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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 (σp).

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

$$\Delta g = \frac{\overset{\bullet}{I}_{BB} + I_{BC} + \hat{I}_{CB} + \hat{I}_{CC}}{\overset{\bullet}{L}_{BB} + L_{BC} + L_{CB} + \hat{L}_{CC}} = 0.103\,\sigma_P \text{ (Rendel and Robertson, 1950)}$$

* 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 ($\approx$ 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:

$$r_t = P_t \, r_{t-1} + E Q^{t-1} s$$

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 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.
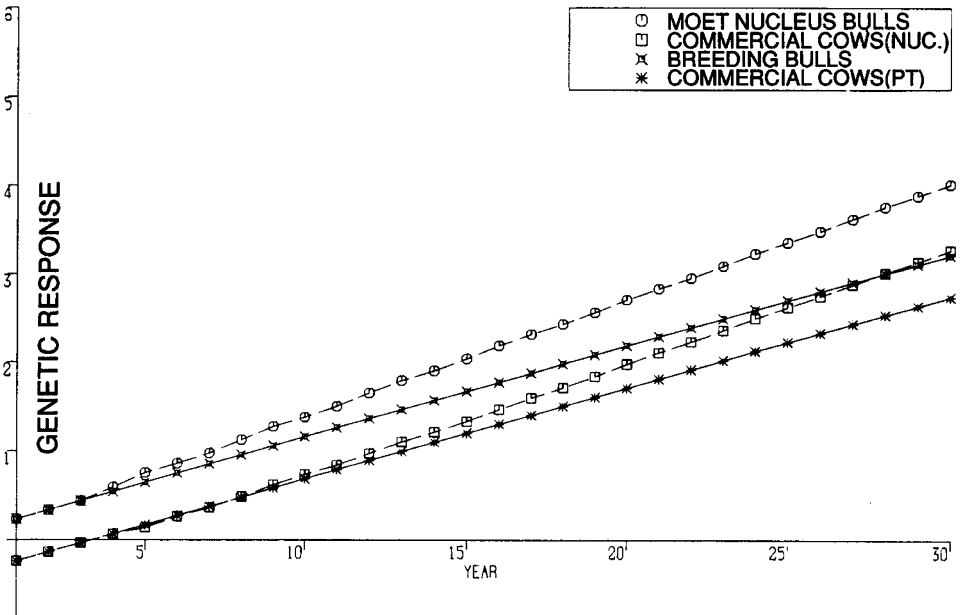
ADULT SCHEME (8 PROGENY PER DONOR)

Fig. 1. Genetic response of animals born in a progeny testing (PT) and adult MOET nucleus scheme.
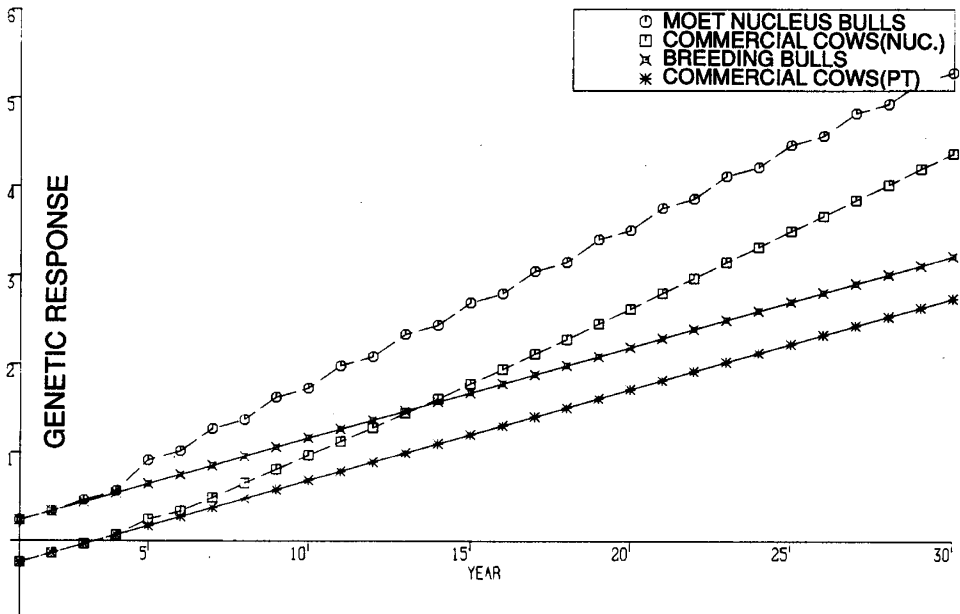
JUVENILE SCHEME (8 PROGENY PER DONOR)

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

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 $\approx 0.3 \, \Delta g$ 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.
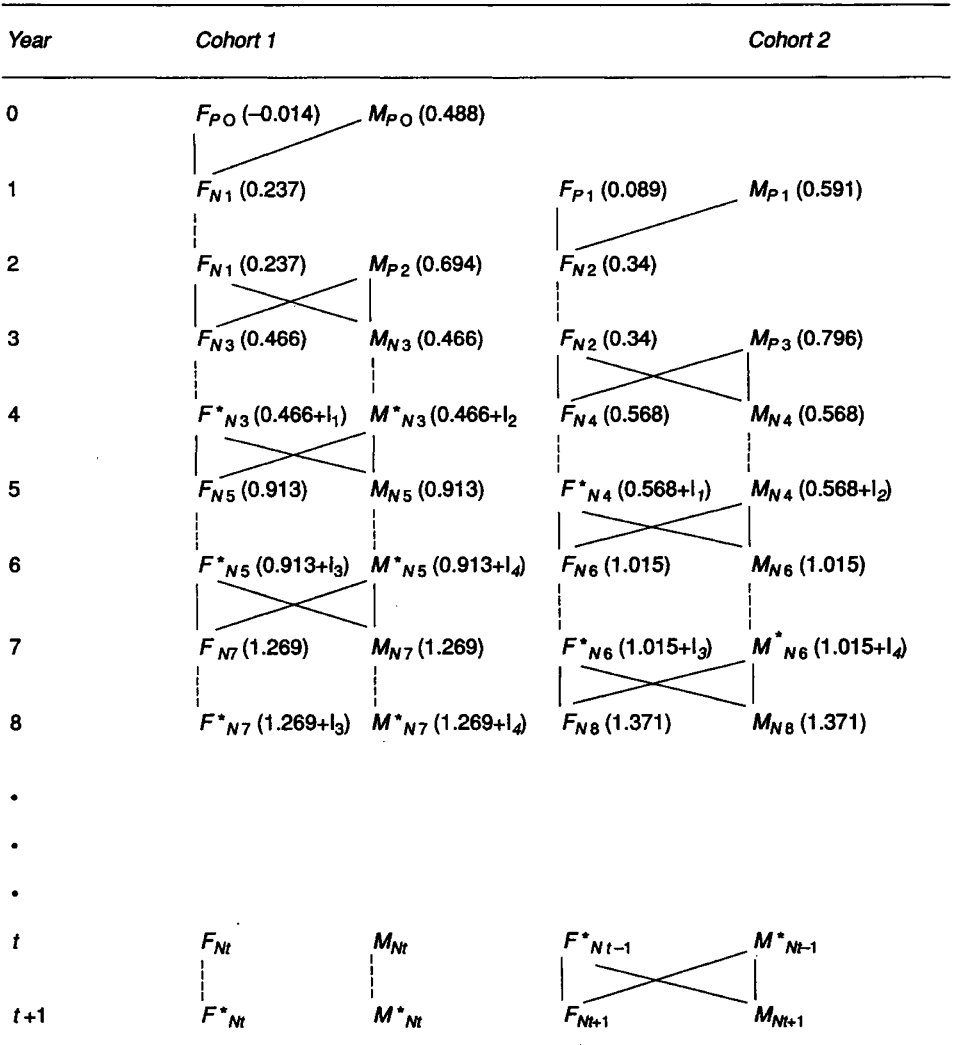
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Appendix 1

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.