226 (-13.2)	0.252 (-3.3)	0.236 (-9.4)	0.221 (-15.4)
ΔF	4.63 (0.5)	4.30 (-6.5)	4.09 (-11.2)	4.74 (3.1)	4.35 (-5.6)	4.02 (-12.7)	4.74 (3.0)	4.37 (-5.0)	4.04 (-12.2)

For all 9 schemes, the reductions in genetic gain were primarily a consequence of changes in selection intensities. Even with the variation in egg numbers, sex ratios and survival rates, each donor had a high probability of contributing a single male for selection, so that the total number of male candidates was not substantially reduced. Male selection intensities decreased from 1.21 to 1.17 only. By comparison the need to use 8 and 16 cows from outside the top ranking 32 cows resulted in changes in the female selection intensity from about 1.22 to 1.09 and 0.98.

When the top 32 cows were donors, rates of inbreeding were up to 3% higher with variable rather than fixed family sizes. However, when some of the top cows failed to produce eggs and the female selection intensities fell, inbreeding rates were reduced by up to 13%. Thus the increase in inbreeding due to variable family sizes (Falconer, 1981) was less important than the reduction in inbreeding due to relaxing the selection pressure on males and, most importantly, on females.

(b) Factorial mating designs

The effects of variation in family sizes on genetic response, the components of response and the rates of inbreeding, averaged over generations two to six, are shown in Table 14. Genetic gain was 1-4% lower than with fixed family sizes, due mainly to changes in male selection intensities.

Allowing for variation in sex ratios and in survival rates reduced response by 1 and 4% with two and four sires mated to each dam respectively. Including variation in the number of eggs recovered per flush reduced response by an additional 2% with two sires per dam, but it increased response slightly with four sires per dam. This slight improvement in response with four sires per dam

TABLE 14

The effect of variation due to biological factors in factorial MOET nucleus schemes on genetic gain, the five components of response and the rates of inbreeding. Eight sires and 32 donors were selected. 'Each donor had four flushes, with a mean of four eggs and a variance of 0, 4 or 16 eggs per flush. No full brothers were eligible for selection. The results were averaged over generations two to six (inclusive). The standard errors are similar to those previously described. The figures in brackets are the percentage change in results compared to schemes with fixed family sizes

	No. sires mated to each dam					
	2			4		
	Variance of egg no. per flush			Variance of egg no. per flush		
	0	4	16	0	4	16
σ_g	0.435 (-0.1%)	0.437 (0.4%)	0.434 (-0.3%)	0.433 (0.0%)	0.436 (0.5%)	0.435 (0.3%)
r_M	0.380 (-1.8%)	0.388 (0.3%)	0.383 (-1.1%)	0.367 (-2.9%)	0.381 (0.8%)	0.384 (1.7%)
i_M	1.520 (-2.9%)	1.494 (-4.6%)	1.461 (-6.7%)	1.698 (-8.1%)	1.669 (-9.7%)	1.619 (-12.4%)
r_F	0.539 (1.2%)	0.542 (1.6%)	0.536 (0.4%)	0.532 (0.8%)	0.537 (1.8%)	0.535 (1.4%)
i_F	1.234 (-0.2%)	1.231 (-0.4%)	1.229 (-0.6%)	1.233 (-0.5%)	1.232 (-0.6%)	1.231 (-0.7%)
ΔG	0.272 (-1.0%)	0.273 (-0.9%)	0.265 (-3.4%)	0.279 (-4.4%)	0.285 (-2.4%)	0.281 (-3.8%)
ΔF	4.98 (0.7%)	4.97 (0.5%)	4.96 (0.2%)	4.95 (-5.3%)	5.03 (-3.7%)	5.13 (-1.9%)

was probably due to chance since, as with hierarchical mating designs, increased variation in egg numbers reduced the number of male candidates, as no full brothers were eligible for selection (see Table 5).

Although variation in family sizes reduced the number of males considerably (by 10-44%), the male selection intensities changed relatively little (by 3-12%). These changes agreed with expectations based on finite numbers of candidates (Becker, 1975) and were relatively small because the fraction of males selected in each situation was quite low.

As in the hierarchical design schemes, variation in family sizes tended to increase inbreeding while lower selection intensities tended to reduce inbreeding. With two sires per dam, inbreeding was changed very little. With four sires per dam, inbreeding was reduced by 2-5% due to a greater relaxation in selection pressure.

DISCUSSION

In small populations, selecting as intensely as possible may not be the optimal strategy. By relaxing the restriction on selecting full brothers, male selection intensities were increased but at a cost. Genetic variances were reduced due to stronger selection pressures and increased rates of inbreeding, which in turn resulted in lower accuracies of selection. The balance between these components of response meant that despite increasing the number of male candidates by up to four fold, genetic gain was only 1-8% higher. In addition, animals born were more inbred and response to selection was more variable.

Thus, allowing more than one son per dam to be eligible for selection provided little increase in response to selection and had considerable disadvantages. Furthermore, it reduces the

possibilities of within dam selection of males for beef traits, for physiological indicators of milk yield or for other similar traits.

The importance of the number of daughters per dam should be assessed from results with eight sires selected since, apart from the smallest schemes, selecting few (four) sires produced far higher rates of inbreeding and more variable responses to selection without increasing the mean response.

With the number of recorded cows constant, small family sizes (two daughters per dam) yielded substantially reduced responses. Rates of response with families of four or eight daughters per dam were fairly similar although the larger family size produced higher rates of inbreeding. This increase in inbreeding, as well as the longer time required to collect the neccessary number of embryos and its consequent effect on generation intervals, suggests that medium sized families may be optimal in the long term. When setting up the nucleus scheme, because of the substantial impact on response, larger family sizes may be more advantageous.

Variation in family sizes in MOET nucleus schemes had similar consequences whether hierarchical or factorial mating designs were used. Assuming all selected cows produced eggs, changes in family sizes brought about by differences in sex ratios, in survival rates and by variation in the number of eggs per donor reduced response to selection by 1-4%. These results, support those of Jansen and Schlote (1987) who concluded from simulation studies that the effect of variation in family sizes in hierarchical schemes was small.

However, failure to collect any embryos from some selected cows, and hence the need to use genetically inferior animals as replacements, had the largest effect on response. This was very much a consequence of reduced intensities of selection. As the size

of the reductions in selection intensities agreed well with deterministic predictions (e.g. Becker, 1975), the potential impact of such factors on genetic gain can be approximated quite well without simulation.

As with any theoretical work, these conclusions depend on the model used. It was assumed that a given percentage of superovulated cows yielded no eggs, that there was no correlation between milk yield and failure to produce eggs, that the repeatability of egg numbers between flushes was zero and that the distribution of eggs from the remaining cows was normal. To date no direct information on these assumptions has been presented.

It was also assumed that despite recovering no eggs from some cows, the number of donors remained constant. In practice, this would require replacing the top ranking cows that produced no eggs with animals of lower genetic merit, thus superovulating more cows. If they were not replaced, the number of candidates (both males and female) would fall proportionally and the response to selection could be substantially reduced since the accuracies as well as the intensities of selection would be affected.

Since selection was for a sex-limited trait, the reduction in the number of males did not result in any loss of information or a reduction in accuracies of selection. In a beef MOET scheme or in a dairy MOET scheme where males provide records (e.g. of physiological indicators), further reductions in response would be expected.

Embryo sexing has been described as a useful tool for reducing the number of embryo transfers and recipients needed when one male per sibship is eligible for selection and a hierarchical mating design is used (Nicholas and Smith, 1983). However, because of the risk of embryos failing to survive to selection, the advantages may have been overestimated. If fewer male embryos are

transferred, the probability of failing to produce a single male for selection is increased. For example, with a 50% probability of an embryo leading to a candidate for selection, transferring three male embryos per dam would on average leave 12% of dams without sons.

The importance of getting embryos from the top cows was shown by the substantial drop in response following the use of genetically inferior cows. The magnitude of this reduction will depend on the female replacement rate. Let us assume that 32 cows are to be selected, but that eight produce no eggs, thus requiring inferior replacements. With 2, 4 and 8 daughters per dam the proportion of females selected increases from 50%, 25% and 13% to 63%, 31% and 16% respectively. The greater the family size, the less important the problem becomes. However, with small or medium sized families, this is by far the most important of the four factors examined.

SUMMARY

This study examined the effects of removing some of the assumptions made in previous chapters concerning family sizes. Firstly, the number of sons and daughters per dam was varied in MOET nucleus schemes using hierarchical mating designs. With four or eight sires and 32 dams selected, increasing the number of sons per dam from one up to four achieved 1-8% higher rates of response but at the expense of increased variation in response and 10-56% higher rates of inbreeding. With four or eight sires and 16, 32 or 64 dams selected, the number of daughters was set to 2, 4 or 8 (with one son per dam in each case). For schemes of equal size, responses were lower with two daughters per dam but were fairly similar with four or eight daughters per dam while inbreeding rates increased as fewer sires and dams were selected. Secondly, the effects of variation in

family sizes due to biological factors and chance were investigated with eight sires and 32 dams selected and mated in a hierarchical or factorial (two or four sires per dam) mating design. The results were similar with each mating design. When it was assumed that eggs were recovered from all selected cows, changes in family sizes due to differences in sex ratios, in survival rates of embryos to selection and to variation in the number of eggs per donor reduced response by 1-4%. However, when eight or 16 of the top females yielded no eggs, thus requiring the use of inferior replacements, response was reduced by a further 9-13%.

CHAPTER 8

GENERAL DISCUSSION AND CONCLUSIONS

Two strategies by which embryo transfer can be applied to the genetic improvement of dairy cattle have been considered. The first strategy was to use embryo transfer in schemes currently in operation (progeny testing schemes) while the second involved the development of novel breeding schemes to take full advantage of this new technology. This thesis has examined both possibilities although most attention was paid to the latter.

Previous studies have indicated that the use of embryo transfer in progeny testing schemes would have relatively little impact on genetic response. For example, Bradford and Kennedy (1980) concluded that it was unlikely to increase response by more than 10%. The results of Chapters 2 and 3 suggest that, although the impact may still be relatively small, it could be greater than previously considered.

The studies in Chapters 2 and 3 examined the possible implications of using embryo transfer on cows selected to produce young bulls for progeny testing. By evaluating the young bulls bred in this manner at an earlier age using full sib records, it was shown in Chapter 2 that the merit of commercial semen could be increased by 10 to 20% in current schemes. Although increases of this magnitude would be substantial from the viewpoint of the AI organisations which sell semen, the impact on genetic progress would be quite small since the bull to breed cow pathway only accounts for about 20% of the total selection response (Everett, 1984).

The use of embryo transfer on bull dams has two other

effects. Firstly, by increasing the probability of producing a male calf, the female selection intensities are increased because fewer bull dams are selected. Secondly, because the bull dams are of higher genetic merit, their daughters (bred by embryo transfer) are also of higher genetic merit and so many are themselves selected as bull dams in the next generation. The results in Chapter 3 showed that these two effects could increase response by 13%. Taken together, these results suggest that response rates in progeny testing schemes may be increased by up to 20% through using embryo transfer on bull dams and by selecting bulls for commercial use from those evaluated on sib or progeny information.

The use of embryo transfer in new dairy cattle breeding schemes was proposed by Nicholas (1979) and Nicholas and Smith (1983). These MOET nucleus schemes differed considerably from progeny testing schemes due to their centralised breeding structure and by emphasising that animals should be evaluated and selected at an early age with low precision instead of at a later age with high precision. Of the two schemes described by Nicholas and Smith (1983), the emphasis on early selection was stronger in the juvenile scheme (generation interval of about two years) than in the adult scheme (generation interval of about four years).

Previous comparisons of MOET nucleus and progeny testing schemes assumed that both schemes were in operation and that they were improving at a constant rate. Chapter 4 compared the schemes in the situation where an efficient progeny testing scheme was in steady state equilibrium and a juvenile or adult MOET nucleus scheme was being set up.

The results showed that the responses achieved by setting up the MOET nucleus schemes were lower in the early years than expected if they were in equilibrium. Compared to the response expected if

the progeny testing scheme was continued, setting up the adult scheme had relatively little impact in the first 10 years. When compared over a longer time period, the benefits were greater.

In contrast, because of the higher response rates expected and the more rapid dissemination of superior genes to the commercial herd, both the short and long term genetic gains achieved by setting up the juvenile scheme were substantial.

Although the juvenile schemes offer the highest potential rates of response, the practical and theoretical problems associated with recovering eggs from young heifers and with selecting young animals solely on pedigree information seem quite large. Because of this, the adult schemes are currently of greater interest. For this reason, a Monte Carlo simulation study of an adult scheme was undertaken, which was described in Chapters 5 to 7.

The high rates of response originally predicted for adult schemes were derived assuming that the effects of finite numbers and the family structure on selection intensities, and the effects of selection and inbreeding on genetic variances and accuracies of selection could be ignored. The results in Chapter 5 showed that these assumptions may be seriously violated in MOET nucleus breeding schemes.

The simulated rates of response were about 60% (with four sires) and 70% (with eight sires) of the responses predicted under these assumptions. Most of the differences between simulated and expected responses were a consequence of reductions in the between family genetic variances due to selection.

As well as reducing the variability among the candidates for selection, the reduction in the between family genetic variances had an even greater effect on the accuracies of selection because of the extensive use of family information for evaluating the candidates for

selection. This effect was greater for males than females because they produced no records. In juvenile schemes, where both sexes are evaluated solely on pedigree information and (in the absence of physiological indicator traits) no within family selection is possible, this problem could be more substantial.

In practice, the reduction in variances may not present such a big problem. The simulation assumed that the base population of candidates was unselected, but there is likely to have been selection in the population prior to setting up the nucleus herd and so some of the reductions in between family genetic variances may be accounted for. Furthermore, because of improved management conditions, the environmental variances in the nucleus herd may be reduced, thus increasing the heritability.

The schemes simulated in Chapter 5 followed Nicholas and Smith (1983) with a hierarchical mating design and only one son per dam eligible for selection. Results in Chapters 6 and 7 showed that alternative mating designs and selection strategies could be employed to improve these schemes.

Small increases in response were achieved by assortative mating or by lifting the restriction of one son per dam. However, neither strategy was considered worthwhile because of the substantial increases found in the rates of inbreeding and in the variance of response.

Replacing hierarchical with factorial mating designs (factorial schemes) increased response by up to 13%. Inbreeding was unchanged with four sires selected and increased by up to 14% with eight sires selected. Using full brothers from selected sibships (sibship schemes) reduced inbreeding rates by about 30% without adversely affecting response. The combination of these two strategies (factorial sibship schemes) increased response rates by

5-14% and reduced inbreeding rates (with one exception) by 14-30%.

The responses were calculated assuming that the generation intervals were the same as in the hierarchical schemes. Of the breeding schemes outlined, only the factorial schemes may violate this assumption, but in most situations it will make little difference. For example, if donors are flushed three times in the hierarchical scheme to generate families of four daughters and one son per dam, the results in Chapter 6 show that the factorial schemes can still achieve 10% higher rates of response without increasing the generation interval.

In the hierarchical schemes, full brothers are not utilised and they serve no purpose because only one son per dam is eligible for selection. In this situation, any strategy which can use the full brothers to reduce inbreeding and/or which can increase response by generating more male sibships of smaller size will be superior.

However, other conflicting options also exists. It is possible to discriminate and select between full brothers for other potentially important characteristics, such as beef traits. In addition, it may soon be possible to predict the breeding values of males for dairy traits by recording reliable indicator traits on the animals themselves (Woolliams and Smith, 1988).

In both situations, males have their own records and so, they need not be evaluated solely on pedigree information. Because this will reduce the intra class correlations of estimated breeding values between relatives, rates of inbreeding may be reduced.

Thus, these two options may increase response and reduce inbreeding. Whether these alternatives are better than the factorial sibship schemes will depend on the economic importance of the other characteristics (first option) and the genetic parameters associated with the indicator trait (second option). In addition, the extra

cost of testing males should be considered.

A third option, which would be possible if embryo sexing was available, would be to reduce the size of the male sibships. By transferring fewer male embryos, resources could be freed for other uses. However, such a strategy would have to account for the possible reduction in male selection intensities, brought about by male embryos failing to survive to selection and hence reducing the number of male candidates.

Chapter 7 described 18 hierarchical schemes in which the number of embryos transferred ranged from 128 to 2048. The simulated responses ranged from 0.6% to 1.3% per annum (assuming a 15% coefficient of variation and a four year generation interval). Responses were considerably lower than predicted by simple deterministic formulae (0.8% to 2.2% per annum).

Nevertheless, the responses achieved in practice from such breeding schemes may be even lower than predicted by simulation. The genetic model ignored dominance effects and assumed that the trait of interest was controlled by a large number of loci, each with a small and additive effect. Because dominance effects were ignored, it was also assumed that the trait showed no inbreeding depression.

However, several studies have shown that milk production traits are subject to inbreeding depression. For example, Robertson (1954) and Hermas et al. (1987) found that for every 1% increase in inbreeding coefficient, milk yield was reduced by 0.32% and 0.47% respectively. De Roo (1988) also demonstrated that further losses in response could occur in such situations if breeding values were estimated without accounting for differences in inbreeding coefficients between animals.

Furthermore, because inbreeding depression is closely

associated with fitness traits (Falconer, 1981), reproductive performance is likely to decline in schemes with high rates of inbreeding. This could reduce the intensities of selection if either semen quality deteriorated or fewer transferable embryos were recovered and, consequently, fewer animals were born.

For these reasons, as well as to maintain relatively low variances of responses, inbreeding rates should be kept to a reasonable level in MOET nucleus breeding schemes. The results in Chapter 7 showed that inbreeding rates varied considerably between schemes. Sire number was of considerable importance. Inbreeding rates ranged from 0.8% to 1.5% (eight sires) and from 1.5% to 2.3% per annum (four sires). Consequently, schemes with eight rather than four sires are preferred.

If rates of inbreeding less than 1% per annum are considered reasonable, only three of the 18 schemes would be acceptable. Because higher response rates were associated with higher inbreeding rates (due to selection), these three schemes achieved relatively low rates of genetic progress (0.56% to 0.87% per annum).

Altering the mating designs and selection strategies can improve the situation. Table 1 summarises the rates of inbreeding and response for factorial, sibship and factorial sibship schemes. The schemes were of equal size, requiring about 500 embryo transfers, and, in each, 32 dams and eight male sibships were selected. Results with four sibships selected were excluded because of high inbreeding rates (1.3% to 1.9%). For schemes of this size, it was possible to achieve rates of response of 1% per annum with similar rates of inbreeding. Among the schemes with rates of inbreeding below 1%, the factorial sibship scheme gave the highest response.

Apart from the effects of inbreeding, realised responses may be lower than predicted because the simulation assumed that all

TABLE 1

Summary of annual rates of response and inbreeding with different breeding strategies. A 15% coefficient of variation and a four year generation interval were assumed and results are expressed in percentages per annum. Eight male sibships and 32 dams were selected. Each dam had four daughters. Assuming a 50% sex ratio and a 50% survival rate of embryos to selection, about 512 embryos would be needed for each scheme.

	Scheme							
	Hierarchical	Factorial No. of sires per dam			Sibship No. of sons per dam			Factorial Sibship (2 sires per dam and 2 sons per dam)
		2	3	4	2	3	4	
No. of sires selected	8	8	8	8	16	24	32	16
ΔF	1.15	1.24	1.28	1.31	0.88	0.80	0.85	0.95
ΔG	0.98	1.03	1.08	1.10	0.97	0.95	0.95	1.03

selected cows had offspring and that families of equal size were generated. This was investigated in Chapter 7. The results for both hierarchical and factorial schemes showed that changes in family sizes, brought about by differences in sex ratios, in survival rates and by variation in the number of eggs per donor would have little (1-4%) impact on responses, provided all selected cows produced eggs. When some selected cows yielded no eggs, thus requiring the use of genetically inferior animals, the impact on response was more substantial (9-13%).

However, the breeding structure of the schemes simulated in this thesis was relatively simple. The nucleus herd established was closed and, within the herd, discrete generations of selection were followed with animals eligible for selection only once. In practice, other groups of animals (from both outside and inside the nucleus) could also be considered for selection.

With a closed nucleus herd, the use of genetically superior stock from outside the nucleus, if available, was not considered. These individuals would be especially useful in the early stages of the nucleus scheme when information within the herd is scarce. Furthermore, the importation of unrelated genetic stock into the nucleus would be a valuable tool for reducing the inbreeding coefficients of nucleus animals.

Within the nucleus, animals were only eligible for selection when first lactation records were completed. Another alternative would be to allow overlapping generations, in which younger and/or older animals would also be eligible for selection. Additional resources would be needed to retain older animals but not younger animals. By increasing the number of candidates, overlapping generations would permit increased rates of genetic progress and/or decreased rates of inbreeding.

When MOET nucleus schemes were originally described, two important features were noted. The first was that higher rates of response were possible than in progeny testing schemes. The second was that additional benefits would also result from exploiting its centralised breeding structure. While most work has focused on the first point, the second point still remains true.

In livestock species (e.g. pig and poultry) utilising centralised breeding schemes, relatively high rates of response have been achieved. The advantages of centralised breeding schemes, such as nucleus herd schemes, in dairy cattle, have been outlined by Hinks (1978).

By imposing more direct control on the pathways of selection, the gap between expected and realised responses may be substantially reduced. It should also be possible to respond more readily to changes in market requirements. In addition, as a consequence of good management, the heritability, and hence the accuracies of selection, may be increased.

With a closed nucleus herd scheme, the response in the commercial herd depends on the response achieved within the nucleus. In this situation, the benefits of employing expensive technologies, such as MOET, embryo sexing and gene transfer, and of recording economically important traits, such as feed conversion efficiency, within the the nucleus are maximised.

Possible disadvantages of centralised breeding schemes in dairy cattle also exist. Difficulties arise with lowly heritable traits, such as fertility and longevity (Colleau and Mocquot, 1989), and possible genotype by environment interactions may occur. These problems may be reduced by collecting records on secondary traits from commercial herd animals and by selecting nucleus animals under commercial conditions respectively.

The results of this study have shown that the rates of response in MOET nucleus schemes, as originally described, are likely to be lower than predicted. However, given the considerable advantages of centralisation, further research should concentrate on the implications of opening the nucleus herd and the use of overlapping generations so that the substantial benefits from using embryo transfer in nucleus herds of dairy cattle may be realised.

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Animal Breeding Abstracts

Review of the use of embryo transfer in the genetic improvement of dairy cattle

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I.

Abstract

The ability to increase the reproductive rate of the dairy cow with embryo transfer has made it possible to raise selection response through higher intensities of selection and shorter generation intervals. Initially, incorporating embryo transfer into a progeny testing scheme was seen to be its only role in dairy cattle improvement. Three main ways of doing this were examined, but none of them is likely to improve response substantially in an efficient scheme. An alternative method of using embryo transfer is in a Multiple Ovulation and Embryo Transfer (MOET) nucleus breeding scheme. Here, an elite herd is set up, with subsequent selection of animals at an early age based on family information. The rates of genetic response possible can be larger than from a national progeny testing scheme. Responses should be higher from a juvenile (selection before first breeding) than an adult (selection after first lactation) MOET nucleus scheme. As a further alternative, MOET hybrid schemes which use the MOET nucleus herd solely to produce the young bulls needed for progeny testing can also yield greater responses than a traditional progeny testing scheme. A MOET nucleus breeding programme offers additional benefits from the greater control which can be exercised over selection, and the ability to adopt new technologies rapidly. Since the concept of utilising MOET nucleus schemes to maximise genetic progress is relatively recent, many questions have still to be answered concerning their application.

II. Introduction

One of the restrictions to genetic progress in cattle has been the inability of a cow to produce more than one offspring, on average, per year. However, with the development of reliable embryo transfer (ET) techniques in the 1970s, this limitation has been removed.

It is now routine procedure for a cow to be given a hormonal treatment which results in the shedding of a larger number of eggs than normal. Following insemination, the fertilized eggs (embryos) are recovered from the uterus by flushing and subsequently, either directly or after a period of frozen storage, are transferred to recipient cows. On average, 6 good embryos can be expected from each flush, and a 70% conception rate achieved from embryos transferred (Christie, W., personal communication; Hasler *et al.*, 1987). Although these figures are a significant improvement on those in the past, the full potential of the technique is still unexploited, since there are over 20 000 follicles in the ovaries of heifers (Salisbury *et al.*, 1978).

Two distinct methods of applying ET to dairy cattle breeding have been presented in the literature. The first incorporates ET into a conventional progeny testing scheme. The second involves the use of ET in an elite herd, and selection of animals at an earlier age on family information. The aim of this study is to review previous work on the application of the different methods to the genetic improvement of dairy cattle and on the evaluation of their relative merits.

III. Using ET to Increase Genetic Progress in a Current Progeny Testing Scheme

In a conventional progeny testing scheme, each sire is evaluated on the first-lactation records of many daughters spread over several herds. When these records become available, the sire is usually around 6 years of age. Of the tested bulls, only the best are used to breed the next generation of young bulls for progeny testing.

These young bulls are bred from a small number of genetically superior cows in the population. Approximately 6 bull dams are needed to produce each young bull for progeny testing (Hinks, 1978). Most cows in the commercial population are needed to breed female replacements.

Rendel and Robertson (1950) showed that the annual genetic response (ΔG) from a breeding programme operating for a sufficient length of time to be in a steady state could be calculated from $\Delta G = (I_{BB} + I_{BC} + I_{CB} + I_{CC})/(L_{BB} + L_{BC} + L_{CB} + L_{CC})$, where I refers to the genetic superiority of the selected animals and L to the generation interval along each of the four selection pathways. *BB* and *BC* refer to the bull to breeding bull and bull to breeding cow pathways, while *CB* and *CC* refer to the cow to breeding bull and cow to breeding cow pathways. I is a product of (*a*) the accuracy of selection (r_{IA}), which depends on the information available on the animal being evaluated, (*b*) the genotypic standard deviation (σ_g), which depends on the additive genetic variance of the trait of interest, and (*c*) the intensity of selection (*i*), which depends on the proportion of animals selected.

Three main ways have been proposed by which a conventional progeny testing scheme could be improved by ET: (i) by increasing the selection intensity on the cow to breeding bull pathway, (ii) by increasing the selection intensity on the cow to breeding cow pathway, and (iii) by providing further information for evaluation of animals.

1. Using ET on the cow to breeding bull pathway

ET is currently used to produce a high proportion of young dairy bulls for progeny testing in some countries, e.g. in Canada (58%), the USA (50%) and France (50%), and is used to a lesser extent or not at all in others (Cunningham, 1987).

By using ET on bull dams, the probability of getting a male offspring suitable for progeny testing from each bull dam is greatly increased, depending on the number of eggs transferred. Thus, the number of bull dams selected can be much smaller, and selection intensity and response can be increased. Assuming that the cow to bull pathway is responsible for about 25% of total genetic response, Hill and Land (1976) and Cunningham (1976) showed that additional gains of 2-10% could be obtained from ET, depending on the original selection intensities on bull dams and the increase in reproductive rate.

Hansen (1976) and Petersen and Hansen (1976) studied the effect of using ET on the cow to bull pathway in a population of 500 000 dual-purpose cattle (i.e. selected for both beef and dairy traits). In their scheme, 400 young bulls were tested for daily gain, and 40% of these were selected to be progeny tested for milk fat yield. The number of bull calves per bull dam was varied from 0.5 (normal reproduction) to 10 (with embryo transfer), while keeping the total number of young bulls available for selection constant. They showed that when keeping the response for daily gain constant, fat yield could be raised by up to 15% due to increased selection pressure on bull dams.

However, the degree of improvement depends on the effectiveness of bull dam selection previous to applying ET. Thus, Cunningham (1976) examined a similar situation to that of Petersen and Hansen (1977), but with a more intense selection of bull dams, and found that using ET had a reduced impact on rates of genetic progress. Petersen and Hansen (1977) also showed that these responses could yield considerable economic benefits, but the costs of ET were not taken into account. Inbreeding was not considered in these studies, which could be a problem in the schemes with the highest genetic gains, where as few as 50 bull dams supply the 400 bull calves for performance testing.

Kraüsslich (1976) similarly modelled a dual-purpose system with young bulls produced by ET. He found that use of ET could increase genetic gains by 5 to 10%. Furthermore, these could be raised up to 20 to 25% if combined with cyclical inbreeding, where sire-daughter or brother-sister matings would be used to allow selection between partially inbred sons, as proposed by Dickerson (1973). But although the increase in genetic variance due to inbreeding was included, the decrease in genetic variance due to selection (Bulmer, 1971), which would be significant, was ignored.

However, the genetic gains outlined above may be lower in practice, due to uncertainty about the true genetic merit of high-yielding cows. Bradford and Kennedy (1980) pointed out that since potential bull dams lie at the extreme edge of the phenotypic distribution, it is much more difficult to evaluate them accurately than cows at other parts of the distribution. Cunningham (1976) stated that it is doubtful whether the superiority of bull dams selected very intensely can be calculated assuming a normal distribution of underlying genotypic values. Similarly, Van Vleck (1986) suggested treating cows that are 3 to 5 standard deviations above the herd level with caution, and he emphasised the importance and difficulty of distinguishing between genetically superior cows and those given preferential treatment, and so biasing the records upwards.

2. Using ET on the cow to breeding cow pathway

Due to the very high proportion of cows currently needed to breed replacement females, the genetic contribution of the CC pathway is minimal. Thus, considerable scope exists for increasing genetic response by applying ET on this pathway. However, the current high costs of ET rule out this possibility unless ET becomes far less expensive.

Cunningham (1976) stated that using ET on the cow pathway to increase the reproductive rate 20-fold could increase genetic gain by 15 to 30%., assuming the pathway contributes 5 to 10% to the total genetic gain. McDaniel and Cassell (1981) demonstrated that in a 100-cow herd with 5 ET offspring per cow, the selection intensity in the cow to cow pathway is increased three and seven fold when, without ET, 70 and 90% of cows are needed to breed replacements respectively. Nevertheless, they showed that the economic benefits are negligible when compared to applying ET on the cow to bull pathway.

Van Vleck (1981) calculated the expected net present value of genetic gains made by breeding replacement females with ET, using several discount rates and time periods. He showed that although the net present value of returns was greater when ET was used, the costs of the ET work were far greater. He therefore concluded that the use of ET on the cow to cow pathway could only become economically feasible if these costs were reduced by a large multiple.

Navarro-Fierro *et al.* (1986) calculated the increase in milk yield, adjusted for frequency and production of different age classes, over a 20-year period from cows bred using ET. The number of offspring per donor was varied from one up to 100. To measure the response from selecting female replacements only, they assumed that the genetic merit of bulls used was the same with or without ET. They concluded that even after 20 years and with high reproductive rates, the increase in milk yield would not compensate for the direct cost of ET, or indirect cost such as loss in milk production while flushing the best cows.

Using ET on the cow to breeding cow pathway in a national breeding programme seems even less desirable than in a single herd. Hill and Land (1976) pointed out that, of necessity, most of the commercial population would become recipients, and that to carry out an operation on such an immense scale would require considerable improvements in ET technology. Van Vleck (1981) also suggested that by using ET over the whole population, the amount of semen used and sold would be substantially reduced, leading to an eventual reduction in numbers of bulls being progeny tested. Thus, genetic progress in the cow to breed offspring pathways would be made at the expense of the bull to breed offspring pathways.

McDaniel and Cassell (1981) suggested that if cytoplasmic inheritance is shown to be important for dairy traits, gains from breeding replacement females by ET would be higher. However, to date the importance of cytoplasmic inheritance has not been proven. Bell *et al.* (1985) analysed milk records from six herds, all of which had been closed on the female side for at least 30 years, and concluded that cytoplasmic inheritance accounted for 2, 1.8 and 3.5% of the total variation for milk yield, fat yield and fat percentage respectively. However, Kennedy (1986) showed that these results could be explained by random genetic drift alone. Huizinga *et al.* (1986) also claimed to have found evidence for the presence of cytoplasmic effects in milk production traits, but as in the study of Bell *et al.* (1985), random genetic drift was not taken into account. Reed and Van Vleck (1987) compared daughter-dam and daughter-granddam heritability estimates, and found no evidence that cytoplasmic inheritance influenced milk production traits of dairy cattle. Analysis of data on cows bred from ET should prove very useful in determining if cytoplasmic effects, and other effects such as dominance, are important in dairy cattle.

3. Using ET for evaluation of animals

The development of ET techniques has opened up new possibilities for evaluating both dams and sires.

(a) Dam evaluation

Since a donor can have several daughters by ET, this allows progeny testing of individual cows. Powell (1981) showed that adding 10 daughter records to a cow index, which had data on the cow (1 record), her dam (r_{IA} = 0.66), her sire (r_{IA} = 0.97) and her maternal grandsire, would increase the accuracy of the index by 7 and 13% when the daughters were recorded all in one herd or in separate herds respectively. With 50 daughters, these increases in accuracy rose to 10 and 33%.

When the number of individual records on the cow to be evaluated is increased, the relative effect of adding daughter records is reduced. On the other hand, if a cow is evaluated on her own performance only, instead of on a family index, the benefits from adding progeny test data are much higher (Bradford and Kennedy, 1980). McDaniel and Cassell (1981) concluded that although progeny records should be used if available, there would be no advantage in delaying selection decisions to wait for them, since the large increase in generation interval would result in an overall reduction in annual genetic gain.

An alternative way that ET can be used in cow evaluation is to increase the number of full- and half-sib records (Powell, 1981). For example, if one sire is bred to 4 donors, each producing 4 daughters, then each cow evaluated has 3 full-sibs and 12 half-sibs. The accuracy of selection from an index including one lactation record of the cow with her full- and half-sib records is about the same as using 3 records on the cow. The major advantage of this is that the cow selected on the family index is two lactations younger than the cow selected without sib information. Thus, using ET in this manner gives us the opportunity to reduce the generation interval without suffering a loss in accuracy of cow evaluation. This strategy is central to the MOET nucleus schemes considered later.

(b) Sire evaluation

Since sires are currently evaluated with considerable accuracy, there seems, at first glance, to be less scope for improvement using ET. If dam records are included in evaluating sires, progeny testing of dams should increase the accuracy of evaluation (Powell, 1981), but not substantially.

A more useful way in which sire evaluation could be improved is with full- and half-sib data, which would be available much earlier than the sire's progeny test results. After being mated to a wide range of cows from the commercial population when about one year old, males usually have to wait a further 4 to 5 years before their daughters complete their first lactation, and the males can be selected. Smith and Ruane (1987) suggested that bulls for commercial use could be selected from those evaluated on full-sib records when aged about three years, and those evaluated on progeny test data when aged about 5.5-6 years. They found that with 3 to 7 full-sister records available per bull, the genetic merit of the bulls selected for commercial use was 10 to 20% higher than when selection was restricted to bulls evaluated on progeny test data alone. This increased response was a consequence of the reduced generation interval.

(c) Problems

There may well be problems associated with using ET information to evaluate animals. Powell (1981) pointed out that the records of animals born from ET could be subject to bias due to preferential treatment, owing to the relative rarity and expense of ET. Also, accuracy of evaluation may be reduced since management constraints may prevent the spread of a donor's offspring over several herds. Powell (1981) warned that progeny testing of sires could be biased if many of his daughters are bred using ET from a few genetically superior donors. If sib information is used for evaluating animals, there is an increased probability of related individuals being selected, leading to an increase in inbreeding (Burrows, 1984), but with a large breeding population this should not be a serious problem.

IV. Genetic Response Possible with a MOET Nucleus Herd

1. MOET nucleus schemes

Potentially the best way that ET can be used to speed up genetic progress in dairy cattle is by setting up a multiple ovulation and embryo transfer (MOET) nucleus scheme. This involves creating a nucleus herd of elite males and females, concentrating testing and selection in the herd, and selecting at an early age using family information.

Nicholas (1979) was the first to examine the possible impact of a MOET nucleus scheme on dairy cattle improvement. He showed that rates of gain equal to those possible from an efficient national progeny testing scheme could be made in a 500-cow herd. This idea was later elaborated (Nicholas and Smith, 1983) and since then, MOET nucleus breeding schemes have been the subject of much interest. Practical MOET nucleus herds have been established in Denmark, France and the United Kingdom.

The basic scheme of Nicholas (1979) was similar to that suggested by Land and Hill (1975) for beef cattle. For the beef system, Land and Hill (1975) assumed a fixed number of cows in the herd, with non-selected females used as recipients. Thus, the selection intensity of females was dependent on the number of eggs transferred per donor and on the total herd size. Animals of both sexes were chosen by mass selection with a generation interval of two years, the minimum possible for beef cattle.

Nicholas (1979) examined the effect of using ET and a family selection index on the genetic response for a sex-limited trait in a 500-cow herd comprising both donors and recipients. In all three schemes outlined, females were selected on their dam's first-lactation record, with a short generation interval of two years but with a low accuracy of selection ($r_{IA} = 0.25$). Males were selected on their dam's first record (pedigree selection scheme) or on a family index utilising full-sib, half-sib and dam records, with a generation interval of 3.6 years (sib selection scheme). In the third scheme, the nucleus herd supplied 30 young bulls for progeny testing, and nucleus replacements were bred both

from young males selected on their dam's first-lactation record and from the top two progeny tested sires. Each selected male was mated to 8 donors.

Nicholas (1979) showed that the genetic response possible was substantially higher from all three schemes than from a progeny testing programme in the herd, and could even be as high as from a national progeny testing scheme. Of the three schemes, the pedigree scheme was always the least effective, and the sib scheme was only superior to the third scheme including progeny testing when the number of eggs per donor was high (leading to an increased selection pressure on males and females).

Annual inbreeding rates ranged from 0.15 to 1.2%, and were highest for the pedigree scheme and lowest with progeny testing of sires. However, these rates are probably underestimated. In all three schemes, each female would have the same breeding value as her full-sisters, since only dam performance is used in evaluation. Similarly, full-brothers would be ranked together in the sib and pedigree schemes. Thus, selection is between full-sib groups rather than between individuals and, due to selecting full-sibs, inbreeding rates would be considerably higher than calculated.

The schemes of Nicholas (1979) were expanded by Nicholas and Smith (1983) into two further schemes. In the first scheme, instead of selecting on the dam's first-lactation record only, the pedigree scheme was modified to allow selection of both sexes at 12 months of age using information from the dam's family, i.e. the dam's own record, her sisters' records, her half-sisters' records and her dam's records. This they called the juvenile scheme.

In the sib scheme proposed by Nicholas (1979), males were selected on their full-sibs', half-sibs' and dam's records. This was retained in the second scheme described by Nicholas and Smith (1983). In addition, females were to be selected on the same information plus their own first-lactation record, giving a generation interval of 3.67 years. This they called the adult scheme.

Genetic gains possible were calculated for various numbers of offspring per donor and donors mated per male. They demonstrated that higher rates of genetic gain (by up to 80%) could be made in MOET nucleus schemes compared with a national progeny testing scheme. Rates of improvement in the juvenile scheme were higher than in the adult scheme, emphasising the benefits of reducing the generation interval. By including information on the sire's family, instead of only the dam's, the advantage of the juvenile scheme would be increased even more (Woolliams and Smith, 1988).

Rates of response from these studies were calculated assuming that the MOET nucleus and progeny testing schemes were running for a sufficient length of time, so that both were in steady-state equilibrium. Ruane and Smith (1988) examined the genetic response possible from using bull parents (*BB* and *BC*) from an efficient steady-state progeny testing scheme to set up a MOET nucleus breeding herd, and compared it to the response expected if the bull parents were used, as normally, to produce young bulls for progeny testing. They found that the differences in genetic response of animals at birth were small for the adult scheme but substantial for the juvenile scheme over the first 10 years. After 20 years, the genetic response of MOET-bred stock over stock bred in the progeny testing scheme was about 55% (juvenile scheme) and 20% (adult scheme).

Nicholas and Smith (1983) reduced the problem of inbreeding by allowing only one male to be eligible for selection from each donor. This lowered the intensity of selection in males. No restriction was placed on females. In the juvenile scheme, all females in a full-sib group will rank the same and be selected, which will raise inbreeding rates. In addition to the problem of selecting full-sibs, using a family index will increase inbreeding rates, since related individuals will be evaluated on overlapping information, resulting in relatives being ranked closely together (Burrows, 1984).

Although the theoretical rates of progress predicted for the MOET schemes are quite high, there are factors affecting these rates which were not taken into account. By selecting on a family index in a small population, the selection intensity is reduced (Hill, 1977). In addition, rates of inbreeding and hence inbreeding depression are both increased. Another danger, due to the small population size, is that of genetic drift leading to the chance fixation of genes and increased variation in the response to selection, so that the response in any individual scheme is uncertain (Nicholas, 1980).

Juga and Maki-Tanila (1987) simulated an adult MOET scheme with 128 females and 32 males eligible for selection each generation. Although not taking account of the reduction in response or variance due to inbreeding, the genetic gain was still substantially lower than predicted from formulae assuming the population to be improving at a constant rate, as used by Nicholas and Smith (1983). For example, with four sires selected, eight donors mated to each sire and eight progeny per donor, the response was reduced by over 33%. The most likely reason for the reduced response is that the extensive use of family information, combined with the small population size, effectively resulted in selection between families rather than between individuals.

If population size is the major limitation to genetic progress, the question must be addressed as to how large the population should be before there is a significant probability of getting all or most of the expected genetic gains. This problem is discussed by Nicholas (1980). In the juvenile scheme, with much shorter generation intervals and total dependence on family information for evaluating candidates for selection, these problems are likely to be exacerbated.

Annual genetic gain is calculated by summing the genetic superiorities of selected animals and dividing by the average generation interval. In a MOET nucleus scheme, where animals are young when selected, there may be an increase in annual genetic gain from further reducing the generation interval through using part-lactation records of performance, depending on the reduction in genetic

merit of selected animals. The genetic and phenotypic correlations between part- and full-lactation milk yields are quite high (e.g. Auran, 1976), and so the potential benefits from selecting on part-records in MOET nucleus schemes should be investigated.

Selection index theory has been used in previous studies for evaluating response in MOET nucleus schemes. In practice, Best Linear Unbiased Prediction (BLUP) methods would be preferred. These would allow for the spread of animals over different spatial and temporal groups, for the genetic trend in the population, and for the inclusion of information on all relatives and ancestors in evaluating animals. Kennedy and Schaeffer (1987) examined the possible effects of new technologies such as ET, cloning, sexing and gene transfer on the genetic evaluation of animals, and showed how existing BLUP procedures should be modified to deal with them.

Other questions have still to be answered regarding the actual running of the MOET scheme, such as whether selected donors or sires should be eligible for selection for more than one year, and what effect this would have on rates of inbreeding and response. Also, it is extremely unlikely that all transfers would be carried out together, and so this would probably lead to transferring blocks of embryos over the whole year. It would be important to manage the transfer of embryos so that all offspring could be accurately evaluated and response optimised.

Large variation has been found in the number of eggs recovered from any flush (Seidel, 1981). Thus, a practical problem which should be considered is whether it is preferable to carry out a fixed number of flushes on each donor or to continue flushing until all or a fixed number of donors give a certain minimum number of eggs. The first strategy should lead to increased variation in family size, the second to a slightly extended generation interval.

There will also be variation in the sex ratio within individual families. Like variation in embryo numbers per flush, this may also affect both the accuracy and intensity of selection. For example, if each transferred embryo has a 50% chance of survival to selection, the sex ratio is 1:1 and six embryos are transferred, there is an 18% chance of getting no females for selection.

No studies have yet been carried out on the implications of these two sources of variation of family structure for response in the MOET nucleus scheme. These problems are likely to be more severe in the juvenile scheme than in the adult scheme, because fewer embryos can be recovered from a young, immature donor than from a mature donor (Gordon, 1983).

2. Hybrid MOET-progeny testing schemes

The idea of using the MOET nucleus herd to produce young bulls for progeny testing, as proposed by Nicholas (1979), has been developed by Christensen (1984) and in great detail by Colleau (1985). In the "MOET × conventional" hybrid schemes of Colleau (1985), the generation interval for females is low, and the nucleus herd is used to produce all young bulls needed for progeny testing. Only progeny tested sires are used for breeding. He described three schemes. In all three, nucleus females are selected to produce both the young bulls and the nucleus female replacements.

In scheme *A*, all nucleus females are flushed twice, when 16 and 18 months old, and then put in calf at 20 months. After 6 months of the lactation, donors are selected on their own performance, assuming a genetic correlation of unity between a six-month and a full-lactation record. At selection, the donors' offspring are 9 months old, and so the generation interval is substantially reduced. This reduction is made possible by transferring embryos from all females, without knowing at the time whether or not they will be selected.

In scheme *B*, embryos are transferred from donors after selection based on their first-lactation record. Thus, the generation interval is almost doubled compared to scheme *A*, but the number of embryos transferred, and hence recipients needed, is substantially reduced. The third scheme, *B'*, is the same as scheme *B*, but with an equal number of embryos transferred as in scheme *A*. These schemes were compared with a highly efficient progeny testing scheme and the juvenile scheme described by Nicolas and Smith (1983), although with a slightly longer generation interval than they proposed.

When the schemes are compared keeping the total number of transfers constant, scheme *A* is at least 10% superior to the progeny testing scheme over a wide range of donor family sizes, and is always better than *B'* and *B*. When the number of offspring born per donor is low, scheme *A* is superior to the juvenile MOET nucleus scheme, but with high numbers of offspring the juvenile scheme is best.

The reranking of the schemes according to the number of offspring per donor is due to the higher sensitivity of the MOET nucleus scheme to ET success rates compared with the hybrid schemes. This sensitivity is a consequence of the dependence of genetic gain in the MOET nucleus schemes on only two pathways, both using ET. With the hybrid schemes, the bull to cow and bull to bull pathways are unaffected by variability in ET rates.

Truncation selection reduces the genetic variance in parents by a factor of $1 - kr^2_{IA}$, where r_{IA} is the accuracy of selection and k is a term which depends on the selection pressure applied and which increases as selection becomes more intense (Bulmer, 1971). Colleau (1985) showed that the reduction in genetic variance for the juvenile MOET scheme was almost negligible compared with that for the progeny testing and MOET hybrid schemes, due to the lower accuracy of selection of animals of

both sexes. When the reduced genetic variance was accounted for, he demonstrated that the annual genetic gain in the juvenile MOET nucleus scheme compared with the progeny testing and hybrid MOET schemes was increased by about 25 and 20% respectively. Accounting for the Bulmer effect in the adult MOET nucleus scheme would also increase genetic gains relative to the schemes with progeny testing, but to a lesser degree than the juvenile MOET nucleus scheme, because animals are evaluated with greater accuracy.

Annual rates of inbreeding were much lower in the hybrid schemes than in the juvenile scheme, due to the longer generation interval. Of the three hybrid schemes, the inbreeding rate was highest for *A*, due to the shorter generation interval on the female side.

Colleau (1986) examined the effect on response of opening up the nucleus in scheme *A* to foreign genetic material. He showed that if genetically superior bulls, progeny tested in a foreign population, were available for use in the nucleus, this would allow a much more rapid diffusion of their superiority throughout the population than with a conventional progeny testing scheme. This would be a considerable advantage for a country with a population lagging behind in genetic merit that wished to upgrade its stock. Dissemination of superior foreign genes to the commercial herd would be even faster with MOET nucleus schemes (Nicholas and Smith, 1983) than with MOET hybrid schemes, since the generation interval on the bull to commercial cow pathway is considerably shorter.

Christensen (1984) and Christensen and Liboriussen (1986) also favoured a hybrid scheme over a pure MOET nucleus scheme. They found that even with high rates of genetic gain in the nucleus, moderate selection pressure on progeny tested bulls was sufficient for their breeding values to be superior to those of young bulls within the nucleus. However, the comparison they made was between the average genetic merit of selected progeny tested bulls and of unselected nucleus bulls, which biased calculations in favour of the progeny tested bulls.

3. Other aspects of MOET and dairy cattle breeding

(a) Physiological indicators

Genetic progress for dairy traits has been hampered by the fact that they can only be measured in the female. If it was possible to measure a trait significantly correlated with milk yield in both sexes before reproductive age, this would be advantageous. Studies on thyroxine degradation rates and more recently on blood urea nitrogen levels suggest that such a trait may exist. Woolliams and Smith (1988) studied the effect of an indicator trait, such as blood urea nitrogen level, on genetic response for milk yield. They showed that the possible increase in genetic gain due to using the indicator trait was greater with MOET nucleus schemes than with progeny testing schemes. In comparing Nicholas and Smith's (1983) adult and juvenile MOET nucleus schemes, the effect of an indicator trait on the juvenile scheme was most favourable.

The increases in response were achieved by adding individual and family measurements of the indicator trait to the family index for milk yield. In the juvenile scheme, even when including the sire's family information, the accuracy of selection is low, leaving considerably more scope for improvement than in the adult scheme. This increased accuracy explains the greater response.

(b) Other factors in MOET nucleus versus progeny testing schemes

The dependence on a single herd in MOET nucleus schemes for genetic progress allows a greater degree of control over selection than in a conventional progeny testing scheme. By controlling the environment, heritability should increase, and so improve the accuracy of breeding value estimation (Christensen and Liboriussen, 1986). However, the possibility of genotype by environment interaction arising must be guarded against by testing and selecting in commercial conditions.

A problem of far greater possible consequence is that of disease occurring in the MOET nucleus herd. To prevent this, stringent health regulations must be applied. Nicholas and Smith (1983) also suggest keeping nucleus stock of different ages in different locations. This should reduce the impact of any outbreak of disease.

Van Tassell and Van Vleck (1987) estimated the actual genetic gain that has been made for milk production in progeny testing schemes, and found that the gap between theoretical and actual progress was substantial. Preferential treatment of animals, selection for other traits, and selection of parents of bulls with lower-than-possible selection intensities and at an advanced age were all responsible for the gap. With a MOET nucleus scheme, these problems can be minimised, and the gap between theoretical and actual genetic progress narrowed.

It should be possible in MOET nucleus schemes to select for economically important traits normally not included in dairy cattle breeding programmes. In the current climate of quotas in milk production, selection for food conversion efficiency and for beef traits may be worthwhile.

In general, the lower the effectiveness of a current progeny testing scheme, the greater the impact that ET can have. It could also be argued that there is a greater need for an efficient breeding scheme to replace it. In a country lacking the infrastructure necessary to run an effective national

progeny testing scheme, a MOET nucleus scheme, due to its centralised nature, would be a useful alternative (Hinks, 1978; Land 1986).

(c) Other advantages and potential developments of ET technology

In this study, the potential impact of ET on genetic gain alone has been examined. It may also prove beneficial in other ways in some special cases. The problem of getting offspring from high yielding cows that are infertile, due to disease or injury, may be overcome using ET. For example, it may allow brucellosis-positive donors to have brucellosis-negative offspring (Youngs *et al.*. 1986). Also, female carriers of harmful recessive genes causing diseases such as bovine syndactyly can be detected by progeny testing with ET (Johnson *et al.*, 1980).

ET can also be used for the expansion and conservation of rare or valuable stocks. Indeed, the initial role of ET in North America in the 1970s was in the production of high-priced animals from the continental beef breeds. Many arguments have been put forward for the conservation of rare livestock breeds, such as the advantages it could offer in meeting possible changes in future market requirements. The storage of frozen embryos and their expansion when needed provide a useful method of conservation (Smith, 1984).

ET can be used to increase the twinning rate by transferring two embryos to each recipient. If one embryo is placed in both uterine horns of an unmated recipient, twinning rates in pregnant recipients of more than 70% can be achieved (Anderson *et al.*, 1979). The net result is an increased number of progeny per donor without having to increase the recipient herd size. Alternatively, it could be used as a strategy to produce the same number of offspring but from a smaller recipient herd. The main disadvantage of twinning is the high proportion of freemartin heifers produced when embryos of opposite sex are transferred together. However, depending on ET success rates, the actual number of fertile females available for selection may not be reduced compared to the situation where each recipient receives only one embryo. Embryo sexing would solve the freemartin problem, and twinning could be a very useful breeding strategy.

The technique of splitting bovine embryos has been available since 1981, but has not been used widely so far. Currently, embryos are seldom split more than twice, producing four genetically identical embryos. The net result is a greater number of offspring per donor, despite the lower survival rates of split embryos compared to whole embryos. Currently, the application of this technique to dairy cattle breeding seems limited. The intensity of selection is not increased, since the animals are genetically identical. However, it can be used to improve the accuracy of selection. Split embryos can also be used to estimate maternal effects, genetic trends and genotype-environment interactions (Brem, 1986).

Some attention has been paid to the potential applications of clones produced by the further development of embryo splitting (Nicholas and Smith, 1983) or cell culture techniques (Van Vleck, 1981). The potential gains described give a very substantial genetic lift. Using selected clones in the commercial herd could increase genetic merit by over 25% (Nicholas and Smith, 1983). Van Vleck (1981) warned that the validity of quantitative genetics theory may be doubtful when selecting animals for cloning which are several phenotypic standard deviations above average.

Nicholas and Smith (1983) suggested one method of selecting cloned animals which should overcome any such problems. Firstly, the best animals in the population would be selected to produce embryos which would be the potential candidates for cloning. Each embryo is then split several times, some are stored, and some are transferred. Selection between clones is made on the basis of first-lactation records. The remaining cloned embryos of the selected clones are then further multiplied and supplied to the commercial herd. The genetic variance of the breeding population can be maintained by keeping the same numbers of selected females (clones) and males as in a conventional breeding system.

Although it is not yet possible to sex sperm or embryos reliably prior to transfer, these techniques may be available in the near future. In addition to preventing freemartins with twinning, sexing could also reduce the number of embryos transferred and recipients needed. If selection of males is restricted for inbreeding purposes so that only one son per donor is eligible for selection, the number of male embryos transferred can be greatly reduced.

V. Conclusion

The development of a technology which enables us to increase the reproductive rate of the cow will have a considerable impact on genetic improvement in dairy cattle. However, by applying this ET technology to an efficient current progeny testing scheme, little extra gain can be made. Instead, alternative breeding strategies must be designed which exploit the novel opportunities the technique presents. Two such schemes are the MOET nucleus and the MOET hybrid breeding schemes. Based on current ET success rates, both schemes should yield rates of genetic response superior to those possible from current progeny testing schemes.

However, by selecting animals in a MOET nucleus scheme from a small population using family information, potential problems such as inbreeding, random genetic drift and reduced selection intensities may be quite significant. These problems are likely to be greater in the juvenile (selection before first breeding) than in the adult (selection after first lactation) MOET nucleus schemes. More work is needed to determine how serious a danger these potential problems represent to genetic progress, and how they can be reduced or overcome.

Improvements in ET technology have been quite considerable in recent years, and should be even greater in the future. Lu *et al.* (1987) described a reliable *in vitro* fertilization system for bovine embryos which makes it possible to accumulate large numbers of embryos for research purposes at a low cost. Thus, for example, it should soon be feasible to recover much higher numbers of embryos per donor, sex them, and split them as often as required. Breeding schemes using ET will be at an advantage since they will be able to adopt these new technologies rapidly. These developments will further enhance the merits of the MOET nucleus schemes in which all genetic gains are derived from pathways using ET, compared with the MOET hybrid schemes, where only two of the four pathways depend on ET.

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Original article

The genetic response possible in dairy cattle improvement by setting up a multiple ovulation and embryo transfer (MOET) nucleus scheme

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Summary — The genetic response in an efficient progeny testing scheme, improving at a constant annual rate of 0.103 phenotypic standard deviations, is compared to that possible from setting up a multiple ovulation and embryo transfer (MOET) nucleus scheme at a given year zero using bull parents from this scheme as nucleus herd founder animals. Two MOET nucleus schemes are described; juvenile, with selection before first breeding, and adult, with selection after first lactation. Four years of selection of bull sires are needed to set up the nucleus herds. Setting up the juvenile nucleus herd is less costly than the adult nucleus herd, since only 2 years of selection of bull dams are needed instead of 4. With 8 progeny per donor surviving to selection in the juvenile nucleus scheme, the average genetic response of nucleus bulls and commercial cows born at year 20 is 60% and 53% higher than the corresponding response of breeding males and commercial cows born in the same year if the progeny testing scheme is continued. With an adult nucleus scheme, responses are 24% and 16% higher. Short-term gains are more substantial from the juvenile than from the adult nucleus scheme. The discounted genetic response of the commercial herd, summed over the first 10 years, is equivalent for the adult nucleus and progeny testing schemes, but is over 40% higher for the juvenile nucleus scheme. When summed over the first 20 years, the juvenile scheme proves equally superior.

multiple ovulation – embryo transfer – dairy cattle – genetic gain

Résumé — La réponse génétique rendue possible par la mise en place de la superovulation et du transfert d'embryons dans les noyaux de sélection chez les bovins laitiers. *La réponse génétique obtenue dans un schéma efficace de testage sur descendance, correspondant à un taux annuel de 0,103 écart-type phénotypique, est comparée aux possibilités apportées par la mise en place de la superovulation et du transfert d'embryons dans un noyau de sélection, en utilisant les pères à taureaux du premier schéma comme animaux, fondateurs du noyau. Deux schémas sont envisagés: juvénile, où la sélection a lieu après la première lactation. Il faut quatre ans de sélection des pères à taureaux pour constituer les noyaux. Il est moins coûteux de mettre en place le troupeau «juvénile» que l'«adulte» car deux années de sélection des mères à taureaux, au lieu de quatre, sont nécessaires. En supposant que 8 descendants par donneuse survivent dans le schéma juvénile, le gain génétique moyen chez les taureaux du noyau et chez les vaches commerciales*

nées la même année, 20 ans après la mise en place du schéma, sont respectivement supérieurs de 60 et de 53% par rapport à la poursuite du testage sur descendance. Avec le schéma adulte, les accroissements de la réponse sont respectivement de 24 et de 16%. Les gains à court terme sont plus importants avec le schéma juvénile. Le progrès génétique actualisé sommé sur les dix premières années dans le troupeau commercial est équivalent au schéma de testage sur descendance, dans le cas du schéma adulte, mais est accru de 40% avec le schéma juvénile, Le schéma juvénile s'avère aussi supérieur sur la période de 20 vingts.

superovulation – transfert d'embryons – bovins laitiers – progrès génétique

Introduction

Few alternative breeding strategies to rival the progeny testing of sires in dairy cattle breeding have been proposed in the past (Hinks, 1978). One which has received considerable attention in recent years was proposed by Nicholas (1979), using multiple ovulation and embryo transfer (MOET) within a single dairy herd as a means to increase response rates. This idea was elaborated by Nicholas and Smith (1983). They showed that the steady state rate of response of MOET nucleus schemes could be significantly superior to that of an efficient progeny testing scheme. The steady state response rate is calculated presuming that a breeding programme has been carried out for a sufficient length of time such that the population is improving at a constant rate. It could be argued that this is not the relevant comparison to make, since progeny testing schemes are already in operation, whereas MOET nucleus schemes are only being initiated now.

In dairy cattle breeding, the effect of a single round of selection on the genetic merit of animals in later generations is not constant until many years after selection. Hill (1974) proposed that the response from the selection of parents be calculated by multiplying the genetic superiority of parents by the proportion of their genes present in later generations (the gene flow method). The aim of this study is to use this method to evaluate the short and long term genetic response possible from establishing a MOET nucleus herd using the best progeny tested bulls and bull dams and then selecting within the closed MOET breeding herd.

Materials and Methods

The selection goal is economic merit, which is determined primarily by milk yield and so is taken to have a heritability value of 0.25 and a repeatability of 0.5. For simplicity, genetic gain is expressed in standard deviation units (σ_P).

Progeny testing scheme

A conventional progeny testing scheme in steady state equilibrium is described in Table I. One hundred young bulls are progeny tested annually. The best 12 are chosen for use on the commercial herd after being evaluated on 50 effective daughters. The best 4 are selected as bull sires. Each selected bull is used for 1 year only. It is assumed that 1% of cows are selected to be bull dams after completing 3 full records, and that there is no effective selection of cows to breed cows.

Table I. Estimated genetic change in a conventional progeny testing scheme (in SD units).

Pathway	*Percent selected (%)*	*Selection intensity i*	*Accuracy of selection r*	*Heritability $_{1/2}$ h*	*Genetic superiority I(op units) (irh)*	*Generation interval L(yr)*
Bull to bull (BB)	4	2.15	0.88	0.5	0.94	6.75
Bull to cow (BC)	12	1.67	0.88	0.5	0.73	6.28
Cow to bull (CB)	1	2.67	0.65	0.5	0.86	6.25
Cow to cow (CC)	100	0	–	–	0	4.74

$$\Delta g = \frac{\dot{I}_{BB} + \dot{I}_{BC} + \hat{I}_{CB} + \hat{I}_{CC}}{\dot{L}_{BB} + \dot{L}_{BC} + \hat{L}_{CB} + \hat{L}_{CC}} = 0.103\,\sigma_P$$ (Rendel and Robertson, 1950).

* 10% of commercial herd bred to young bulls.

Thus I_{BC} = (0.9) (0.731) + (0.1) (0).

L_{BC} = (0.9) (6.75) + (0.01) (2).

Rendel and Robertson (1950) showed that the annual genetic gain (ΔG) of a breeding scheme in steady state equilibrium can be calculated from:

$$\Delta g = \frac{I_{BB} + I_{BC} + I_{CB} + I_{CC}}{L_{BB} + L_{BC} + L_{CB} + L_{CC}}\,\sigma_P$$

where I and L refer to the genetic superiorities and generation intervals of selected animals, and B and C represent bulls and cows respectively. Thus the average genetic merit of all offspring born in year 1, resulting from selection and mating at year 0, can be set to zero by subtracting $\Delta G(L_{BB} + L_{BC} + L_{CB} + L_{CC})$ from the genetic superiorities of their parents. However, because of the higher genetic merit of bull parents over cow parents, there is a difference (D) at birth in the genetic merit of males and females. Thus the average merit of breeding males born is:

$$\frac{(I_{BB} - \Delta g L_{BB}) + (I_{CB} - \Delta g L_{CB})}{2} = 0.24\,(= D/2)$$

The average merit of all females born is:

$$\frac{(I_{BC} - \Delta g L_{BC}) + (\hat{I}_{CC} - \Delta g \hat{L}_{CC})}{2} = -0.24\,(-D/2)$$

Thus the average merit of breeding males born at year one is $D/2$. These are mated to 10% of the commercial cow herd for progeny testing. The term commercial cow herd is used to define the 99% of cows that are not selected as bull dams. Thus, their main role is in yielding milk in their own lifetime, and they are not used to breed males in the next generation. The average merit of all females born at year 1, which can be considered as the average merit of cows born in the commercial herd, is $-D/2$. With the scheme in a steady state, the average merit of breeding bulls born at year 20 over the offspring born in year 1 is:

$D/2 + 19\ \Delta g = 2.19\ \sigma_P$.

The average merit of commercial cows born at year 20 is:

$-D/2 + 19\ \Delta g = 1.72\ \sigma_P$.

MOET nucleus schemes

The 2 main schemes which propose using MOET to increase rates of genetic gain are the MOET nucleus schemes (Nicholas and Smith, 1983) and the MOET hybrid schemes (Colleau, 1985). These have been reviewed by Ruane (1988). In the MOET hybrid schemes, females are selected on first lactation performance while breeding males are progeny tested. In the MOET nucleus schemes, males are not progeny tested but instead are selected at an early age on family information in the same way that the females are. In this study, we have only investigated the genetic response from establishing a MOET nucleus scheme.

Nicholas and Smith (1983) examined 2 types of MOET nucleus schemes–adult and juvenile. In the adult scheme, animals are selected after the first lactation. Males are evaluated on their full sibs', half sibs' and dam's records; females are evaluated on the same information plus their own lactation record. In the juvenile scheme described here, animals are selected before first breeding using not only family information of the dam as proposed by Nicholas and Smith (1983) (*i.e.* records on the dam, her full sibs, her half sibs and her dam) but also of the sire (*i.e.* records on his full sibs, his half sibs and his dam). The generation intervals of the 2 schemes are 3.75 and 2 yr respectively, which are slightly longer than those used by Nicholas and Smith (1983).

In setting up the MOET nucleus herds, 4 bull sires and 64 bull dams are selected as nucleus founder animals. Since the number of nucleus founder males is equal to the number of bull sires normally selected in the progeny testing scheme, their genetic superiorities are equal. Although the number of nucleus founder females is much smaller than the number of bull dams normally used to produce young bulls for progeny testing, their genetic superiorities are conservatively assumed to be equal. This is to allow for factors such as possible preferential treatement of top animals and avoiding selection of closely related cows.

Responses are calculated with 64 selected donors producing 4, 8 or 16 candidates for selection in the next generation. With 4 candidates per donor, the correlation of true with expected breeding values for juvenile animals (males or females), adult males and adult females is 0.42, 0.54 and 0.64 respectively. As the number of progeny per donor is raised to 16, this correlation increases by $\approx$ 10%. Assuming a 50% survival rate of the embryo to selection age, the total number of embryos transferred and recipients needed is 512, 1024 and 2048 respectively. With a 50% sex ratio, the proportion of females selected as replacement donors is 1/2, 1/4 and 1/8 respectively. In order to reduce inbreeding, only 1 male per full sibship is eligible for selection. A mating ratio of 16 females per sire is used so the proportion of full sibships selected, from which one male is chosen randomly, is 4/64.

Selection intensities for MOET nucleus and progeny testing schemes are calculated under the assumptions of an infinite population size and unrelated candidates for selection. If the finite population size is accounted for, selection intensities would be reduced slightly. For example, in the adult scheme with 8 progeny per donor the selection intensities for males and females respectively would be reduced from 1.968 and 1.271 to 1.911

Table II. Age structure of the British dairy cow commercial herd (based on the national milk records 5-year survey 1981/1982).

Age when progeny born	*Frequency (%)*
2	11.80
3	23.76
4	22.60
5	11.06
6	10.28
7	7.83
8	5.37
9	3.21
10	1.94
11	1.16
12	0.58
13	0.26
14	0.10
15	0.05
	100.00

Thus commercial cows born in any year will receive 5.9% of their genes from 2-year old cows, 11.88% from 3 year old cows, etc. The average age of cows at the birth of their daughters is 4.74 yr.

and 1.252. The corresponding reduction in annual response of all schemes would be quite small (≈ 2%) and of almost equal magnitude for the nucleus and progeny test schemes. Accounting for genetic relationships between candidates for selection is more problematic, but would have a greater effect on the MOET nucleus than the progeny testing scheme.

As in the progeny testing scheme, 12 nucleus bulls are selected annually (the best from 64) for use on the commercial herd for one year. The structure of the cow commercial herd is taken from the British Milk Records survey 1981/1982 and is shown in Table II. In evaluating the response from MOET nucleus schemes using Hill's (1974) method, the herd is split into yearly groups to make computation easier. The methods of setting up the 2 MOET nucleus systems are different and need to be considered separately.

Juvenile scheme

Nucleus founder animals are selected as described at years 0 and 1. Selection of the resulting offspring before breeding is not possible, since no milk records are produced in the MOET nucleus herd by that time. Since progeny tested sires are expected to have a higher genetic merit than unselected MOET nucleus males, they are bred to 64 unselected MOET nucleus females at years 2 and 3. The offspring born (both male and female) can then be selected using the first lactation records of the females and progeny test data of the sires. From year 4 onwards the nucleus herd is closed, and from year 6 onwards evaluation of candidates for selection is based on nucleus herd information only. This is shown in Appendix 1. Nucleus males are used on the commercial herd when 14 months old for 1 year, giving a generation interval of 2.42 years.

Adult scheme

To establish the herd, 4 rounds of selection of nucleus founder males and females are needed at years 0, 1, 2 and 3. However, at year 3 they are selected (to accommodate the gene flow method) to produce only 75% of the nucleus animals, the remaining 25% being bred from within the nucleus. From year 4 onwards, nucleus stock are selected on MOET nucleus information to breed all nucleus replacements. Nucleus sires are also selected for use on the commercial herd for one year, with a generation interval of 4.08 years.

Calculation of genetic progress

This can be subdivided into 2 steps – the calculation of genetic progress from: 1) the early rounds of selection when the nucleus herd is being established; and 2) repeated selection within the nucleus once the herd is established.

Selection within the closed nucleus herd is carried out annually, without overlapping of sires or dams between years, and genetic gains were calculated using the GFLOW programme (Brascamp, 1978) of the Hill (1974) gene flow method. Genetic gains from the early rounds of selection were calculated using a modified version of this program which accounted for changes in the population structure in the early rounds of selection when setting up the nucleus herd. These results were then added to those from repeated selection. The response at year t (r_t) from one early round of selection along a given selection pathway is calculated by:

$$r_t = P_t\ r_{t-1} + EQ^{t-1}s$$

where the P,E and Q matrices describe respectively the movement of all genes in the whole population, along the given selection pathway and by ageing alone in the whole population (Hill, 1974). The vector s defines the genetic superiority of selected animals. A small example to illustrate the method is shown in Appendix 2.

For both MOET nucleus schemes, it is assumed that the nucleus founder males and females are of equal merit to the bull sires and bull dams from the progeny testing scheme. Taking the average genetic merit of all offspring born in the progeny testing scheme at year 1 as zero, then the genetic merit of nucleus founder sires at year 0 is $I_{BB} - L_{BB}\ \Delta g + D/2 = 0.49$ and of nucleus founder dams at year 0 is $I_{CB} - L_{CB}\ \Delta g - D/2 = -0.01$.

Since the progeny testing scheme is in steady state, the merit of nucleus founder stock used increases by $\Delta\ g$ each year. Thus for example the merit of nucleus founder sires selected at years 1, 2 and 3 is $0.49 + \Delta\ g$, $0.49 + 2\Delta\ g$ and $0.49 + 3\Delta\ g$ respectively. Similarly, the merit of bulls used on the commercial herd at year 0 is $I_{BC} - L_{BC}\ \Delta g + D/2 = 0.25$ and of cows used to breed replacements at year 0 is $I_{CC} - L_{CC}\ \Delta\ g - D/2 = -0.72$.

In any commercial enterprise the timing of returns can be crucial to its success. The process of discounting allows us to discriminate between short and long term genetic gains so that the earlier the gains are accumulated, the greater the discounted response. An inflation-free discount rate of 5% per annum, which also allows for risk, is used (Bird and Mitchell, 1980). The returns from a national dairy cattle breeding programme can be seen as the increase in milk yield from the commercial herd cows due to selection. Thus the discounted genetic merit of the commercial herd was calculated.

Table III. The expected genetic response (in phenotypic SD units) of newborn adult nucleus males and commercial females. The difference in genetic response compared to breeding males and commercial cows respectively born in the progeny testing scheme is shown in brackets.

Animals	*Year born*	*Progeny per donor surviving to selection*		
		4	*8*	*16*
Nucleus males	10	1.18 (0.01)	1.38 (0.22)	1.56 (0.39)
	20	2.23 (0.04)	2.71 (0.52)	3.13 (0.94)
	30	3.27 (0.05)	4.02 (0.80)	4.65 (1.43)
Commercial cows	10	0.67 (–0.02)	0.74 (0.05)	0.80 (0.11)
	20	1.69 (–0.02)	1.98 (0.27)	2.23 (0.51)
	30	2.73 (–0.01)	3.27 (0.53)	3.73 (0.99)

Table IV. The expected genetic response (in phenotypic SD units) of newborn juvenile nucleus males and commercial females. The difference in genetic response compared to breeding males and commercial cows respectively born in the progeny testing scheme is shown in brackets.

Animals	*Year born*	*Progeny per donor surviving to selection*		
		4	*8*	*16*
Nucleus males	10	1.52 (0.36)	1.73 (0.57)	1.90 (0.74)
	20	2.97 (0.78)	3.51 (1.31)	3.97 (1.78)
	30	4.42 (1.20)	5.29 (2.07)	6.03 (2.82)
Commercial cows	10	0.88 (0.20)	0.97 (0.28)	1.04 (0.35)
	20	2.27 (0.56)	2.62 (0.91)	2.92 (1.21)
	30	3.71 (0.97)	4.37 (1.63)	4.95 (2.20)

Results

The expected genetic response of nucleus males and commercial cows born after 10, 20 and 30 years for 4, 8 and 16 progeny per donor is shown in Tables III and IV for the adult and juvenile MOET nucleus schemes respectively. Results for 8 progeny per donor are also shown in Figures 1 and 2.

The importance of ET success rates and herd management is shown by the significant increases in response achieved with higher numbers of progeny per donor. With 4, 8 and 16 progeny per donor the predicted superiority of juvenile nucleus bulls born at year 20 over breeding males born in the progeny testing scheme is 36, 60 and 81%. With the adult MOET nucleus scheme, the figures are 2, 24 and 43%. The commercial herd lags behind the nucleus herd in genetic merit. The corresponding figures for the commercial herd at year 20 are 33, 53, and 70% for the juvenile and –1, 16 and 30% for the adult MOET nucleus schemes. Although genetic gain increases with the number of progeny

per donor, the costs of running the scheme also become more expensive. In deciding what the optimum size of the scheme should be, account should be taken of the extra costs needed as well as the greater returns possible from increasing the family size.

Further comparison between the schemes will be made with 8 progeny per donor. The gap between the predicted genetic merit of animals bred from the nucleus and progeny testing schemes increases with time, as shown by Figures 1 and 2. For the adult scheme, the average merit of nucleus bulls born in the first 3 years is the same as those breeding bulls born in the progeny testing scheme. The nucleus bulls born at year 4 are slightly superior, and from then on they become progressively better. Commercial cows bred to nucleus sires exceed these bred to progeny tested sires from year 9 onwards. After that, the gap between them diverges.

For the juvenile nucleus scheme, response is far more substantial in the early years than with the adult scheme. By year 10, the genetic response of newborn potential breeding males is almost 50% higher in the MOET nucleus scheme than in the progeny testing scheme. Thus by year 15, the difference between them is equivalent to about 10 years' genetic gain of the progeny testing scheme. This increased genetic response is passed down to the commercial cow herd so that by year 15 the average genetic merit at birth of the commercial cows is higher than that of the progeny testing scheme breeding bulls at birth.

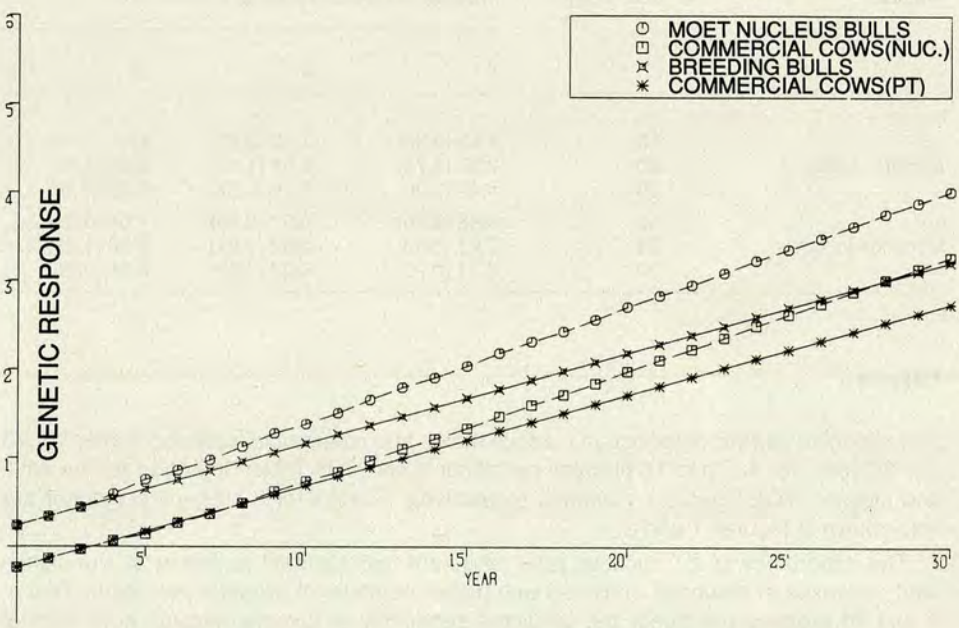
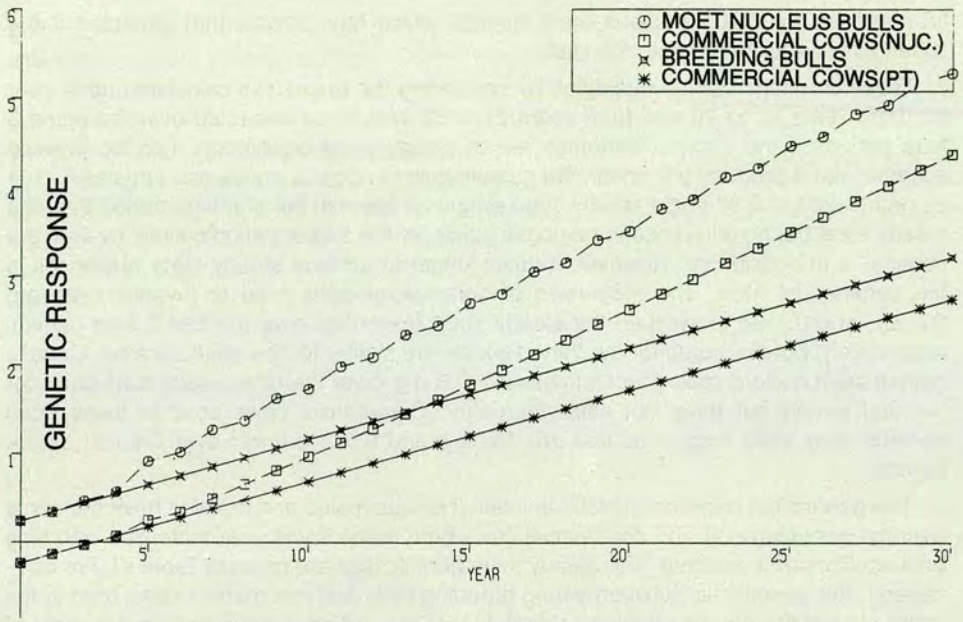


Fig. 1. Genetic response of animals born in a progeny testing (PT) and adult MOET nucleus scheme.



JUVENILE SCHEME (8 PROGENY PER DONOR)

Fig. 2. Genetic response of animals born in a progeny testing (PT) and juvenile MOET nucleus scheme.

In a MOET nucleus scheme, the steady state response to selection depends only on 2 selection pathways, selection of sires to breed nucleus offspring and donors to breed nucleus offspring. The expected steady state rates of annual genetic change are given in Table V. In setting up a nucleus scheme, genetic response in the nucleus herd fluctuates in the early years before stabilising at the steady state rate of response. In addition, it takes longer to stabilise in the commercial herd because of the time needed to disseminate the genetic progress from the nucleus to the commercial tier. This results in a gene-

Table V. Expected steady state annual genetic gain given in phenotypic SD units. The expected difference in genetic response between animals born in a MOET nucleus and progeny testing scheme after 20 years is given in brackets.

Scheme	*Progeny per donor surviving to selection*		
	4	*8*	*16*
Juvenile	0.145 (0.84)	0.178 (1.5)*	0.207 (2.08)
Adult	0.104 (0.03)	0.132 (0.58)	0.155 (1.04)

*1.5 = 20 (0.178 – 0.103).

tic response of MOET nucleus bred animals which lags behind that expected if the scheme is in equilibrium from the start.

These time lags can be quantified by comparing the responses calculated up to year 10, from years 11 to 20 and from years 21 to 30 with those expected over the same 3 time periods if the nucleus schemes are in steady state equilibrium. For the juvenile scheme with 8 progeny per donor, the genetic gain of nucleus males and females is 0.11 σ_P (equivalent to 0.63 years steady state progress) lower in the first time period than the steady state but no difference in response exists for the 2 later periods, since by then the scheme is in equilibrium. However, it takes longer to achieve steady state responses in the commercial herd. The responses of commercial cows bred to juvenile sires are 2.2 Δg and 0.7 Δg lower than the steady state responses over the first 2 time periods respectively, but are equal for the third. Results are similar for the adult scheme. Genetic gain of adult nucleus males and females is $\approx$ 0.3 Δg lower than the steady state gains for the first period but does not differ thereafter. Commercial cows bred to these adult nucleus sires yield responses that are 1.6 Δg and 0.5 Δg lower over the first 2 time periods.

The genetic lag between nucleus animals (nucleus males and females have the same average genetic merit) and commercial cows born in the same year increases with time until equilibrium is reached. The steady state genetic lags are given in Table VI. For comparison, the genetic lag between young breeding bulls and commercial cows born in the same year in the progeny testing scheme is 0.47 σ_p, which is equivalent to 4.6 years of improvement. The genetic lag in the MOET nucleus scheme is:

$$\Delta g\,(L_{BC} + L_{CC}) - (I_{BC} + I_{CC})$$

where *C* refers to commercial cows. With the MOET nucleus schemes, the genetic lag is increased quite significantly due to the subdivision of the population into selected (nucleus herd) and non-selected (commercial herd) levels.

The summed genetic merit of commercial cows born in the first 10 and 20 years of the MOET nucleus schemes, discounted to the present, is compared to that from commercial cows in the progeny test scheme. The results are given in Table VII. With 8 progeny per donor, discounted genetic returns from the juvenile scheme are much higher over the first 10 years compared to returns from the progeny testing and adult schemes which are roughly equal. When compared over 20 years, the juvenile scheme is still far superior

Table VI. Steady-state genetic lag in SD units (with the equivalent number of years annual genetic gain of each scheme in brackets) between nucleus animals and commercial cows born in the same year.

Scheme	*Progeny per donor surviving to selection*		
	4	*8*	*16*
Juvenile	0.74 (5.1)	0.96 (5.4)	1.15 (5.6)
Adult	0.54 (5.1)	0.75 (5.7)	0.93 (6.0)

Table VII. The summed discounted genetic response of commercial cows born in the first 10 or 20 years with a MOET nucleus scheme compared to those born over the same years in the progeny testing scheme (100). Discount rate is 5%.

Years born	*Juvenile scheme Progeny per donor*			*Adult scheme Progeny per donor*		
	4	*8*	*16*	*4*	*8*	*16*
1–10	133%	143%	152%	92%	101%	109%
1–20	131%	147%	161%	97%	110%	121%

while returns from the adult scheme are slightly higher than from the progeny testing scheme.

Discussion

The results demonstrate that genetic response can be increased substantially within a short time by setting up a MOET nucleus scheme using the top animals from an efficient progeny test scheme. The larger the nucleus scheme established (in terms of the number of embryos transferred), the greater the predicted response.

The response of newborn nucleus animals is superior to that of newborn progeny test breeding bulls from early on and, as a consequence of the shorter generation intervals, this superiority is passed on to future generations of nucleus and commercial herd animals more quickly in the juvenile than in the adult scheme. Thus genetic response is more rapid in both the early and late years from the juvenile scheme.

Genetic gains achieved in practice are likely to be lower than those predicted here for both the progeny test and MOET nucleus schemes. The reasons for the observed gap between expected and realised genetic gains in progeny test schemes have been well discussed elsewhere (Van Vleck, 1977; Van Tassell and Van Vleck, 1987). The extensive use of family information combined with the small population size in MOET nucleus schemes should result in higher inbreeding rates (Burrows, 1984), lower selection intensities (Hill, 1977) and greater variation in the response to selection due to genetic drift than expected. These problems are likely to be much worse in the juvenile than in the adult scheme (Ruane, 1988).

The largest response in the early years is expected to come from setting up a juvenile rather than an adult MOET nucleus scheme. This also has the additional advantage of requiring only 2 years of selection of nucleus founder females instead of 4. A practical system may be to set up a juvenile nucleus scheme, run it for a given length of time and then open the herd to new genetic material. This system should allow high genetic gains to be made in the early years as well as guarding against the problems previously referred to. However, due to the increased genetic lag of the commercial herd (see Table VI) it may be more difficult to find commercial cows within the population of sufficiently

high genetic merit for use in the nucleus herd. The trading of genetic material of high merit between different MOET nucleus schemes may be the preferred method of introducing novel genetic stock.

Another alternative would be to change from a juvenile to an adult scheme after a given length of time. This could be done quite simply by deferring selection until the first lactations of the female candidates are complete. Other strategies exist and should be considered, such as the possibility that instead of selecting both sexes on parental pedigree from year 4 onwards in the juvenile scheme as described, females could be selected using their own performance with males selected on parental pedigree.

In this study schemes were compared chiefly under the assumption of 4 daughters and 1 son per donor surviving to selection. It should be possible to obtain such numbers in the adult scheme with a generation interval of 3.75 years. However, at present it may not be possible to achieve this family size within the 2–year generation interval described for the juvenile scheme, since embryo recovery rates are lower in immature donors compared to mature donors (Gordon, 1983). To date, little emphasis has been placed on improving embryo recovery rates in young heifers, and so considerable scope for improvement exists. The ability to produce large numbers of embryos for research purposes by methods such as *in vitro* fertilisation (*e.g.*, Lu *et al.*, 1987) should mean that current MOET sucess rates will be improved in the future.

Smith and Ruane (1987) examined the merits of using young sires, bred by MOET and evaluated on full sister first lactation records, in addition to older progeny tested sires on the commercial herd. They showed that the genetic merit of commercial semen using the top animals from both groups could be increased by 10 – 20% in this manner. The question could be asked here whether it would be worthwhile to progeny test the young nucleus bulls and then select the top 12 bulls for commercial use from the young nucleus bulls evaluated on MOET nucleus information and the older nucleus animals evaluated on progeny test data. The answer seems to be no. With 4, 8 and 16 progeny per donor, the genetic merit of the 12 commercial bulls is highest when 10, 11 and 12 young juvenile nucleus bulls and 7, 8 and 9 young adult nucleus bulls are chosen, respectively.

Thus further testing of MOET nucleus sires using progeny test information produces few sires of sufficiently high merit to be selected for use on the commercial herd, especially compared with young juvenile sires. In addition, with a MOET nucleus breeding scheme, improvements on the bull to breed commercial cow pathway do not increase the annual rate of genetic gain. Thus for the adult scheme with 4 progeny per donor, when progeny testing of MOET nucleus bulls has most impact, the annual rate of genetic gain of commercial cows remains unchanged, but their genetic merit compared to nucleus animals (the genetic lag) is reduced by 15%. Given the considerable costs of progeny testing it is unlikely that progeny testing nucleus bulls for use on the commercial herd would be worthwhile.

It may be useful to set up a nucleus breeding scheme in developing countries which lack the infrastructure necessary to maintain an efficient progeny testing scheme (Hinks, 1978; Land, 1986). Nucleus founder stock could be selected from foreign gene pools (if appropriate) and the resulting embryos imported to form the base population. Assuming no genotype-environment interaction, the expected genetic response of bulls born at different years is as shown in Tables III and IV. The genetic response of commercial cows born over time will depend on the population structure and the genetic lag.

Conclusion

The short term gains from setting up an adult MOET nucleus scheme using genetic stock from an efficient progeny testing scheme are quite small compared to those expected from continuing with the progeny testing scheme, but are significant in the long term. In contrast, both the short and long term genetic gains from setting up a juvenile MOET nucleus scheme are quite substantial.

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Appendix 1

Setting up the juvenile MOET nucleus scheme. *M* and *F* represent males and females; *P* and *N* represent animals from the progeny testing scheme and MOET nucleus scheme. The generation interval is 2 years. The genetic merit of animals is given in the brackets. I_1 and I_2 are the genetic superiorities of nucleus females and males used to breed nucleus offspring respectively, evaluated on nucleus records of the dam and her family and progeny test data of the sire. I_3 and I_4 are the genetic superiorities of nucleus females and males used to breed nucleus offspring respectively, evaluated using nucleus herd information on both the sire and the dam. These superiorities are calculated in Appendix 2. The unbroken lines represent reproduction, the broken lines ageing. The asterisks refer to selected nucleus animals.

Year	*Cohort 1*		*Cohort 2*	
0	F_{PO} (–0.014)	M_{PO} (0.488)		
1	F_{N1} (0.237)		F_{P1} (0.089)	M_{P1} (0.591)
2	F_{N1} (0.237)	M_{P2} (0.694)	F_{N2} (0.34)	
3	F_{N3} (0.466)	M_{N3} (0.466)	F_{N2} (0.34)	M_{P3} (0.796)
4	F^*_{N3} (0.466+I_1)	M^*_{N3} (0.466+I_2	F_{N4} (0.568)	M_{N4} (0.568)
5	F_{N5} (0.913)	M_{N5} (0.913)	F^*_{N4} (0.568+I_1)	M_{N4} (0.568+I_2)
6	F^*_{N5} (0.913+I_3)	M^*_{N5} (0.913+I_4)	F_{N6} (1.015)	M_{N6} (1.015)
7	F_{N7} (1.269)	M_{N7} (1.269)	F^*_{N6} (1.015+I_3)	M^*_{N6} (1.015+I_4)
8	F^*_{N7} (1.269+I_3)	M^*_{N7} (1.269+I_4)	F_{N8} (1.371)	M_{N8} (1.371)
•				
•				
•				
t	F_{Nt}	M_{Nt}	F^*_{Nt-1}	M^*_{Nt-1}
t+1	F^*_{Nt}	M^*_{Nt}	F_{Nt+1}	M_{Nt+1}

Appendix 2

An example to illustrate how the expected genetic response of newborn juvenile nucleus offspring is calculated (given in SD units). Each donor produces 8 progeny as candidates for selection.

Contribution to the cumulative genetic response by year

Year nucleus offspring born	*Year of selection of parents*										*Cumulative genetic response*
	0	1	2	3	4	5	6	7	8	9	
1	0.237[1]										0.237
2	0	0.34[1]									0.34
3	0.119	0	0.347								0.466
4	0	0.17	0	0.398							0.568
5	0.119	0	0.347	0	0.447[2]						0.913
6	0	0.17	0	0.398	0	0.447[2]					1.015
7	0.119	0	0.347	0	0.447	0	0.356[3]				1.269
8	0	0.17	0	0.398	0	0.447	0	0.356			1.371
9	0.119	0	0.347	0	0.447	0	0.356	0	0.356		1.624
10	0	0.17	0	0.398	0	0.447	0	0.356	0	0.356	1.727

[1] Bull dams and bull sires are used. How these values are derived can be seen in Appendix 1 and in Materials and Methods. Only half this genetic merit is passed on in subsequent generations because nucleus males are not used at years 2 and 3.

[2] $0.447 = 1/2\ (I_2 + I_1)$ (see Appendix 1).
$= 1/2\ (i_m r_m h + i_f r_f h) = 1/2\ ((1.968)(0.5522)(0.5) + (1.271)(0.5522)\ (0.5))$.

[3] $0.356 = 1/2\ (I_4 + I_3)$ (see Appendix 1)
$= 1/2\ (i_m r_m h + i_f r_f h) = 1/2\ [(1.968)(0.4396)(0.5) + 1.271\ (0.4396)(0.5)]$.

r_m and r_f represent the correlation of true with expected breeding values for males and females respectively, and are calculated using selection index theory.