Increased Rates of Genetic Change in Dairy Cattle by Embryo Transfer and Splitting

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ABSTRACT

Possibilities for increased rates of genetic change in dairy cattle through embryo transfer and embryo splitting are examined, using the MOET (multiple ovulation and embryo transfer) systems proposed by Nicholas (1979). These involve embryo transfer from one year old females (juvenile scheme, generation interval 1.8 years) and from females after 1 lactation (adult scheme, generation interval 3.7 years), with use of males at similar ages. Though selection, is less accurate than in conventional progeny testing, the annual rate of genetic improvement can be increased, and even doubled. If the number of transfers is restricted and the inbreeding rate is limiting, the adult scheme for both sexes is preferred. A scheme with 1024 transfers per year and 512 females milk-recorded per year will sustain a rate of genetic improvement some 30 percent above that possible by a conventional national progeny testing program. Because of the relatively small number of animals involved, it is argued that greater control over recording, breeding and selection should be possible, leading to a larger proportion of the possible genetic gains being realized in practice. Other advantages, and disadvantages of MOET systems, and their integration in dairy cattle improvement are discussed.

INTRODUCTION

Breeders of dairy cattle have appreciated the advantages of improved reproductive rates in their work. Artificial insemination is now widely exploited, both for its commercial and genetic advantages. Embryo transfer is now feasible, and embryo

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splitting to give identical twins has been achieved (Willadsen, 1979; T. Williams and P. Elsden, personal communicaltion). In 1979, Nicholas proposed the use of embryo transfer from immature heifers, which theoretically allows faster rates of genetic change than conventional progeny testing systems.

The objectives of this paper are to review this proposal, to find the optimal conditions under which it should be operated and to consider how to adapt and integrate it into a national improvement program. The value of embryo splitting will also be examined, and the extension to developing large clones will be considered.

METHODS

Conventional program.

As a base to assess the value of the new techniques consider first a conventional progeny testing program with artificial insemination (AI), as in the UK. Some 150 young bulls per year are progeny tested in testing herds, on about 50 daughters each (contemporary comparison weighting of about 30). An efficient plan would be to use the best 2 bulls for one year to breed bulls, and the best 10 bulls for three years to breed cows. To obtain 150 young bulls, some 600 cows would be selected as bull dams. Selecting at an intensity of 1/25, and on 3 lactation records, would require a recorded cow population of about 50,000 cows. The annual rate of inbreeding is largely determined by the number of bulls (n_{bb}) per year to breed bulls and the generation interval (L), and is approximately $1/(8L^2n_{bb})$. The genetic superiority of the parents and their age when their offspring are born are given in Table 1. The estimated equilibrium genetic change is about 0.1 phenotypic standard deviation (SD) units per year. This corresponds to the figure of 2% of the mean per year (coefficient of variation of 20%) usually quoted as the maximum possible rate (Robertson and Rendel, 1950; Skjervold and Langholtz, 1964; Lindhé, 1968). It is theoretically possible to obtain higher rates, by more intense selection and by more accurate selection of females (including information on sires and grandsires); VanVleck (1982) suggests rates as high as 3% per year. With large pedigree recorded populations the

levels of inbreeding with such schemes are low, from 0.1 to 0.2% per year.

In practice the rates of realized genetic change in milk yield are much lower than the possible rates, and range from 0.5 to 0.75% of the mean in different countries (VanVleck, 1977). This is partly due to inefficiencies in the system (for example, in the cb path in Table 1) and also to selection for other traits, especially type and functional traits.

Multiple Ovulation and Embryo Transfer (MOET)

Several workers concluded that embryo transfer would contribute little to the rate of improvement of dairy cattle in traditional progeny testing schemes, because increases in the selection differential of cows to breed bulls would be small in an efficiently operated improvement scheme (e.g., McDaniel and Cassell, 1981). However, there may be advantages in practice, by increasing the probability of obtaining a suitable bull calf from each selected contract mating arranged. If embryo transfer could be applied in all commercial herds, then the rate of improvement in a progeny testing program could be increased by some 15% (VanVleck, 1982).

Nicholas (1979) suggested an alternative method of using MOET to increase the rate of genetic response. It is based on reducing the generation interval and tolerating less accuracy in selection, and requires much smaller numbers of recorded cattle. One scheme, his pedigree scheme, involves selection among transferred sons and daughters when they are 12-13 months of age, on the basis of their dam's (the donor) first lactation record. In his other scheme, the sib scheme, selection of transferred males is delayed until their female sibs have completed their first lactation, so that males can be selected on an index using sib and dam performance.

In this paper we shall expand on these proposals by adding information on other relatives in selection of both males and females. We shall use the terms, juvenile scheme (J) for selection at one year of age, adult scheme (A) for selection at 3 years of age, and these will refer to the methods of selection for each sex separately. The time schedules for each scheme in each sex are shown in Table 2. The generation interval for the juvenile

scheme is about 1.8 years and for the adult scheme is about 3.7 years; Nicholas (1979) used 2 years and 3.6 years, respectively. These compare with the average generation interval in a conventional progeny testing system of about 6.3 years.

The information on relatives available for the two schemes is shown in Figure 1. It can all be combined optimally for selection by conventional family selection methods in a selection index (see Appendix). Here the genetic responses are evaluated for both sexes on both the juvenile and adult schemes, with and without information on relatives (16 combinations in all).

Parameters and symbols used, corresponding to those of Nicholas (1979) where possible, are given in Table 3. In order to derive general results, the genetic changes have been evaluated for large population selection differentials (that is ignoring the number of transfers). The responses for any finite number of transfers can be estimated by adjusting for the finite population selection differentials (Burrows, 1972). With (y/2) female progeny per donor available at selection, the proportion selected is (2/y) for females. The corresponding proportion selected in males is (2/xy), with (y/2) full sib males being selected from the best full sibships. However, this would lead to a much increased rate of inbreeding, so selection of males is restricted to the proportion 1/x, equivalent to the maximum of one male per full-sibship. (Since all male full sibs will have the same estimated breeding value, semen from all of them can be used.) Both cases have been evaluated, but the main results are given for the latter case, the equivalent of one male per sibship, since this is considered the more reasonable in practice. The annual genetic change can be evaluated as

$$\frac{i_m r_{G_m I_m} \sigma_G + i_f r_{G_f I_f} \sigma_G}{L_m + L_f}$$

where i_m and i_f are the selection differentials for males (m) and females (f), r_{GI} is the correlation between the genotypic value of the individual and the index in selection, σ_G is the genetic standard deviation, and L is the generation interval.

The genetic drift variance and the rate of inbreeding depend on the numbers selected for breeding and on the generation interval. The variance of the predicted response can be derived taking account of the drift variance, following Hill (1974). Only a proportion of the embryos transferred will be available for selection in the next generation. Here a conception rate of 0.7 and a survival rate to selection of 0.7 have been assumed, giving $s \doteq 0.5$. With a total of T transfers per year, there will be $D = sT/y$ donors per year and $S = D/x$ sires per year. In the juvenile scheme, females are used as donors before their record or index is available. Those donors which are not subsequently selected will have their progeny sibships culled and effectively will leave no progeny. Since the proportion selected in females is 2/y, the effective number of donors per year entering the breeding herd is $2D/y = D^*$ in the juvenile scheme. The approximate rate of inbreeding per year is estimated as

$$\frac{1}{8L^2}\left(\frac{1}{S} + \frac{1}{D^*}\right).$$

For the adult scheme, donor females are already selected, so $D^* = D$. The rate of inbreeding may well be higher than estimated, since selection will tend to be of whole sibships of females rather than of individuals, and the selection indexes will select related individuals (Robertson, 1961). On the other hand, if semen from all the males in a selected sibship was used, this would reduce the rate of inbreeding and reduce the genetic drift variance.

Embryo splitting

Splitting of embryos to give identical twins, or triplets, has been recently achieved, and could become possible routinely. Selection accuracy could then be increased because records on genetically identical individuals would be available. The genetic responses possible with such splitting, into $v = 2$, 4 and 16 identical individuals, have also been evaluated using selection indexes as before. However, the selection intensity among males and among females has not been increased, because this would lead to use of

genetically identical males, and of females, and to much higher rates of inbreeding. Thus the total number of transfers has been increased (by 2, 4 and 16 times) to maintain the same rates of inbreeding (ΔF).

Embryo Sexing.

If it were possible to sex embryos before transfer, a limit might be set on the number of male embryos transferred. This would reduce the number of transfers required, or allow a larger effective breeding population with the same number of total transfers. For example, the equivalent number of transfers with say 3 male progeny at selection would be ($vy \geq 6$)

$$Tvy/(3 + \tfrac{1}{2}vy).$$

With $y = 8$ genetically different progeny per donor, and $v = 2$ identicals per progeny, the equivalent number of transfers would be 1.45 times T, so the total number of transfers could be reduced from 2000 to 1450.

Cloning.

If it were possible to continue the splitting process, large clones of genetically identical individuals could be developed. This might be from embryos, or from somatic cells (recently achieved by Hoffner and Di Bernardino, 1980 in amphibians). Though neither is currently possible in mammals, it is interesting to sketch out the implications for genetic improvement.

Dealing with repeated embryo splitting and storage, there are three steps in improvement. The first is the genetic lift obtained by selecting the parents of the embryos to be cloned. This lift corresponds to the selection of parents of bulls, and in Table 1 (paths bb and cb) corresponds to about 4 years of genetic improvement.

The second phase is in the selection of the best clone, which would then be multiplied and used by embryo transfer into commercial females, so that the population would consist largely of the best, or few best, clones. The optimum number of clones to test and the optimum number (n) of individuals per clone can be derived following

Robertson (1957) for progeny testing methods. The estimated genetic improvement in standard deviation units is

$$iH^2\sqrt{\frac{n}{1+(n-1)H^2}}$$

where i is the standardized selection differential for proportion p selected and H^2 is the heritability in the broad sense (including dominance and epistatic effects). With a total testing capacity of N and with C clones selected, the optimum test number per clone (n=pN/C) can be derived from

$$\frac{C(1-H^2)}{NH^2} = \frac{2p(z-xp)}{2px-z}$$

where x and z are the deviate and the ordinate corresponding to p in the normal distribution. With H^2=0.3 and C=1 for N=1000 and 10,000 the optimum proportions selected are 0.75% and 0.12%, with 8 and 12 individuals tested per clone, and with 125 and 830 clones, respectively. The genetic responses are 1.32 and 1.68 phenotypic standard deviation units, corresponding to 13 and 17 years of the annual genetic change theoretically possible by a conventional progeny testing program. This response is obtained 4 years after forming the clones, the time needed to grow, test and select them on first lactation records. Because of the time interval, two stage or multi-stage selection of the clones is unlikely to add much in dairy cattle.

The third phase would be in the increased rate of annual genetic improvement. Relying on the few best clones would narrow the genetic base, so a larger number of selected clones would be used to reconstitute the gene pool, and generate a new set of clones for testing. With no limits to the number of transfers, the rate of inbreeding could be set at any required level. Various mating and selection plans could be used. However, the rates of annual genetic change could at least be as great as those achieved with the MOET and embryo splitting, considered earlier.

RESULTS

To keep the results general, the genetic changes were evaluated for large population selection differentials, and using the number of progeny available at selection, rather than

the number of transfers. The responses for finite numbers in selection and for different conception rates and survival to breeding age can be accomodated later for any specific situation. In practice some allowance in numbers would need to be made for any inefficiency in use of the MOET techniques and of imbalance among sexes and numbers between sibships.

Results in Table 4 show the value of including information on relatives when making selections. The annual response is increased appreciably by using a selection index, rather than only the dam II♀ record (juvenile scheme) or the dam I♀ 3 records (adult scheme).

Theoretically the proportion selected in males could be 1/x times that for females, with x donors per male. However, as discussed earlier, this would involve selecting all males from the best full-sibships, and would increase the rate of inbreeding, especially with larger sibships. The alternative of selection equivalent to one male per sibship is thus preferred here. The difference in genetic response between the two selection policies is evident from Table 4. In the case involved (8 progeny per donor, 8 mates per sire) some 10-30% more response would be made with the more intense selection in males.

The main results of the paper are presented in Table 5, showing the rates of genetic change and inbreeding with different combinations of progeny per donor and donors per male and with index selection of males and females. For comparison of response, it is useful to remember the rate possible with a progeny testing system is about 0.1 SD (Table 1), corresponding to 100 units in Table 5. Most of the MOET systems could exceed this, often by substantial margins. The juvenile scheme applied to both sexes (JJ) gives a greater rate of response than the adult scheme in both sexes (AA). Combinations of the two schemes for males and females (JA and AJ) are intermediate. In addition, as the number of progeny per donor and the number of females per male increases, the responses continue to climb, up to 90% more than possible by conventional progeny testing. However, before becoming too enthusiastic about the possible rates of response, it is important to consider the rates of inbreeding incurred, or to calculate the total number of

transfers needed to maintain a required rate of inbreeding.

The rate of inbreeding was calculated for a total of 1000 transfers (500 progeny surviving to selection) per year. The actual rate can then be scaled up or down as a multiple of 1000. The results show that very much higher rates of inbreeding occur with the juvenile scheme than with the adult scheme. This is due to the lower generation interval in the juvenile scheme, and because only a proportion of the donors become effective donors, the rest and their progeny being culled at the next selection. The inbreeding rate is highest when both sexes are selected on the juvenile scheme (JJ), least on an all-adult scheme (AA) with the others (JA) and (AJ) intermediate. It can be seen from Table 5 that in order to obtain the higher rates of response with the juvenile scheme (JJ), more than four times as many transfers per year would be required to maintain the same rate of inbreeding as in the AA scheme. With 1000 transfers per year only a few MOET systems can sustain as low a rate of inbreeding (0.1%-0.2% per year) as a national progeny system, and these show little extra possible response. Thus either more transfers per year would be needed, or a higher rate of inbreeding would have to be tolerated.

Two ways to reduce the number of transfers needed would be to improve conception and survival rates, and to transfer fewer male embryos, if the embryos could be sexed. For example, in the case with 8 donors per male and 12 progeny per donor, improvement of the conception-survival rate(s) from 50 to 60% would reduce the number of transfers by 17%, and transferring only 4 males instead of 12 per donor would reduce it by 33%. In the AA case, these would reduce the rate of inbreeding from 0.2% to 0.12% per year.

The advantages of embryo splitting in increasing further the rates of response are shown in Table 6. Again substantial gains can be obtained, some responses exceeding twice the rate possible with progeny testing. Since the accuracy of selection is improved by having genetically identical individuals, the juvenile scheme shows greater responses than the adult scheme. However, to maintain the same rate of inbreeding, the number of transfers would have to be increased by the same factor as the splitting factor.

The genetic response from the breeding, selection and large scale commercial use of large clones is shown in Figure 2. The results are expressed in terms of the number of years of annual genetic change theoretically possible by progeny testing. There is an initial genetic lift equivalent to 4 years of genetic change by selecting the parents of clones, as for parents of bulls in an AI selection program. After three years the performance of the clones will be known, and the best can be selected for widespread commercial use, the progeny being born in year 4 and being some 13-17 years ahead of an AI population. An appropriate number of the best clones, to maintain a broad genetic base, is mated at year 4 to give a new round of clones and the best clones of the new round are available at year 8. As shown in Table 6, rates of response of more than twice the rate possible by progeny testing can be achieved with embryo splitting and this is used as the subsequent rate of response in Figure 2. After 16 years the difference between breeding and use of clones and a progeny testing system corresponds to about 30 years of annual genetic change of the latter, and continues to increase over time.

DISCUSSION

There seem good possibilities for some of the new techniques of reproduction physiology to affect our methods of breeding and improvement of dairy cattle. Some of the techniques considered here are already available (embryo transfer), some are experimentally possible (embryo splitting) and some are not yet possible (production of large clones). Another review of the possible use of new techniques is given by VanVleck (1982) in the context of improving progeny testing systems. In both these studies, no new genetic or selection principles are involved, and all the results rely on well established and proven theories of selection and selection response.

The main object of this paper was to try to optimize the MOET system and to adapt it for practical application. Results show that where the number of transfers possible is limited, and inbreeding is important, the adult (AA) scheme (with a 3.7 year generation interval) is preferred. A proposed practical scheme, possible with 1982 technology, is

outlines below. To use embryo transfer staff and facilities efficiently, a continuously operating adult (AA) scheme is proposed, with 4 transfer periods (each of 2 months transfer and one month off) per year. With a total of T = 1024 transfers per year, an inbreeding rate of 0.24% per year is obtained. Numbers involved are given in Table 7 and are derived as follows. Using a dash to refer to figures for a 3 month period, we have T' = 256 transfers per period, which requires D' = sT/y = 0.5(256)/8 = 16 donors per period, where s ≐ 0.5 represents the combined effect of 70% conception and 70% survival to selection. These 16 donors each produce y = 8 offspring (4 males, 4 females), giving a total of 64 males (16 x 4 full sib groups) and 64 females available for selection. The young bulls are kept until they have semen frozen; the equivalent of one bull per full sibship to minimize inbreeding. Within periods one bull (or bulls) from the best full sibship (1/16) is selected, along with the 16 best indexing 16 first lactation cows. The 16 selected females are mated to the selected bull(s), and to the bull(s) selected in the two previous periods, to provide variation and overlap, otherwise the groups in the different periods would be genetically closed. Note that the heifers are not remated until their lactation record is available. Alternatively they could be selected on part (5-6 month) record, reducing the generation interval to 3.2 years. At this stage there will be 3 full lactation records and one part record available on the dam. With finite numbers selected, the loss in standardized selection differential is ½(1.968 + 1.271 - 1.766 - 1.256) approximately 0.1 SD, which is equivalent to a 7% reduction in selection differential. Use of older bulls from the two previous periods increases the generation interval by 3%. These factors collectively lower the annual genetic change to 0.129 SD units per year,about 30% greater than possible with conventional progeny testing. The estimated standard error of the prediction is 0.023 SD units. Thus with testing and recording some 512 cows per year, and transfer of 1024 embryos per year, a practical MOET scheme could be equivalent to a full national program of recording and progeny testing.

Apart from the much smaller number of animals involved, there are several other

advantages of a MOET scheme like the one proposed above. Comparisons among contemporaries are balanced, and environment and management conditions can be better controlled. Both of these could lead to more accurate selection. Animals can be recorded more often and special traits may be recorded and used in selection. Dairy cattle are amomalous in that selection is usually only on outputs, and inputs are usually not considered. With a MOET scheme, feed intake (throughout life) could be measured and the life time efficiency of milk production could be included in the criterion for selection. Another advantage in countries where dairy cattle contribute to meat production, is that males can be performance tested for beef traits, and selected within sibships, with no loss of selection differential for dairy traits. However, it would be better to combine all the information in a selection index (including correlations among traits and data on carcass traits of unselected sibs). If genotype-environment interactions were of concern, sibships could be divided across environments. With the shorter generation interval, the returns from a MOET program are obtained sooner than from a progeny testing system. Finally, and perhaps most important in achieving the responses possible, the breeding and selection would be under control of a single agency so that selection differentials on defined breeding criteria could be realized in practice.

However, the role of a MOET scheme may not be to replace progeny testing but to provide a nucleus herd of the type envisaged by Hinks (1978), for breeding young bulls for progeny testing. This is because producers may prefer well proven bulls, rather than young bulls of high average merit, but with much variation. The same problem exists for the large population half-sib selection scheme proposed by Owen (1976) though it is competitive with progeny testing systems. However, a MOET scheme producing young sires could well double the rate of genetic improvement, compared with current shcemes, and on a national basis would have a high benefit-cost ratio even with the present high cost of embryo transfer. As transfers become less expensive, the total number of transfers could be increased, and the inbreeding rate reduced. Then juvenile (JJ) MOET

schemes would be preferred because of the higher genetic gains possible.

There is also an opportunity in setting up a MOET scheme to take advantage of the initial genetic life (shown in Figure 2) possible within a population or to select nucleus stocks from any superior populations. Indeed since it will take 2-3 generations before differences in annual response become apparent, the main early benefits could come from these opportunities. The MOET scheme should not be seen as a closed breeding unit, but individuals with the highest breeding values would be used, whatever their source. The same would apply within the scheme, for example by reusing superior males and females over several MOET periods.

Two disadvantages of a MOET scheme are the disease risk to a single nucleus, and reliance on a single breeding unit for national improvement. The first could be overcome by holding different age groups in the MOET scheme at different locations, and the second by relying on international competition, or a competition among MOET units within a country.

If embryo splitting techniques could be extended to develop large clones, then rates of genetic improvement can be greatly accelerated, as shown here and by VanVleck (1982). However, there would also be very large benefits in commercial production, since cloning and sexing would allow 1) production of animals of the desired sex and of the required genotype at each birth (e.g., beef genotypes for dairy cows); 2) increased uniformity; 3) clones of hybrids; 4) artificial twinning (in beef cattle); and 5) rapid repopulation and dissemination. Some of these and others are discussed by Seidel (1980).

VanVleck (1982) has considered the value of embryo transfer, sexed sperm and cloning in progeny testing systems, and has shown that appreciable improvements in genetic response can be obtained. However, the results assume widespread use of embryo transfer in <u>all</u> commercial herds. He also points out that the accuracy of the cow to bull (cb) path is less accurate than specified, due to special treatment of cows likely to be bull mothers. This would be avoided with a controlled MOET scheme. The possibility of

obtaining the high selection differentials in a wide spread national improvement program is also in doubt because of competing interests. Different perspectives are also taken on two aspects of cloning, on the value of storing embryonic (juvenile) material while testing clones and on further genetic improvement after the first round of cloning. These papers sketch out some of the possibilities with the new techniques in reproductive physiology. The important feature is that they be considered, discussed and used where appropriate to improve our cattle populations for efficient production of animal food products.

REFERENCES

Burrows, P. M. 1972. Expected selection differentials for directional selection. Biometrics 28:1091-1100.

Hill, W. G. 1974. Variability of response to selection in genetic experiments. Biometrics 30:363-366.

Hinks, C. J. M. 1978. The use of centralized breeding schemes in dairy cattle improvement. Animal Breeding Abstracts 46:291-297.

Hoffner, N. J. and M. A. di Bernardino. 1980. Developmental potential of somatic nuclei transplanted into meiotic oocytes of Rana pipens. Science 209:517-519.

Lindhé, B. 1968. Model simulation of AI-breeding within a dual purpose breed of cattle. Acta Agric. Scand. 18:33-39.

McDaniel, B. T. and B. G. Cassell. 1981. Alternative uses of embryo transfer and their effect on the rate of genetic change. J. Dairy Sci. 64:2484-2492.

Nicholas, F. W. 1979. The genetic implications of multiple ovulation and embryo transfer in small dairy herds. 30th Meeting European Ass. Anim. Prod., Harrogate, England, CG1.11.

Owen J 1975. Selection of dairy bulls on half-sister records. Anim. Prod. 20 : 1–10.

~~Nicholas, F. W. 1982. The effect of multiple ovulation and embryo transfer or response to selection and rate of inbreeding in an individual dairy herd. Animal Production (Submitted).~~

Robertson, A. and J. M. Rendel. 1950. The use of progeny testing with artificial insemination in dairy cattle. Journal of Genetics 50:21-31.

Robertson, A. 1957. Optimum group size in progeny testing and family selection. Biometrics 13:442-450.

Robertson, A. 1961. Inbreeding in artificial selection programs. Genetical Research, (Cambridge), 2:189-194.

Seidel, G. E. 1980. Potential applications of cloning in animal industry. 9th Inter. Congress in Animal Reproduction and Artificial Insemination, Madrid.

Skjervold, H. and H. J. Langholtz. 1964. Factors affecting the optimum structure of AI-breeding in dairy cattle. Zeitschrift fur Tierzuchtung und Zuchtungsbiologie 80:26.

Van Vleck, L. D. 1977. Theoretical and actual genetic progress in dairy cattle. Proc. Inter. Conf. Quant. Genetics. Edited by E. Pollak, O. Kempthorne and T. B. Bailey. Iowa State University Press, Ames, Iowa.

Van Vleck, L. D. 1982. Potential genetic impact of artificial insemination, sex selection, embryo transfer, cloning and selfing in dairy cattle. In New Technologies in Animal Breeding. Edited by G. Seidel. Academic Press.

Willadsen, S. M. 1979. A method for culture of micro-manipulated sheep embryos and its use to produce monozygotic twins. Nature 277:298-300.

Table 1. Estimated genetic change and genetic lag in a conventional progeny testing improvement program.

	Age at birth of progeny (years) A	Genetic superiority (SD units) I	Genetic superiority (years) G = I/R	Genetic lag (years) G-A	
Bulls to breed bulls (bb)	6.5	1.05	10.1	3.6	2.0
Cows to breed bulls (cb)	6.5	0.71	6.8	0.3	
Bulls to breed cows (bc)	7.5	0.72	6.9	-0.6	-2.0
Cows to breed cows (cc)	4.5	0.11	1.1	-3.4	

Annual genetic change = $R = \frac{1.05 + 0.71 + 0.72 + 0.11}{6.5 + 6.5 + 7.5 + 4.5} = 0.104$ SD units.

Table 2. Schedule for MOET: juvenile and adult schemes.

Month	Juvenile scheme	Adult scheme
1	Born	Born
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13	Select on pedigree, MOET	
14		
15	Mate	Mate
16		
17		
18		
19		
20		
21		
22	MOET progeny born	
23		
24	Calve	Calve
25		
26		
27		
28		
29		
30		
31		
32		
33		
34	Complete lactation, select	Complete lactation, select ♂ and MOET
35	MOET progeny for MOET	
36		Mate for further lactations
37		
38		
39		
40		
41		
42		
43		
44	MOET progeny born	MOET progeny born
Generation interval	22 months = 1.83 years	44 months = 3.67 years

Table 3. Parameters and symbols.

Heritability	h^2	(0.25)
Repeatability	t	(0.35)
Generation interval (years)	L	$(L_m+L_f)/2$
Transfers per year	T	
Progeny at selection, per year	sT	(s=0.5)
Donor females per male	x	
Progeny at selection, per donor	y	
Donors per year	D	(sT/y)
Effective (selected) donors (Juvenile scheme)	D*	(2D/y)
Sires per year	S	(D/x)
Inbreeding rate per year (approximate)	ΔF	$\frac{1}{8L^2}(\frac{1}{S}+\frac{1}{D^*})$
Identicals per embryo	v	

Table 4. Annual genetic change with MOET[a] (in phenotypic standard deviation units)

Comparison of 1) selection on dam record versus index selection including relatives and 2) selection on only one breeding male per sibship (upper values) versus all males from the best sibships (Lower values).

				Female selection			
				Juvenile scheme		Adult scheme	
			Number of males selected per sibship	Dam record	Index[b]	Dam record	Index[b]
Male selection	Juvenile scheme	Dam record	1	0.100	0.116	0.076	0.117
			all	0.120	0.136	0.090	0.130
		Index	1	0.120	0.136	0.090	0.130
			all	0.148	0.164	0.108	0.149
	Adult scheme	Dam record	1	0.079	0.089	0.066	0.097
			all	0.097	0.108	0.080	0.110
		Index	1	0.119	0.130	0.097	0.127
			all	0.152	0.163	0.121	0.152

[a]MOET; 8 progeny per donor, 8 mates per sire.

[b]Index ; as shown in the Appendix.

Table 5. Annual genetic change and inbreeding rate (per 1000 transfers) for several possible MOET systems. Both males and females are selected on the appropriate index

		Donors per male[c]											
		8				16				32			
		Progeny per donor				Progeny per donor				Progeny per donor			
Male	Female	4	8	12	16	4	8	12	16	4	8	12	16
Annual genetic change (SD units x 1000)													
J[a]	J	110	136	150	158	127	153	166	175	142	168	181	189
J	A	097	130	147	158	109	142	159	170	120	152	168	179
A	J	109	130	141	148	130	150	161	168	148	168	178	185
A	A	099	127	141	150	116	143	156	165	130	156	170	179
Inbreeding rate[b] per year (% x 100) (per 1000 transfers/year)													
J	J	30	72	125	191	54	119	197	287	102	215	340	478
J	A	12	24	36	48	23	45	68	90	44	88	131	175
A	J	13	32	56	85	24	53	88	127	45	96	151	212
A	A	7	13	20	27	13	25	38	51	25	49	74	

[a] J = Juvenile, A = Adult.

[b] For comparison, the normal inbreeding rate in a national progeny testing scheme may be about 1% per year, corresponding to 10 units in the table.

[c] Only one male (or equivalent) selected per sibship.

Table 6. Possible rates of annual genetic change (in SD units) with MOET and embryo splitting (with T, 2T, 4T or 16T transfers).

Embryo splitting		Donors per male											
		8 Embryos per donor				16 Embryos per donor				32 Embryos per donor			
Male	Female	4	8	12	16	4	8	12	16	4	8	12	16
J[t]	J												
	X1	110	136	150	158	127	153	166	175	142	168	181	189
	X2	121	148	161	170	139	165	178	187	154	180	193	202
	X4	130	157	171	179	148	175	188	197	164	191	204	213
	X16	141	169	182	191	160	188	201	210	176	204	218	227
J	A												
	X1	097	130	147	158	109	142	159	170	120	152	168	179
	X2	107	142	159	170	119	153	170	181	130	163	180	191
	X4	115	151	168	179	127	163	180	191	138	173	190	202
	X16	124	162	180	191	137	174	192	204	148	185	203	215
A	J												
	X1	109	130	141	148	130	150	161	168	148	168	178	185
	X2	117	137	148	155	137	158	168	175	156	175	186	192
	X4	122	143	153	160	143	163	173	180	161	181	191	198
	X16	127	148	159	165	148	168	179	185	166	186	197	203
A	A												
	X1	099	127	141	150	116	143	156	165	130	156	170	179
	X2	107	135	149	158	123	151	164	174	137	164	178	187
	X4	113	141	155	165	128	157	171	180	142	170	184	193
	X16	118	148	162	172	134	163	178	187	147	177	191	200

[t]J = Juvenile, A = Adult.

Table 7. Proposed MOET improvement program, using the adult (AA) scheme, with 1024 transfers per year (70% conception, 70% survival) with 8 progeny per donor at selection and 16 donors per male.

	Per period (3 months)	Per year
Transfers	256	1024
Calves born	179	716
Bulls for semen freezing	16(64)[a]	64(256)
Heifers lactation 1	64	256
Donors	16	64
Cows lactation 2	16	64
Cows lactation 3	16	64
Cows lactation 4	16	64
Bulls used	1(4)+2(8)[b]	4(16)

[a] 1 bull (or 4 bulls) frozen per full sibship.

[b] From 2 previous periods.

Generation interval = 3.7 years.

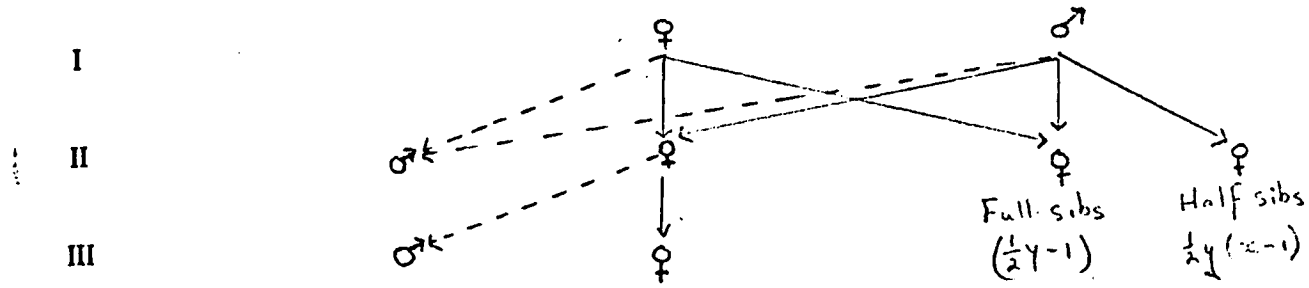
Inbreeding rate approximately

$$\frac{1}{8}\frac{1}{(3.7)}2\left(\frac{1}{4}+\frac{1}{64}\right) = 0.24\% \text{ per year.}$$

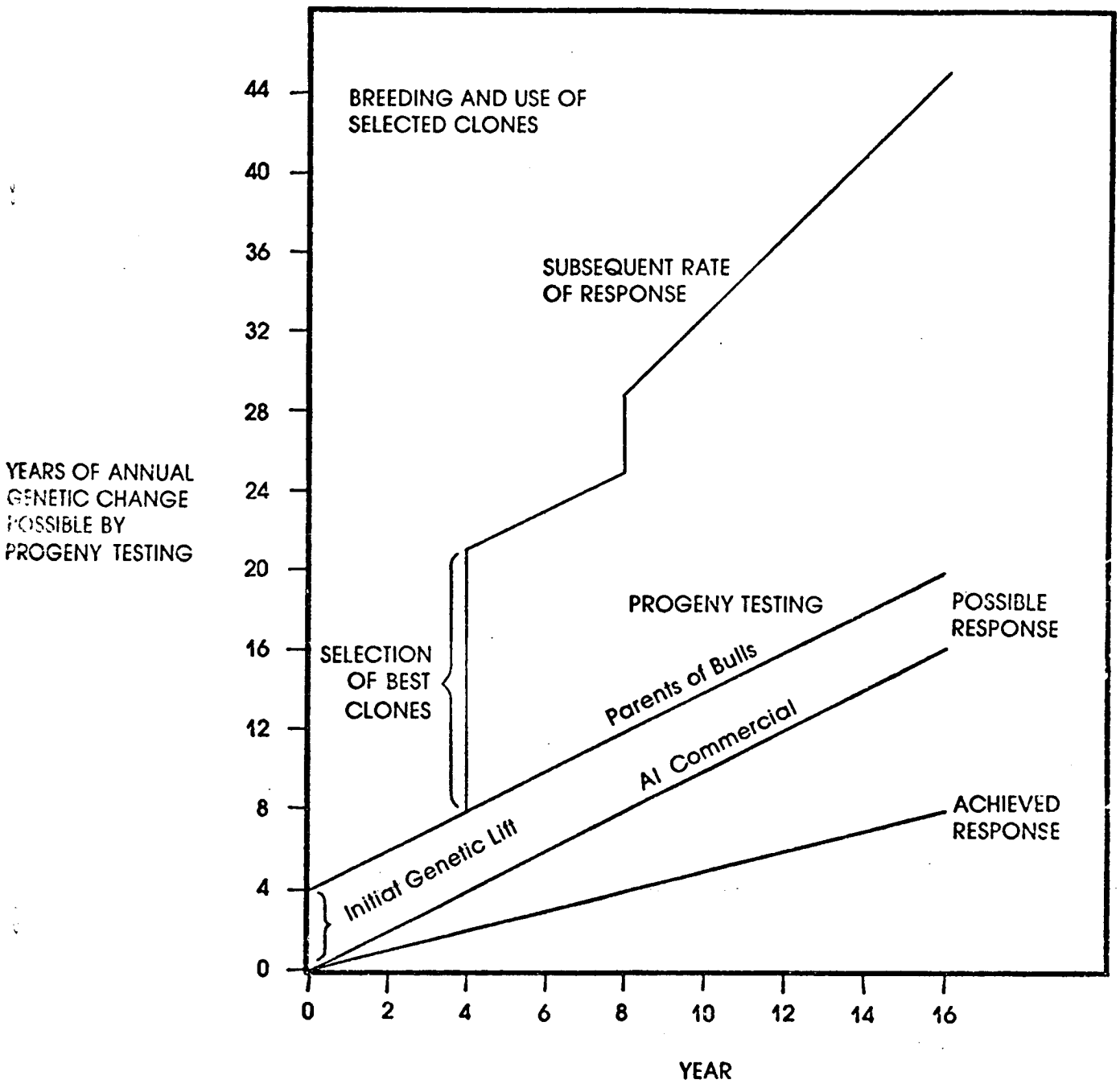
Annual genetic change = 0.129 SD units/year.

Figure 1

Generation



Scheme	Candidates for selection	Age at selection	Method of selection	Selection criteria
Juvenile	III ♂, or III ♀	1 year	Dam record Index	II ♀ (1 record) I ♀ (3 records) II ♀ (1 record) II ♀ Full sib aunts (~~y/2~~ x 1 record) (½y-1) II ♀ Half sib aunts ((x-1)y/2 x 1 record)
Adult	II ♂, or II ♀	2.9 years	Dam record Index	I ♀ (3 records) I ♀ (3 records) II ♀ (1 record) II ♀ Full sibs (~~y/2~~ x 1 record) (½y-1) II ♀ Half sibs ((x-1)y/2 x 1 record)


YEARS OF ANNUAL GENETIC CHANGE POSSIBLE BY PROGENY TESTING
44
40
36
32
28
24
20
16
12
8
4
0
BREEDING AND USE OF SELECTED CLONES
SUBSEQUENT RATE OF RESPONSE
PROGENY TESTING
POSSIBLE RESPONSE
SELECTION OF BEST CLONES
Parents of Bulls
AI Commercial
Initial Genetic Lift
ACHIEVED RESPONSE
0
2
4
6
8
10
12
14
16
YEAR

Appendix

Example. Matrix to derive a selection index for female II ♀ in Figure 1 for a MOET adult (A) scheme.

Phenotypic matrix (Standardized)

Dam[a] I	Donor[b] II	Full-sibs	Half-sibs	Genetic vector Donor II
$\frac{1+(d-1)t}{d}$	$\frac{1}{2}h^2$	$\frac{1}{2}h^2$	0	$\frac{1}{2}h^2$
$\frac{1}{2}h^2$	1	$\frac{1}{2}h^2$	$\frac{1}{4}h^2$	h^2
$\frac{1}{2}h^2$	$\frac{1}{2}h^2$	$\frac{1+(n-1)\frac{1}{2}h^2}{n}$	$\frac{1}{4}h^2$	$\frac{1}{2}h^2$
0	$\frac{1}{4}h^2$	$\frac{1}{4}h^2$	$\frac{1+(n-1)\frac{1}{2}h^2+n(x-1)\frac{1}{4}h^2}{nx}$	$\frac{1}{4}h^2$

[a] Dam I with d records. Others all with 1 record.
[b] Female has n=y/2 full sibs and n(x-1) half sibs.

Figure 1.

Pedigree showing the relationships between candidates for selection and relatives from whom milk production records are available. Definitions of x and y are given in Table 3.

Figure 2.

Possible genetic response from the breeding and use of selected clones compared with that possible from progeny testing.

"Possibilities with embryo transfer and splitting in dairy cattle improvement"

Questions and Answers

1. P. Miller

What assumptions were made for the pedigree and sib selection schemes regarding achieved response to selection compared with theoretical maximum?

C. Smith

The figures presented are for theoretically possible genetic changes with the embryo transfer schemes. These were compared with theoretically possible changes with national progeny testing programs. However, the arguement was make that with a controlled small embryo transfer scheme, a higher proportion of the possible changes might be achieved in practice since there would be better standardisation and recording and less loss in selection differential due to attention payed to traits of little economic importance.

2. J. W. Hardiman

Do you think embryo transfer would offer a significant advantage to the swine breeder?

C. Smith

No. The pig already has a good reproductive rate, so only a little extra would be gained. I've estimated this in a paper in Livestock Production Science. Even then very large facilities are required, and it would be unlikely to be economically worthwhile.

3. A. W. Nordskog

Assuming embryo transfer will increase genetic gain by, say a factor of 2, over gains from conventional breeding methods, this would, of course, be beneficial to the consumer, but what is it's benefit to the producer?

C. Smith

Yes, the main and long term benefit is to the consumer in terms of the more efficient production of human food. The producer would benefit from early use of improved stocks in competition with other producers (and countries) and the industry would benefit in competition with other products, and so in staying in production.

4. G. W. Friars

How did you estimate the standard deviation due to drift?

C. Smith

The standard error of the estimate of the predicted genetic change is calculated from the genetic drift variance. With a generation interval of 4 years, and 4 males and 64 females per year, the generation effective size is about 60. The drift variance is thus $h^2\sigma p^2/60$. The response per generation is about $4x0.13\sigma \pm \sqrt{.25/60}\sigma$, that is $.52\sigma \pm 0.065\sigma$. Of course, drift becomes less important with time since the response increases as t (time) and the drift standard error as $\sqrt{t}$.

5. K. Goodwin

What is the basis for your estimate of 2.3% genetic gain per year in pigs?

C. Smith

The estimate of a 2.3% genetic gain per year in lean tissue food conversion ratio for British tested pigs is based on deviations from two control herds (maintained at two Universities), over a 7 year period of comparisons at UK control testing stations. Details are in press in Animal Production.

6. P. Miller

How many such elite populations should operate in a country such as the US?

C. Smith

Theoretically only one elite MOET population is necessary; if you discount the risks and are sure of your breeding objectives. However, it would be useful to have several units in competition with one another, whether nationally supported or financed by breeding groups such as your own. The US could easily support or warrant 10-15 such units. The other advantage would be to select in the different units for different objectives (high v average fat percent) or different conditions (concentrate v pasture feeding) or for dual purpose v. dairy cattle. Currently everyone is breeding for the same objectives with the same genetic base. Operation of several schemes would allow diversity not possible on a national progeny testing system, and might cover some of the risks of having changing requirements negate some of our current improvements.