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PREDICTION OF GENETIC CHANGES IN SMALL CLOSED CATTLE  
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Gwang-Joo Jeon

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**PREDICTION OF GENETIC CHANGES IN SMALL CLOSED CATTLE POPULATIONS  
EMPLOYING MULTIPLE OVULATION AND EMBRYO TRANSFER TECHNIQUES**

By

Gwang-Joo Jeon

A DISSERTATION

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## ABSTRACT

### PREDICTION OF GENETIC CHANGES IN SMALL CLOSED CATTLE POPULATIONS EMPLOYING MULTIPLE OVULATION AND EMBRYO TRANSFER TECHNIQUES

By

Gwang-Joo Jeon

Breeding schemes employing multiple ovulation and embryo transfer techniques promise a greater rate of genetic response than current AI progeny testing schemes. This is due to shorter generation intervals, higher intensity in selecting cows for replacements, more progeny from genetically superior females, and potential for more intensive control on selection criteria relative to large populations such as entire U.S.

This study examined genetic changes and random genetic drift in three small closed dairy cattle populations using a stochastic simulation model. Results from the stochastic simulation were compared to those from the deterministic models.

Two populations with 88 breeding females and one population with 352 breeding females using multiple ovulation and embryo transfer breeding schemes were generated by stochastic simulation. Selection was strictly for first lactation milk yield. Ignoring and restricting inbred matings were also examined for their impact on genetic responses.

In closed finite populations, effective population size, inbreeding, and linkage disequilibrium have major influences on genetic responses and genetic drift. The reduction in genetic variation due to

inbreeding and linkage disequilibrium was taken into account in the simulation. The results indicated that strict restriction on inbreeding slowed genetic progress but was less of a problem in a larger population. The smaller population, ignoring inbred matings, showed a rapid rate of inbreeding. Linkage disequilibrium reduced genetic variation as significantly as inbreeding in the three populations.

Genetic responses and drift in small closed populations were also estimated by deterministic models and then compared with those from stochastic simulation results. In deterministic models, Rendel and Robertson's equation and gene flow model were modified to account for reduced accuracies and heritabilities due to inbreeding and linkage disequilibrium in each generation. Generally, deterministic models gave similar estimates to stochastic models for genetic responses. Reduction of genetic variation due to linkage disequilibrium is as important as that due to inbreeding. When conservative restriction on inbreeding was applied in the mating schemes to a small herd, deterministic methods did not give similar estimates to stochastic models for genetic responses in later generations.

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## 1. INTRODUCTION

Traditionally, the main concern of animal breeders have been maximum improvement of animals' genetic potential, which returns the most profit to them. The maximum improvement of genetic potential requires several factors such as proper statistical procedures to accurately rank animals and good managerial practices to allow animals to express their genetic ability. In general, any breeding program should be judged in several ways, not only the maximum improvement of the traits but also the monetary returns from the improved traits (Hill, 1971).

Recently, new technology termed multiple ovulation and embryo transfer (MOET), has been developed with the potential to a faster genetic progress than artificial insemination (AI) progeny testing schemes. From theory of genetic progress formulized by Rendel and Robertson (1950), which was initially based on the selection index by Hazel (1943), genetic progress is described as a function of selection intensity, accuracy of the evaluation, genetic variation, and generation interval for each transmitting path of genetic materials. Among these factors, MOET breeding scheme should most benefit selection intensity and generation interval. A major advantage of MOET is that several progeny from selected parents utilizing genetically inferior cows as recipients. As a consequence, the selection intensity of cow to cow path becomes much higher than the conventional AI progeny testing scheme.

The study of MOET breeding schemes in comparison to the conventional AI progeny testing scheme has been done using empirical

simulation by several people. They showed that the genetic progress from a MOET scheme was much greater than that from the conventional AI breeding scheme. Many studies using the formula of Rendel and Robertson's equation or gene flow model using transition probability method in estimation of genetic responses has been neglected for the effect of inbreeding and linkage disequilibrium. The inbreeding and linkage disequilibrium, however, substantially reduce the genetic variation depending on the population size and selection intensity. This may partially explain the discrepancy between the realized and the estimated genetic changes (Ven Vleck, 1981). Especially, in a small finite population, inbreeding and linkage disequilibrium should be closely monitored.

This study was divided into two investigations:

- (1) Stochastic simulation modeling of small closed populations using MOET techniques was studied to examine genetic changes considering the reduction in variance due to inbreeding and linkage disequilibrium.
- (2) Comparison between stochastic and deterministic models in estimation of genetic changes with and without consideration of inbreeding and linkage disequilibrium.

## 2. REVIEW OF LITERATURE

2.1 INTRODUCTION: In traditional AI progeny testing breeding schemes, selection of future parents requires two stages which takes approximately 6 years on average: In the first stage, parents are selected based on their pedigree information and in the second stage they are re-evaluated based on their own or progeny performance. Due to the limitation of single progeny from females in conventional AI progeny testing scheme, genetic improvement is achieved mainly through the use of thousands units of semen from selected sires.

Recently, a new technology called MOET, termed by Nicholas and Smith (1983), has been developed and implemented in some commercial herds. MOET schemes have a promising feature based on theory. The main advantages of MOET application to a population are; 1) more offspring from selected females 2) reduced generation intervals 3) easier to transport embryos than adult animals 4) new borns have easier adaptation to the environment of herds than adult animals 5) quick test for a carrier of recessive traits due to short generation intervals 6) reduced risk of disease transmission 7) increase numbers of rare or endangered species. Several authors (proposed application of MOET breeding schemes and reported faster genetic responses than conventional AI progeny testing populations (Nicholas, 1977, Van Vleck, 1977, Nicholas and Smith, 1983, Ruane, 1988)).

2.2 MULTIPLE OVULATION AND EMBRYO TRANSFER (MOET): The initial embryo transfer was conducted in a rabbit as early as 1891. Up to 1971, most embryo transfer work has been done as a laboratory tool for the study

of reproduction. Since 1975, embryo transfer has become an acceptable tool for use in cattle breeding (Critser et al., 1980). This acceptability is partly due to the nonsurgical collection technique. Multiple ovulation and embryo transfer involves several procedures (Seidel, 1989).

2.2.1 SUPEROVULATION: When a heifer is born, the ovary contains about 200,000 oocytes. These oocytes are formed during fetal development. After birth, no new oocytes are made. Those present degenerate and disappear from the ovary by puberty. This process of degeneration is called atresia, which continues throughout life. Superovulation is defined as the treatment of a female with the hormones that cause more ova to be ovulated at one time than normal. One hormone used is follicle-stimulating hormone (FSH) which is secreted by the pituitary gland located at the base of brain. Another is pregnant mare's serum gonadotropin (PMSG). Superovulation is also called multiple ovulation. Timing of superovulation depends on the estrous cycle which varies from cow to cow. The time to induce superovulation, for example, is day 15 if a cow will have a 19-day cycle, or at day 19 if she has a 23-day cycle.

2.2.2 EMBRYO RECOVERY: About 5 days after superovulation with FSH hormone, artificial insemination is conducted. If the semen and eggs meet at the proper time fertilization occurs. The fertilized egg is called an embryo. In cattle, embryos are recovered 6 to 8 days after estrus. After 9 days, recovery and pregnancy rates are slightly

reduced. Embryo recovery is usually by a nonsurgical method. The success of embryo recovery depends not only on the age of embryo but also on the technique and the skill of the technician. About 50 to 80% of embryos are recovered.

2.2.3 STORAGE OF EMBRYO: If recovered embryos must be immediately transferred, This should be done between 20 min to 24 hr. In most cases, it is necessary to store embryos until appropriate recipients are available. To maintain the viability of embryo is important. For short-term storage, they are usually kept under 0 to -10 degree Celsius for several days without much loss of viability. For long-term storage, they are deep-frozen in liquid nitrogen at -196 degree Celsius.

2.2.4 RECIPIENTS: The recipients are not necessarily genetically inferior cows. They must be in good health including fertility, conformation, and milking ability. In general, there are more losses of calves from heifer recipients than cow recipients.

2.3 MOET BREEDING SCHEMES: Ruane (1988) made a good review on various MOET breeding schemes. In the conventional AI progeny testing scheme, the bull to bull path contributes most to the genetic improvement. MOET breeding schemes improve the genetic progress through the increase in the reproductive rate of the female allowing a larger emphasis on selection of female candidates. As a consequence, selection intensity of the cow to bull path increases because fewer cows are



required to obtain the bulls for progeny testing.

Land and Hill (1975) examined the potential genetic progress of growth rate in beef cattle employing MOET. In their scheme, cows and bulls were assumed to have the first progeny at 2 years of age and 90 % of cows calving any year survived to the following year. If the embryo does not survive, then, the recipient received a second transfer. All recipients were assumed fertile. The main advantage in the scheme was the number of calves reared from each donor cow. They reported that the growth rate by MOET can be almost twice the conventional performance testing program.

Petersen and Hansen (1977) studied the MOET aspect in bull to cow path in dual cattle populations, where selection emphasis was on butterfat and growth rate. By doubling the number of sons per dam, which resulted in halving the number of selected cows, there was about 8% increase in butterfat yield.

Nicholas (1979) first examined the potential genetic progress by MOET in dairy cattle. In his scheme, females were selected based on their dam's first lactation record and generation interval was assumed 2 years. This resulted in relatively a lower accuracy of .25. Males were selected based on their dam's first lactation record, or a family index using full-sib, half-sib, and dam's first record. All schemes obtained higher genetic responses than the conventional AI progeny testing scheme.

Following Nicholas's work (1979), Nicholas and Smith (1983) were first to examine two MOET schemes that they termed Juvenile and Adult schemes. The basic principle of the juvenile and adult schemes are

equivalent to the first and second stage selection, respectively, of conventional AI progeny testing scheme. The generation interval for juvenile scheme is slightly less than 2 years. This is about one third that of conventional AI progeny testing scheme. The generation interval for their adult scheme was 3.7 years. The results showed that by using various numbers of progeny per donor and numbers of donors per sire, the genetic responses from both juvenile and adult schemes, or combination of two schemes exceeded the genetic responses from the conventional AI progeny testing scheme by up to 80 percent.

Powell (1981) studied the effects of embryo transfer resulting in additional progeny information on evaluation of cows and bulls. He showed that the repeatability of cow index increased from .43 for a cow having one daughter to .49 for 10 daughters. He also pointed out that ET can be used in cow evaluations to increase the number of full-sib and half-sib records, which eventually shorten the generation interval because the use of 3 full-sibs and 12 half-sibs gives about the same accuracy as cow's own 3 records (Ruane, 1988).

McDaniel and Cassel (1981) investigated the impact of ET on genetic progress and concluded that ET can increase cow index dollars up to 17% when 10 offspring per dam were obtained versus one offspring. For herd replacements, percentage of cows to maintain herd size is significantly reduced to 3.5 % when 20 offspring per dam is possible.

Juga and Maki-Tanila (1987) studied the effect of various number of donors per sire and number of sires used. They reported that selecting only one sire used on all cows obtained less than one percent of genetic progress more than conventional AI progeny testing breeding

scheme per year. They suggested the optimum breeding design was adult MOET scheme with selection of 2 sires and 16 donors per sire, which resulted in 1.26 % increase per year.

Wooliams and Smith (1988) re-examined the work of Nicholas and Smith (1983), where information on paternal pedigree was not included in the index. They suggested inclusion of this information increased the selection response in juvenile scheme 25 to 30%. They also studied the effect of including indicator traits. Indicator traits are defined as those traits which give indirect information on the traits being selected. For example, blood urea nitrogen (BUN) as indicator trait for milk yield. The value of indicator traits depends on the magnitude of the co-heritability which is defined as genetic correlation between two traits times the corresponding heritabilities of the two traits. The use of indicator traits may also allow earlier selection in both male and females, which makes the generation intervals shorter.

Bradford and Kennedy (1980) pointed out that there exist some difficulties in selection of potential bull-dam donors because they are at the extreme edge of the phenotypic distribution. Cunningham (1976) mentioned that the underlying genetic distribution of selected bull-dams may not follow the normal distribution due to the intensive selection.

**2.3.1 ACCUMULATION OF INBREEDING:** Since MOET breeding schemes produce more than one progeny from the selected parents, more full-sibs and half-sibs are expected than with conventional AI progeny testing schemes. This increases the rate of inbreeding. The effects of

inbreeding are two: 1) reduction in variance and 2) inbreeding depression. The higher level of inbreeding in the population causes animals to be more related and thus, the population is less variable. Since the variation is key in selection, less variation may slow the rate of genetic progress. The inbreeding depression refers to the reduction of mean phenotypic value of the characteristics connected with reproduction or physiological efficiency. With the usual dominance model of inbreeding depression, there exist a linear relationship between inbreeding coefficient and performance in unselected populations (Hill, 1986). Hill also pointed out that the effect of population size ranging from 10 to 160 animals are trivial for 5 generations. The rate of inbreeding is directly associated with the effective population size. This was first introduced by Wright (1931). The restriction of population size increases the homozygosity within the population and is introduced in terms of the concept of the idealized random breeding population, which is known as the effective population size.

Under selection and artificial insemination, the inbreeding coefficient in a population is much higher than that estimated from the random mating population of equal size, because parents do not contribute to the next generation equally (Toro et al., 1988). Robertson (1961) pointed out that inbreeding under individual selection is expected to be much greater than that calculated from the actual number of parents when both heritability of the trait and selection intensity is high.

With no selection and random mating of parents, the rate of

inbreeding is simply defined as (Falconer, 1980):

$$\Delta F = 1/(4N_m) + 1/(4N_f)$$

where  $N_m$  and  $N_f$  are number of selected males and females. Then, the level of inbreeding in the  $t^{\text{th}}$  generation becomes:

$$F_t = 1 - (1 - \Delta F)^t$$

where  $F_t$  is the average inbreeding in the  $t^{\text{th}}$  generation. In reality, random mating without selection would not be practiced in commercial herds. Therefore, the inbreeding rate by the formula above is expected to be much less than the realized inbreeding rate.

Another formula for annual expected inbreeding was given by Hill (1972):

$$\Delta F = (1/N_m + 1/N_f)/(8 \times L^2)$$

where  $L$  is an average generation interval of males and females. These two formulae assume that the generations are discrete and selected parents have the equal probability of contributing to the next generation. However, the rate of inbreeding in overlapping generations equals the rate of inbreeding in discrete generations if the the number of individuals entering the population each generation and the variance of lifetime family size are equal (Fewson and Nitter, 1987). Johnson (1977) developed a method for estimation of inbreeding using a transition probability matrix method (Hill, 1974):

$$F_{(t+1)} = P F_t P' + D$$

where  $P$  is a matrix specifying the path of genes between the different age groups and has a stochastic nature; and  $D$  is a diagonal matrix whose elements depend on the number of individuals in each age group. This formula, however, does not take into account the complex situation

of the four pathways of transmitting genetic materials. Fewson and Nitter (1987) designed a formula to estimate the rate of inbreeding in a single cycle selection of the four pathways:

$$\Delta F = P'QP$$

$$= \begin{bmatrix} 1/4 & 1/4 & 1/4 & 1/4 \end{bmatrix} \begin{bmatrix} 1/2N_{mm} & 1/2N_{mf} & & \\ 1/2N_{mf} & 1/2N_{mf} & & \\ \hline & & 1/2N_{fm} & 1/2N_{ff} \\ 0 & & 1/2N_{ff} & 1/2N_{ff} \end{bmatrix} \begin{bmatrix} 1/4 \\ 1/4 \\ 1/4 \\ 1/4 \end{bmatrix}$$

$$= 1/32(1/N_{mm} + 3/N_{mf} + 1/N_{fm} + 3/N_{ff})$$

where P can be extended such that for an example, male to male (mm) path can be subdivided into a group of young bulls (q proportion) and the proven bulls (1-q proportion) and young cows with a proportion of r and an old cows with a proportion of (1-r). Then, P' is redefined as:

$$P' = [.25s \ .25(1-s) | .25q \ .25(1-q) | .25 | .25r \ .25(1-r)]$$

As a consequence, Q becomes a size of 7x7 matrix.

Toro et al. (1988) examined four different methods of mating policy for the minimization of inbreeding; 1) random mating (RM) 2) minimum coancestry (MC) 3) weighted selection (WS) and 4) the combination of MC and MS (MW). They found the MW system gives the lowest inbreeding coefficient of the methods.

**2.3.2 LINKAGE DISEQUILIBRIUM:** Selection in the parental generation creates a reduction of variance in the progeny generation. This is known as linkage disequilibrium, or gametic phase disequilibrium (Falconer, 1981). The consequence of reduced variance

due to parental selection can be simply viewed as the distribution theory. Since only the right tail-side of parental population is selected as parents, the distribution of these selected parents is no longer the same as the original population. The reduced variance due to selection can be denoted (Falconer, 1981):

$$V(p)' = (1-k)V(p)$$

where  $V(p)'$  is the phenotypic variance in the selected parents;  $V(p)$  is the phenotypic variance in the whole population;  $k$  is the reduction factor and redefined as  $i(i-x)$ , where  $i$  is the selection intensity and  $x$  is the deviation of the truncation point from the population mean in standard deviation units. Then, the reduced genetic variance of  $V(g)'$  equals  $(1-kh^2)V(g)$ .

Bulmer (1971) derived the linkage disequilibrium in more detail by regressing the progeny on parents:

$$y = a + bP_1 + bP_2 + e$$

where  $a$  is an intercept;  $b$  is a regression weight; and  $e$  is error.

Taking the variance ( $V$ ),  $V(e)$  is  $(1-.5(h^2)^2)V(y)$ , where  $V(y)$  is a total phenotypic variance. The equality of  $V(e)$  and  $(1-.5(h^2)^2)V(y)$  is defined by rewriting the above equation:

$$y = a + b(P_1 + P_2) + e$$

By knowing that the covariance between an offspring and one parent is  $(1/2)h^2V(y)$ , then,

$$\text{Cov}(y, P_1+P_2) = h^2V(y)$$

$$V(P_1+P_2) = 2V(y), \text{ therefore,}$$

$$\begin{aligned} b &= \text{Cov}(y, P_1+P_2)/V(P_1+P_2) \\ &= .5h^2 \end{aligned}$$

Then, the residual variance can be computed;

$$V(y) = b^2V(P_1+P_2) + V(e)$$

$$\begin{aligned} V(e) &= V(y) - 2b^2V(y) \\ &= (1-.5h^4)V(y) \end{aligned}$$

Finally, the variance in progeny generation after selection in parental generation becomes:

$$\begin{aligned} V(y^*) &= b^2V(P_1) + b^2V(P_2) + V(e) \\ &= 2b^2[V(y) + dV(y)] + V(e) \\ &= V(y) + .5(h^2)^2dV(y) \end{aligned}$$

where  $V(y^*)$  is a new variance after selection in parental generation.

The second term in the RHS of equation above,  $.5(h^2)^2dV(y)$ , is the amount of reduction in variance in progeny generation due to parental selection, where  $d$  is expressed as:

$$d = [V(y^*) - V(y)] / (.5(h^2)^2V(y))$$

This equation was extended to the situation of selection of several generations such that:

$$V(a)_1 = V(a)_0 + d_1$$

$$V(y)_1 = V(y)_0 + d_1$$

where  $V(a)_1$  and  $V(y)_1$  are additive genetic and phenotypic variance, respectively, available in the  $i^{th}$  generation;  $V(a)_0$  and  $V(y)_0$  are genetic and phenotypic variances, respectively available in the base generation; and  $d_{i+1}$  is  $.5d_i + .5(h^2)^2dV(y)_i$ .

Bulmer (1971) and Falconer (1981) derivations were restricted to the single trait. Tallis (1987) extended this to the situation where more than one trait is considered. His approach is the same ancestral regression approach as Bulmer's derivation (1971) but the solution



involves an iteration method.

**2.3.3 RANDOM GENETIC DRIFT:** The definition of random genetic drift is simply the random changes of the gene frequency. In small finite populations with random mating, the direction of change is unpredictable (Falconer, 1981). The random genetic drift is a joint function of effective population size, heritability of the traits, and selection intensity.

Hill (1974) showed the derivation for estimating the random genetic drift. For  $N_m$  males selected from  $M_m$  and  $N_f$  females selected from  $M_f$ , where  $M_m$  and  $M_f$  are total number of males and females, respectively, available for selection, the random genetic drift variance, then, can be computed as:

$$\sigma_d^2 = .25\sigma_a^2 \{ [1-(1-C_m)h^2]/N_m + [1-(1-C_f)h^2]/N_f \}$$

where  $C_m$  and  $C_f$  are coefficients of order statistics for selected males and females;  $N_m$  and  $N_f$  are number of selected males and females.

The importance of random genetic drift can be thought of as how much difference we can expect between the expected and the realized genetic responses. All breeders wish to minimize the difference. Nicholas (1980) reported that for a simple mass selection program with selection intensity of  $i$  and heritability of  $h^2$ , the size of population required for the coefficient of variation of genetic response to be  $\alpha$  after  $t$  generations can be approximated by a simple function,  $1/(\alpha i h)^2 t$ .

**2.4 PREDICTION OF BREEDING VALUES:** Methods of predicting breeding values have been developed from selection index method with best linear

prediction (BLP) to mixed model equation (MME) with best linear unbiased prediction (BLUP) properties.

In 1937, Smith first developed a selection index for plant design. In 1943, Hazel (1943) developed a selection index for livestock. In their initial studies, no statistical properties such as BLP were defined. Nevertheless, their derivation was proven as BLP, where B refers to best minimizing expected value of error squared, L refers to linear combination of records, and P refers to prediction. The property of BLP for selection index only holds if the records are completely adjusted for the known fixed effects. However, in Hazel's paper, the records were adjusted only for season and line of breed effects.

The selection index is conventionally denoted as:

$$I = b'x$$

$$H = a'g$$

where I is an estimate of true breeding value, H

b is a vector of unknown index weights

x is a vector of records of relatives adjusted for known fixed effects

H is a true breeding value

a is a vector of economic weights, or relative economic importance

g is a vector of true breeding values

Then, the index weights, b, are obtained by:

$$b = P^{-1}Ca$$

where P is a matrix of phenotypic (co)variances among the x

C is a matrix of covariances between x and g

Then, the estimated breeding value of the animal is  $b'x$ , which is an

estimate of H.

Due to its superiority of properties over selection index method, a mixed model equation of BLUP is currently the most common method for evaluation of animals' genetic merit.

In application of MME of BLUP, use of MME has evolved from sire model to animal model. Among these MME, animal model uses the least assumptions and is considered an ideal model among all MME of BLUP. The MME of BLUP was mostly developed by Henderson (1988). A rapid method of constructing the inverse of relationship matrix by Henderson (1976) made the model calculations more feasible in practice. The usual notation of MME is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

where  $\mathbf{y}$  is a vector of records

$\mathbf{b}$  is a vector of unknown fixed effect

$\mathbf{u}$  is a vector of unknown random effect

$\mathbf{e}$  is a vector of unknown random residual

$\mathbf{X}$  and  $\mathbf{Z}$  are known design matrices

The expectation and variances are:

$$\begin{array}{c|c|c|c|} \mathbf{E} & \mathbf{y} & - & \mathbf{Xb} \\ \hline & \mathbf{u} & & \mathbf{0} \\ \hline & \mathbf{e} & & \mathbf{0} \end{array} \quad \begin{array}{c|c|c|c|} \mathbf{V} & \mathbf{y} & - & \mathbf{Z'GZ} + \mathbf{R} \\ \hline & \mathbf{u} & & \mathbf{G'Z'} \\ \hline & \mathbf{e} & & \mathbf{R'} \end{array} \quad \begin{array}{c|c|c|} \mathbf{ZG} & \mathbf{R} & \\ \hline \mathbf{G} & \mathbf{0} & \\ \hline \mathbf{0} & \mathbf{R} & \end{array}$$

where  $\mathbf{G}$  and  $\mathbf{R}$  are known genetic and residual (co)variances and are positive definite. Then, the normal equation to solve for  $\mathbf{b}$  and  $\mathbf{u}$  are:

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{A}^{-1}\mathbf{G} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}$$

Usually, the problem of MME is the large number of equations due to the relationship matrix among animals. Thus, it is sometimes impossible to invert left hand side of the equation and therefore, the equation should be solved iteratively. In a study of a simulated pig population, Sorensen (1988) reported that selecting animals based on MME animal model increased the response about 15% larger than selection based on selection index, which was more beneficial when heritability is lower.

**2.5 PREDICTION OF GENETIC RESPONSES:** Rendel and Robertson (1950) derived the formula for prediction of genetic response based on selection index theory (Hazel, 1943). Genetic progress is a function of accuracy, selection intensity, genetic variability among animals, and generation interval:

$$\Delta G = i \times r_{TI} \times \sigma_a / L$$

where  $i$  is selection intensity,  $r_{TI}$  is accuracy or correlation between estimated and true breeding values,  $\sigma_a$  is additive genetic SD, and  $L$  is generation interval. The assumptions made in the equation above is quite moderate such that all parameters are kept constant over time and also the response is only from a single cycle of selection in a steady state. Therefore, this equation does not tell how many generations are required to reach the steady state. This problem was overcome by the gene flow model, which was based on transition probability matrix

method (Hill, 1974). The gene flow model does take into account the earlier fluctuation of genetic responses.

Most studies of predicting genetic responses have ignored the effect of inbreeding and linkage disequilibrium, which leads to overestimates of the selection responses. Modified equations for these two factors may considerably increase the accuracy of the prediction.

### **3. CHAPTER 1 Stochastic Modeling of Multiple Ovulation and Embryo Transfer (MOET) Breeding Schemes in Small Closed Dairy Cattle Populations**

#### **3.1 ABSTRACT**

Genetic changes and genetic drift in three small closed dairy cattle populations were examined by using a stochastic simulation model. Multiple ovulation and embryo transfer (MOET) and AI techniques were used in two populations with 88 breeding females and one population with 352 breeding females. Selection goal was maximum genetic improvement in milk yield. The reductions in genetic variation due to inbreeding and linkage disequilibrium were taken into account in the simulation. Strict restriction on inbred mating was found to slow genetic progress significantly in the small population but was inconsequential in the larger population. However, ignoring inbred mating in the smaller population caused a rapid accumulation of inbreeding coefficient. Linkage disequilibrium was as important as inbreeding in reducing genetic variation. Genetic drift was much smaller in the larger population.

#### **3.2 INTRODUCTION**

The techniques of multiple ovulation and embryo transfer (MOET) and basic considerations of their application in the genetic improvement of dairy cattle were outlined by Seidel and Seidel (1981) and Van Vleck (1981). A variety of MOET breeding schemes were suggested for dairy cattle in literature starting from juvenile and adult systems in closed populations by Nicholas and Smith (1983) to open systems in large populations by Christensen and Liboriussen (1986). Recently, Ruane

(1988) provided a thorough review on the use of MOET techniques in the genetic improvement of dairy cattle.

Nearly all studies have indicated that breeding schemes employing MOET techniques promised a greater rate of genetic response than current AI progeny testing schemes. This conclusion was based on the argument that MOET would lead to shortened generation intervals, more progeny from genetically superior females, higher intensity in selecting cows for replacements, and more focused selection criteria. However, the comparisons between breeding schemes were based on empirical results from deterministic models with infinite population theory. In prediction of genetic responses at low level of inbreeding, an infinite population theory may be satisfactory in finite populations (Hill, 1967). However, the main weakness in applying infinite population theory in a finite population is that genetic sampling cannot be accounted for. The well-known Rendel and Robertson's equation (1950) for the prediction of genetic response does not take into account inbreeding, linkage disequilibrium, or Bulmer effect (1971), which would reduce genetic variation substantially in finite populations. These weaknesses of using deterministic models to compare breeding schemes, especially infinite populations, can be overcome by using stochastic models. De Roo (1988) used a stochastic model to study breeding schemes in a small pig population, and a simulation study for MOET breeding scheme in dairy cattle was made by Juga and Maki-Tanila (1987). The stochastic model in our study included several improvements over previous models. The simulation approximated: realistic biological and managerial situations in a MOET dairy operation with regard to the

occurrence of breeding decisions and events, including the selection and stocking of semen and embryo banks, on monthly bases. Number of eggs produced per flushing would follow a Poisson distribution. The matings would not be random, but based on ranking from an animal model. Accumulation of inbreeding would be closely monitored and considered in mating decisions.

The specific objectives of this study were to examine genetic responses and genetic drift in small closed dairy cattle populations resulting from using breeding schemes which utilize MOET techniques with milk yield being the sole selection goal. A stochastic simulation model was used to generate results from MOET breeding schemes which were compared to current AI progeny testing breeding schemes. The influences of effective population size, inbreeding, and linkage disequilibrium on genetic variation, response and drift were also of interest.

### 3.3 METHODS

Three MOET breeding schemes in separate closed dairy cattle nucleus herds were simulated over a period of 144 months. Prior to that, however, base populations were established by random mating for 13 months. In all three schemes, the selection goal was genetic improvement in milk yield. The three MOET breeding schemes were:

- (1) MOET1: A total of six males and 88 females in the population. No restrictions were imposed to avoid inbred matings;
- (2) MOET2: Same population size as in MOET1, but matings that would produce inbreeding coefficient greater than .0625 for offspring



were not made.

(3) MOET3: A total of 24 males and 352 females in the population. Same restriction on inbreeding as used in MOET2.

*Parameters for simulation*

The parameters used in all three MOET breeding schemes were:

- (1) Trait: milk yield in first lactation;
- (2) Average milk production in base population: 7,500 kg;
- (3) Phenotypic standard deviation in base population: 1,498 kg;
- (4) Heritability: .4;
- (5) Conception rate: .7;
- (6) Sex ratio: .5;
- (7) Survival rate for males and females (from birth to breeding age): .7;
- (8) Number of eggs per superovulation of a cow: A Poisson distribution with mean five;
- (9) Minimum number of eggs in an egg bank: 50;
- (10) Mortality: .02 per month amongst cows older than 14 months of age; and
- (11) Maximum number of transferable eggs per selected male: 50.

Each of the three MOET breeding schemes was simulated stochastically and was randomly repeated five times. The results in each of the 144 months were used to calculate average genetic changes and genetic drift, which were compared to genetic change from a conventional AI progeny testing scheme for a large population. Theoretical annual genetic gain in a conventional AI population was .02 of population average (Van Vleck, 1981), i.e., 150 kg per year.

Realized genetic gain was assumed to be a third of the theoretical gain (Van Vleck, 1977), i.e., 50 kg per year.

### Simulation of Records

Records were generated by assuming an infinitesimal model (i.e., an infinite number of loci each with a small effect) by

$$y_i = \mu + a_i + e_i \quad [1]$$

where  $y_i$  = phenotypic lactation milk record of the  $i$ th animal;  $\mu$  = mean production of the population;  $a_i$  = additive genetic effect of the  $i$ th animal; and  $e_i$  = random residual. The breeding value of animal  $i$  if parents were unknown,  $a_i$ , was generated by

$$a_i = z\sigma_a, \quad [2]$$

where  $z$  is a random normal deviate and  $\sigma_a$  is the assumed additive genetic standard deviation, or was generated by

$$a_i = .5(a_{i(s)} + a_{i(d)}) + M, \quad [3]$$

where  $a_{i(s)}$  and  $a_{i(d)}$  are true breeding values of sire and dam of the  $i$ th animal and  $M$  is a deviation due to random mendelian sampling which was generated as

$$M = z(.5(1-\bar{F}))\sigma_a \quad [4]$$

where  $\bar{F}$  is the average inbreeding of the parents, and  $.5(1-\bar{F})$  accounts for the reduction of genetic variation due to inbreeding. The additive breeding value,  $a_i$ , was generated at the birth of animal  $i$ , and if she is female a phenotypic milk record was generated 12 months after her first calving. The environmental residual,  $e_i$ , in equation [1] was generated as  $e_i = z\sigma_e$  where  $\sigma_e$  is the assumed residual standard deviation. All the random deviates used in the study were generated from IMSL STAT/LIBRARY (1987).

### Base population

For each of the three MOET breeding schemes, initial unselected base populations can be considered as a random sample of a large unselected dairy population. A base population was generated with a uniform age distribution ranging from one to 23 months, and in gametic phase equilibrium state. Four females were generated per each month of age, and a fixed number of sires was used in the time period for establishing a base population.

The initial founder animals generated in a base population did not have lactation records, and selection could not be applied immediately. Therefore, animals in a base population were random mated for 13 months to allow them to have records for evaluation and selection. Female animals that were 14 months or older were mated while father-daughter matings were avoided. All births resulted in females and no mortality was allowed. At the conclusion of the 13 months, ages of animals would range from one to 36 months.

Starting from the 14th month, for each of the succeeding 144 months, selection and voluntary culling of animals would be based on their breeding values from an animal model. The number of founder animals in a base population was the size of its breeding population and would be kept constant.

### Evaluation of animals

Breeding values were evaluated every month based on their first lactation records using an animal model:

$$y = \mu 1 + Za + e \quad [5]$$

where  $y$  = a vector of the first lactation records;  $\mu$  = an unknown fixed

constant;  $\mathbf{a}$  = a vector of unknown random effects of additive breeding values for all animals in the population, male and female, with and without records;  $\mathbf{e}$  = a vector of random residuals; and  $\mathbf{l}$  and  $\mathbf{Z}$  = incidence matrices corresponding to  $\mu$  and  $\mathbf{a}$ , respectively. The expectation values and (co)variances were;

$$E \begin{bmatrix} \mathbf{y} \\ \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mu \mathbf{l} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \text{ and } \text{Var} \begin{bmatrix} \mathbf{y} \\ \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{ZAZ}'\sigma_a^2 + \mathbf{I}\sigma_e^2 & \mathbf{ZA} & \mathbf{I}\mu^2\mathbf{e} \\ \mathbf{AZ}'\sigma_a^2 & \mathbf{G} & \mathbf{0} \\ \mathbf{I}\sigma_e^2 & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where  $\mathbf{A}$  is an additive relationship matrix for all animals in  $\mathbf{a}$  including inbreeding coefficients. Mixed model equations were constructed using parameter value for  $\sigma_e^2/\sigma_a^2$ . The equations were solved by an iteration method. The solutions for  $\mathbf{a}$  would be used as selection criteria.

### Selection

The best bull among all young bulls of 14 months of age was selected in each month. His semen would be stored in a semen bank, and to be used to fertilize no more than 50 transferable eggs. This restriction should help to reduce the length of generation interval and the rate of inbreeding. Then the best bull of all bulls having semen in storage was used to breed the selected donor females.

The number of donors selected was dependent on the number of fertilized eggs available in the egg bank. The number of eggs in the egg bank was kept at a minimum of 50. For example, if the egg bank had 40 embryos, then two donors would be selected from all open cows that

were 14 months of age or older. The assumption was that the number of fertilized eggs per each superovulation averaged five but followed a Poisson distribution. However, even if the egg bank had 50 eggs or more, still one donor is selected to ensure the availability of superior genetic potential in that given month.

The selection intensity on either the males or females was impossible to enumerate, but they were a function of size of the semen and egg banks, number of eggs per superovulation, number of bulls and donors selected and number of transferable eggs fertilized per bull. These values varied from month to month.

### **Mating**

In all MOET breeding schemes, matings were done to maximize genetic gain in milk yield. However, in MOET2 and 3, those matings that would have resulted in progeny with inbreeding coefficients greater than .0625 were avoided.

This was accomplished by computing the inbreeding coefficients for offspring of all possible matings among selected males and donors. Only those matings which produced the highest expected breeding values but with inbreeding coefficients less than .0625 were chosen. Those conceived donors were flushed, and recovered fertilized eggs were stored in the egg bank. All embryos were ranked by their predicted breeding values, i.e., average of sire's and dam's breeding values. Then, top ranked embryos were transferred to all open cows and heifers each month.

## **Culling**

Involuntary culling was imposed on those cows that failed to conceive after three consecutive breedings. Also, a 2% mortality rate due to diseases and accidents was imposed on cows after completion of first lactation.

Voluntary culling was then practiced to keep the number of breeding females in the populations constant. When population size exceeded the capacity, those open cows that were in second or greater lactations were culled first. If culling was still needed, heifers were culled. Within each culling category of females, culling was done by the magnitude of predicted breeding values in ascending order. Those young bulls that were not selected at 14 months of age were culled. Selected bulls were culled after being used to produce 50 transferable eggs.

After the stochastic process in each of the three MOET populations was simulated over the course of 144 months and repeated for five times, inbreeding, linkage disequilibrium, and genetic response with random genetic drift variation were calculated.

## **3.4 RESULTS**

### ***Inbreeding***

One consequence of inbreeding is a decrease in production due to inbreeding depression. The model used in this study did not include nonadditive genetic effect and thus did not consider inbreeding depression.

Another consequence is reduced genetic variation which is a direct proportion of the average inbreeding coefficient in the population. If

genetic variance is reduced due to inbreeding, the loss would not be recovered unless foreign genetic material is introduced. The accumulation of inbreeding over 12 years in the three MOET populations simulated is presented in Figure 1. MOET1 population with 88 breeding females without restriction on inbreeding accumulated about 22.5% inbreeding after 12 years. MOET2 and MOET3 populations both with restriction on inbreeding reached 4.8% and 3.9%, respectively.

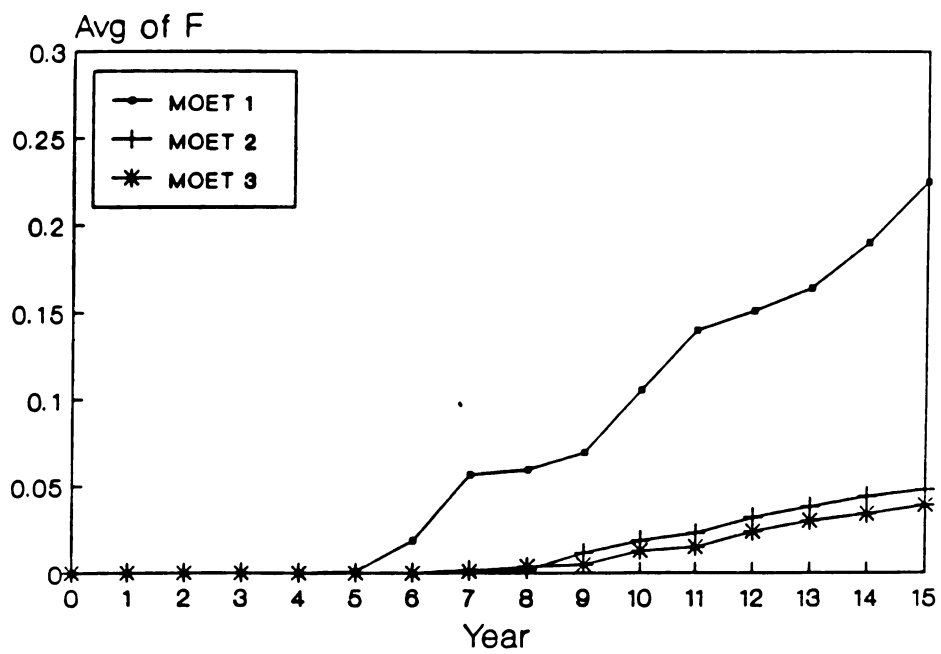


Figure 1. Accumulation of inbreeding in the three MOET populations for 12 years



Should MOET1 population be continued beyond 12 years, inbreeding would soon reach the point where selection would be ineffective due to severe loss of additive genetic variation. In MOET2 and MOET3 populations, genetically superior animals might not be selected due to the restriction on inbreeding, thus hindering the progress of genetic merit in these populations. The breeding scheme in both MOET2 and MOET3 was the same, but MOET3 had a lower rate of inbreeding simply due to a larger population size. The rate of inbreeding in all three MOET populations followed approximately a linear trend.

#### *Linkage disequilibrium*

Selection of parents leads to a reduction of variance in the progeny generation by generating gametic phase disequilibrium, or linkage disequilibrium (Bulmer, 1971). The effect of linkage disequilibrium on additive genetic variance at time  $t$  was expressed as:

$$\sigma_{a(t)}^2 / (1 - \bar{F}) \sigma_{a(0)}^2$$

where  $\sigma_{a(t)}^2$  was the genetic variation at time  $t$ ;  $\sigma_{a(0)}^2$  was the initial genetic variation in the base population; and  $\bar{F}$  was the average inbreeding coefficient in the population at time  $t$ . With increasing selection intensity, a larger reduction of genetic variance due to linkage disequilibrium is expected. The MOET3 population has the largest number of breeding animals, which gave a higher selection intensity on males than MOET1 and MOET2. This resulted in the largest reduction in genetic variance due to linkage disequilibrium of 20.5% for MOET3. The linkage disequilibrium in MOET1 and MOET2 were 17% and 16.8%, respectively.

The amount of genetic variation in each year varied as shown in

Figure 2, 3 and 4. In MOET2 and MOET3, if top ranking bulls could not be used because of restriction on inbreeding in the progeny, bulls from previous generations, who might not be intensively selected, were used, hence more genetic variation among progeny. This should explain why MOET2 showed more fluctuation of genetic variation than MOET1 and MOET3.

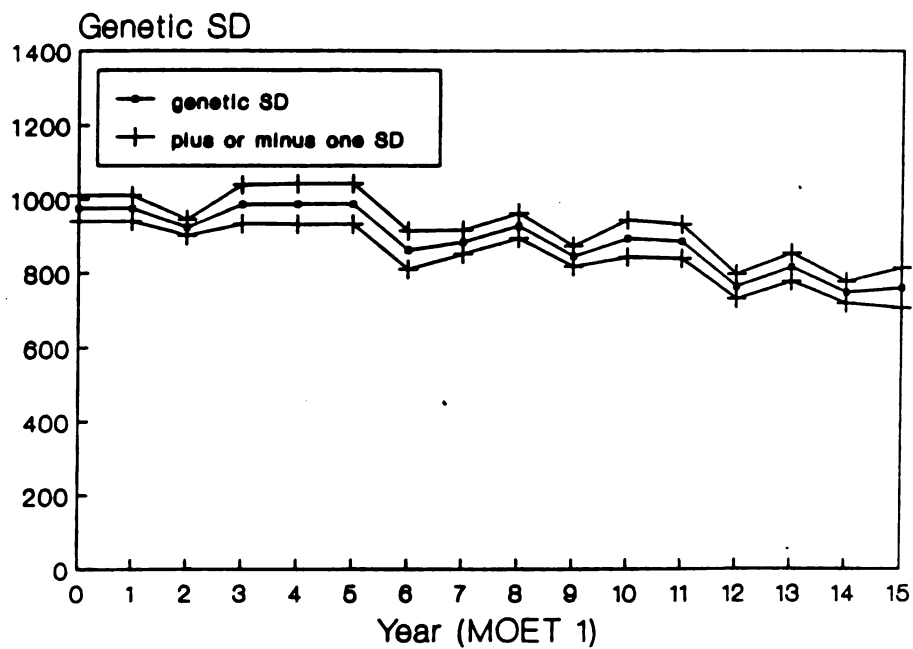


Figure 2. Change in genetic variation in MOET1 population for 12 years

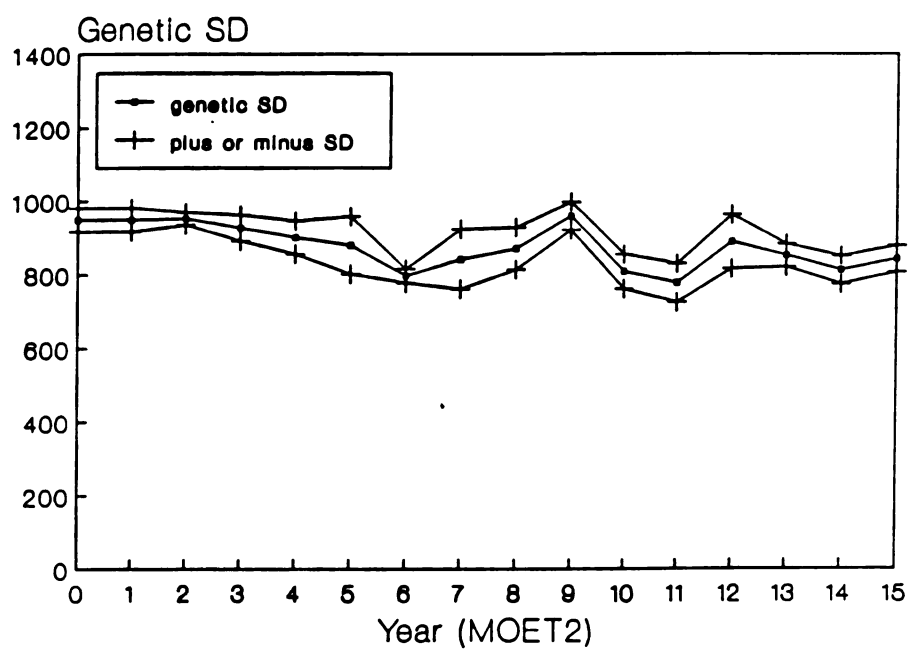


Figure 3. Change in genetic variation in MOET2 population for 12 years

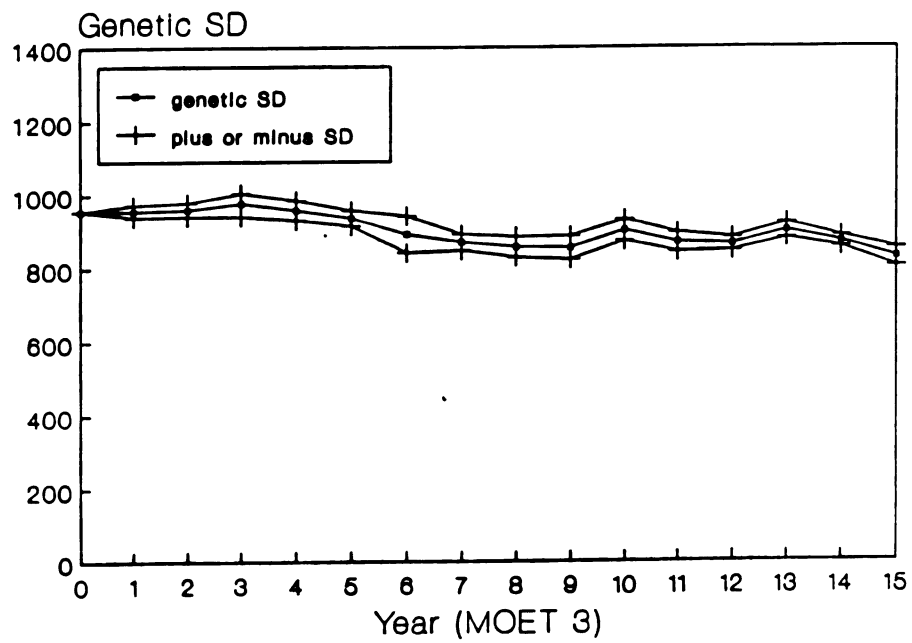


Figure 4. Change in genetic variation in MOET3 population for 12 years

*Genetic response*

The genetic changes from the three MOET schemes were compared to both theoretical and realized genetic progress from a conventional progeny testing AI population. The theoretical genetic progress was assumed to be 2% of production average or 150 kg per year (Van Vleck, 1981), and realized genetic gain was assumed to be one third of the theoretical genetic gain (Van Vleck, 1977) or 50 kg per year. The genetic progress over 12 years are shown in Figure 5, 6, and 7. The genetic means of MOET1 population followed a smooth linear trend and fluctuated less than those of MOET2 and MOET3. This was due to no restriction on inbred matings in MOET1 population. This always allowed the selection of best genetic material in each month. The selection of best animals was not always possible in MOET2 in order to meet the restricted inbreeding criteria, which hindered genetic progress. The same restriction on inbreeding was imposed in MOET3 population, but its genetic trend was similar to that of MOET1. Due to the larger population size, MOET3 population was less affected by the inbreeding restriction and had higher probability of selecting animals that were less related.

The rate of genetic progress in either MOET1 or MOET3 populations was greater than both theoretical and realized genetic gains from the current AI progeny testing population. However, the genetic gain in MOET2 population was less than the theoretical genetic gain from the current AI progeny testing population. This was because of the small number of breeding animals and inbreeding restriction in mating.

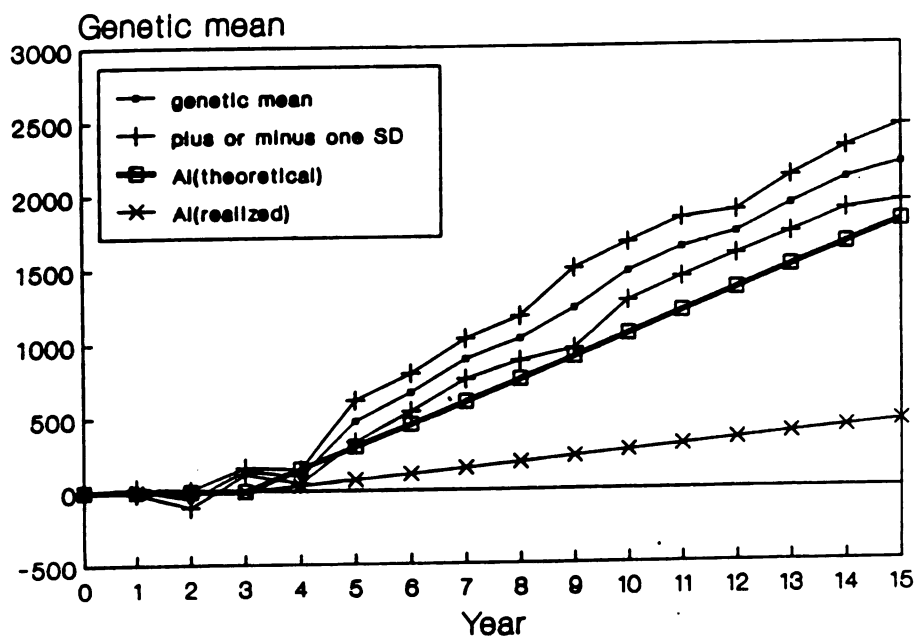


Figure 5. Annual genetic mean with genetic drift variation in MOET1 population for 12 years

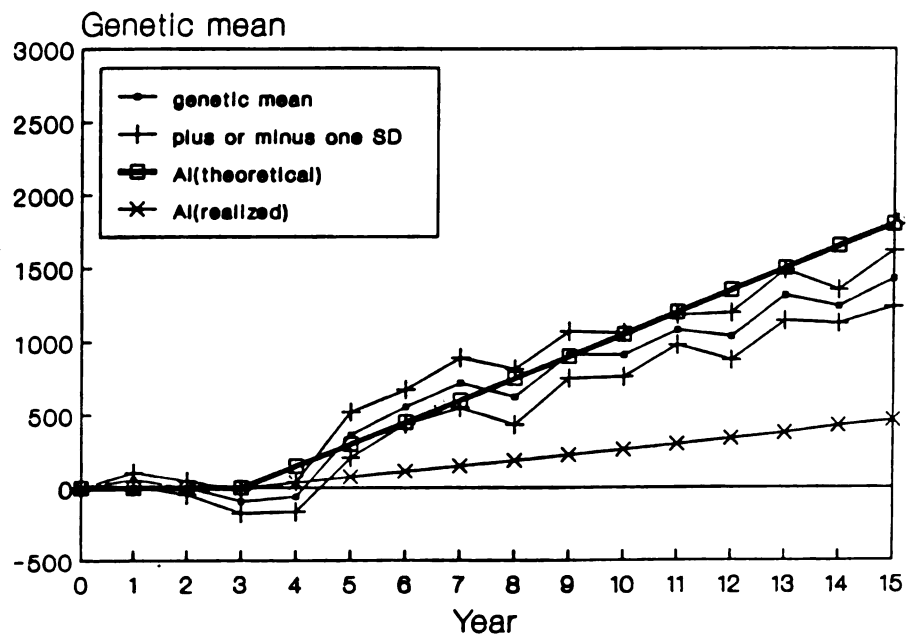


Figure 6. Annual genetic mean with genetic drift variation in MOET2 population for 12 years

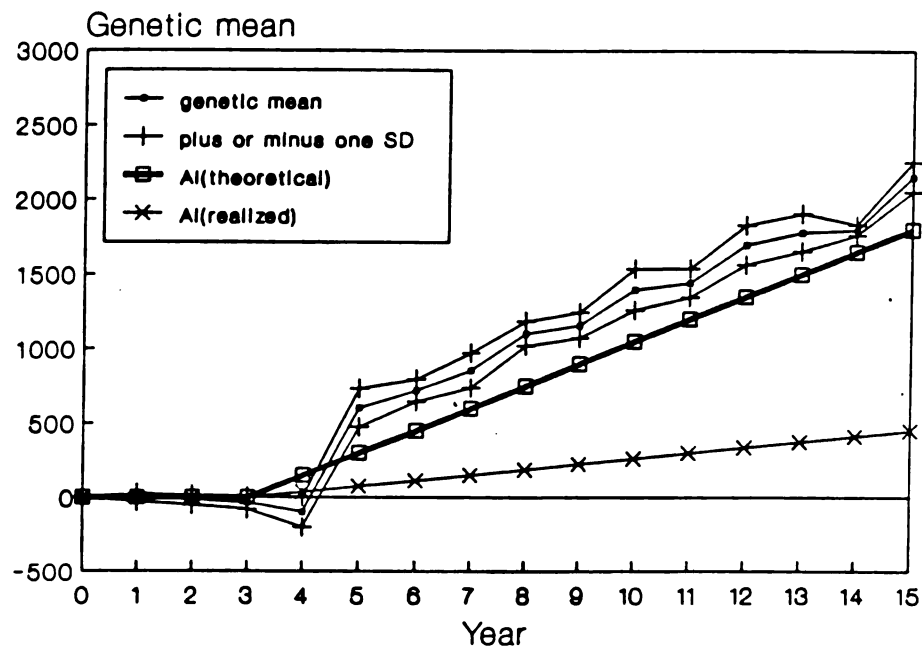


Figure 7. Annual genetic mean with genetic drift variation in MOET3 population for 12 years



### Genetic drift

Many factors contribute to random genetic drift, but it is mainly related to effective population size. The random genetic drift was described in terms of variation in genetic means over five replications and was also shown in Figure 5, 6, and 7.

For the coefficient of variation (CV) of response to be  $\alpha$  after  $n$  generations, given selection intensity of  $i$  and heritability  $h^2$ , the population size required can be approximated by Nicholas (1980):

$$1/n\alpha^2i^2h^2$$

Therefore, imposing higher selection intensity on highly heritable traits for a fixed number of generations would require a smaller population size. On the other hand, for fixed intensity, heritability and size, for  $\alpha$  to be small, relatively large population size would be required. Hence, after 24 years, the CV of genetic mean MOET3 population was the smallest, 4.69%. Those in MOET1 and MOET2 populations were 9.68% and 13.38%, respectively. In MOET2 population, the selection intensity was lower than those in MOET1 and MOET3 populations due to inbreeding restriction and smaller size, thus resulting in the highest CV of genetic mean.

### 3.5 CONCLUSIONS

All three MOET breeding schemes studied achieved higher genetic responses than the realized genetic gain from the current AI progeny testing population. This was accomplished in populations in spite of their small sizes, the closed schemes, and in some cases restrictions on inbreeding. In fact, genetic gains in these MOET populations were higher than not only the realized but also the theoretical maximum

genetic gain possible in the current AI progeny testing schemes. This was true with the exception of the small population with inbreeding restriction. The small population, without restrictions to avoid inbreeding, accumulated a high level of inbreeding. No restriction on inbreeding did not appear to be worthwhile in terms of genetic gain for the time horizon studied. Beyond that, however, selection would become futile due to severe reduction in genetic variation because of inbreeding. Higher selection intensity regardless of population size lead to higher degree of linkage disequilibrium. The reduction in genetic variation due to linkage disequilibrium was as significant as that due to accumulation of inbreeding. Higher selection intensity and larger population size lead to lower random genetic drift, but genetic drift was not significant in all the populations studied.

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#### **4. CHAPTER 2 Comparison of Deterministic and Stochastic Modeling for Genetic Responses in Small Closed Dairy Cattle Populations**

##### **4.1 ABSTRACT**

Genetic responses and drift in small closed populations were studied by stochastic and deterministic models. In closed finite populations, effective population size, inbreeding, and linkage disequilibrium have major influences on genetic responses and drift. Three multiple ovulation and embryo transfer breeding schemes covering a 12 year period were simulated by stochastic models. The results were compared to those from deterministic models. In deterministic models, Rendel and Robertson's equation and Gene Flow model were modified to account for reduced accuracies and heritabilities due to inbreeding and linkage disequilibrium in each generation. Selection intensity, generation interval, and accumulation of inbreeding used in deterministic models were obtained from stochastic models.

Generally, the modified deterministic models gave estimates of genetic responses similar to stochastic models. Reduction of genetic variation due to linkage disequilibrium was as important as that due to inbreeding. However, in the population with a large accumulation of inbreeding, accounting for linkage disequilibrium alone was not as effective as that of inbreeding alone for deterministic models. When conservative restriction on inbreeding was applied in the mating schemes to a small size herd, deterministic methods did not give estimates of genetic responses similar to responses from stochastic models in later generations.

## 4.2 INTRODUCTION

In designing a selective mating plan, an accurate prediction of genetic gain and an anticipation of genetic drift are essential. The deterministic equation by Rendel and Robertson (1950) for the prediction of genetic change in a breeding program is well known and popularly used. However, it is only asymptotically true when the rate of genetic change is in a steady state, which may take many generations. A method to account for the earlier fluctuation of genetic progress before reaching the steady state is the Gene Flow model using the probability transition matrix (Hill, 1976). When the rate of genetic change in a breeding program with a constant selection intensity over time becomes stable, then the two equations, RRE and GFM, would give the same result.

In a small finite population, rate of inbreeding and linkage disequilibrium are major factors that should be closely monitored. These two factors substantially reduce genetic variation and result in slower genetic progress. This contributes to the discrepancy between realized genetic gains in a real population and estimated genetic gains from RRE and GFM. Also, the random genetic drift is essential in small finite populations.

Both RRE and GFM are deterministic in nature and their theoretical formulas do not take into account inbreeding and linkage disequilibrium, or the Bulmer effect (1971), both of which lead to a reduction in genetic variation depending on population size, level of inbreeding, and selection intensity. This may be a partial explanation why only one third of the predicted genetic response has been achieved

in dairy populations (Van Vleck, 1981). The deterministic equation for estimation of random genetic drift given by Hill (1976) also assumes constant parameters over time, ignoring the reduced variance due to inbreeding and linkage disequilibrium.

The deterministic models can be improved to avoid simplifying the assumptions such as heritability, selection accuracy, and variances kept constant throughout the period of breeding plan. The genetic changes can be more accurately studied by a stochastic simulation model. However, the stochastic approach is tedious, costly, and time demanding.

The objectives of this study were: 1) to illustrate a modification in estimation equation for random genetic drift by Hill (4), and Rendel and Robertson's equation and Gene flow model for genetic response, which would account for reduced variances due to inbreeding and linkage disequilibrium; 2) to examine possible improvement in the accuracy of predicting genetic responses by the modified Rendel and Robertson's equation and Gene flow model, and random genetic drift by the modified Hill's equation; and 3) to compare both genetic responses and random genetic drift from the deterministic and stochastic models in three small closed dairy cattle populations employing multiple ovulation and embryo transfer (MOET) technique.

#### 4.3 METHODS

##### Stochastic model

Breeding events in each of the three multiple ovulation and embryo transfer (MOET) populations were simulated monthly for a 12 year period using parameters shown in Table 1. Simulation of each population was

replicated five times. The structure and details of breeding events of the three MOET populations, MOET1, MOET2, and MOET3, were previously described in detail in CHAPTER 3.

Table 1. Parameters used to simulate the three populations using MOET breeding schemes<sup>1</sup>

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Trait : milk yield

Heritability ( $h^2$ ) : .4

Phenotypic SD : 1,498 kg

Production mean : 7,500 kg

Survival rate : .7

Conception rate : .7

Avg. no. eggs/superoovulation : 5 (following Poisson distribution)

No. of founder females ( age 14 mo.) :   88 for MOET 1  
                                                          88 for MOET 2  
                                                          352 for MOET 3

---

<sup>1</sup>Restriction in inbreeding with maximum of .0625 in the progeny was imposed in mating schemes of MOET2 and MOET3. For MOET 1, inbreeding was not considered.

An infinitesimal model at an individual animal level was used to generate records:

$$y_i = \mu + a_i + e_i$$

where  $y_i$  was the first lactation record of the  $i^{\text{th}}$  animal;

$\mu$  was a constant overall mean;

$a_i$  was an additive genetic value of the  $i^{\text{th}}$  animal; and



$e_i$  was the random residual corresponding to the  $i^{\text{th}}$  record.

For genetic evaluation of animals, an animal model was used with a known complete relationship matrix. Accumulation of inbreeding, changes in genetic variance due to inbreeding and linkage disequilibrium, and genetic responses with drift variation were computed each month. The average selection intensity (SI), generation interval (GI) and inbreeding resulting from the stochastic simulation were later used in deterministic models and are summarized in Table 2.

Table 2. Parameters averaged from the 5 replicates of each simulated MOET population that were used in the deterministic equations.

| population | Selection Intensity |        | Generation Interval |        | Inbreeding |
|------------|---------------------|--------|---------------------|--------|------------|
|            | male                | female | male                | female |            |
| MOET 1     | 1.8485              | 1.488  | 2.83                | 3.64   | 22.5%      |
| MOET 2     | 1.6865              | 1.400  | 3.25                | 3.45   | 4.8%       |
| MOET 3     | 1.6865              | 1.400  | 3.25                | 3.75   | 3.9%       |

#### Deterministic models

*Genetic responses.* A summary of the alternative deterministic equations of RRE and GFM used in this study is given in Table 3.

Table 3. Description of modified Rendel and Robertson's equations (RRE) and Gene Flow Models (GFM).

| Models                                                     | description                                                |
|------------------------------------------------------------|------------------------------------------------------------|
| Unmodified:                                                |                                                            |
| Rendel & Robertson Equation (RRE)<br>Gene Flow Model (GFM) | ignoring inbreeding and<br>linkage disequilibrium          |
| Modified:                                                  |                                                            |
| RRE(F)<br>GFM(F)                                           | modified for inbreeding<br>only                            |
| RRE(LD)<br>GFM(LD)                                         | modified for linkage<br>disequilibrium only                |
| RRE(F,LD)<br>GFM(F,LD)                                     | modified for both inbreeding<br>and linkage disequilibrium |

(1) Rendel and Robertson's equation (RRE).

By the selection index theory, Rendel and Robertson's equation (1950) is commonly denoted as:

$$\Delta G/\text{year} = \Sigma G_i / \Sigma L_i$$

where  $\Delta G/\text{year}$  is annual genetic gain;  $G_i$  is genetic superiority of the  $i^{\text{th}}$  pathway;  $L_i$  is generation interval of the  $i^{\text{th}}$  pathway; and  $i=1,2$  with 1 being from bull to produce bull and cow and 2 being from cow to produce bull and cow. For simplification of model calculations, the genetic superiority of the bull was computed based only on pedigree information traced back two generations. For the dam, her first lactation record was also included in addition to the pedigree information. The genetic superiority of the  $i^{\text{th}}$  pathway is:

$$G_i = SI_i \times (r_{TI})_i \times \sigma_a \quad [1]$$

where  $SI_i$  is selection intensity of the  $i^{\text{th}}$  pathway;  $(r_{TI})_i$  is accuracy of the  $i^{\text{th}}$  path, or correlation between estimated and true breeding values;  $\sigma_a$  is additive genetic standard deviation. To compute  $r_{TI}$ , the selection index equation for true breeding value,  $g$ , was set as:

$$I = b'x \quad [2]$$

where  $b$  is a vector of index weights;  $x$  is a vector of phenotypic values adjusted for all fixed effects that were assumed to be of known magnitude. The relatives' information in index equation [1] were dam, dam's full-sib, dam's half-sib, sire's full-sib of females, sire's half-sib of females, and paternal grandam. This index has a similar structure as the one outlined in the paper given by Wooliams and Smith (1988) except indicator traits were not included. The index weights were obtained as  $b = P^{-1}G$ , where  $P$  is the phenotypic covariance matrix of  $x$ ;  $G$  is covariances between  $x$  and  $g$ . Then, the accuracy,  $r_{TI}$ , was computed as:

$$r_{TI} = \sqrt{(b'Pb)}/\sigma_g$$

## (2) Gene Flow Model (GFM).

The gene flow model (GFM) gives a more exact estimation of selection responses than RRE because it accounts for earlier fluctuation of selection responses. The main principle of GFM is to use a recurrence relationship employing the transition probability matrix method developed by Hill (1976). The GFM in matrix notation was:

$$M_i(t) = Tp(M_i(t-1) + S(i)) \quad [3]$$

where  $M_i(t)$  is a vector of genetic means of animals at age  $i$  at time  $(t)$ ;  $Tp$  is the transition probability matrix that specifies the



The genetic responses estimated by equation [4] were obtained by restricting  $s_{mi}$  of [4] in right-hand-side to zero for the initial time period corresponding to their generation intervals of the three MOET populations. The restriction was due to the use of sires from base populations, where all sire were unselected and these unselected sires were used at least for one generation (i.e., selection superiority=0) in initial MOET application to the populations.

### (3) Modified RRE and GFM to account for inbreeding

Reduction of genetic variance due to inbreeding is directly proportional to the level of inbreeding according to the function:

$$\sigma_{a(t)}^2 = (1 - \bar{F}_t) \sigma_{a(0)}^2$$

where  $\bar{F}_t$  is an average inbreeding coefficient in the population at time  $t$ ; and  $\sigma_{a(t)}^2$  and  $\sigma_{a(0)}^2$  are genetic variances at time  $t$  and in base generation, respectively. The simulated populations, MOET1, MOET2, and MOET3, resulted in 22.5%, 4.8%, and 3.9% inbreedings, respectively, after 12 years, which were assumed to follow a linear trend. In computing genetic changes,  $\sigma_a$  of RRE in [1] and  $s_{mi}$  and  $s_{fi}$  of GFM in [4] were adjusted according to annually reduced variances due to  $\bar{F}$ .

### (4) Modified RRE and GFM to account for linkage disequilibrium.

Selection of parental generation induces a reduction in genetic variance in next generation. This reduction in variance is known as linkage disequilibrium or Bulmer effect (1971). The theory derives from a simple regression equation by regressing progeny ( $y$ ) on both parents ( $P_1$  and  $P_2$ ):

$$y = a + b(P_1 + P_2) + e$$

where  $a$  is intercept;  $b$  is regression weight; and  $e$  is error. Taking the variance ( $V$ ),  $V(e)$  is  $(1-.5(h^2)^2)V(y)$ , where  $V(y)$  is a total phenotypic variance. After selection in parents, then the variance in progeny generation becomes:

$$\begin{aligned} V(y^*) &= b^2V(P_1) + b^2V(P_2) + V(e) \\ &= 2b^2[V(y) + dV(y)] + V(e) \\ &= V(y) + .5(h^2)^2dV(y) \end{aligned} \quad [5]$$

where  $V(y^*)$  is a new variance after selection in parental generation. The second term in the right-hand-side of equation [5],  $.5(h^2)^2dV(y)$  is the amount of reduction in variance in progeny generation due to parental selection, where  $d$  can be expressed as:

$$d = [V(y^*) - V(y)] / (.5(h^2)^2V(y))$$

This equation was extended to the situation of selection of several generations such that:

$$V(a)_i = V(a)_0 + d_i$$

$$V(y)_i = V(y)_0 + d_i$$

where  $V(a)_i$  and  $V(y)_i$  are additive genetic and phenotypic variance, respectively, available at the  $i^{\text{th}}$  generation;  $V(a)_0$  and  $V(y)_0$  are genetic and phenotypic variances, respectively available in the base generation; and  $d_{i+1}$  is  $.5d_i + .5(h^2)^2dV(y)_i$ .

(5) Modified RRE and GFM for both inbreeding and linkage disequilibrium.

Reduction in variance due to both  $F$  and  $LD$  can be incorporated into equation [1] and [4]. The reduced genetic variance at time  $t$  due

to both F and LD can be expressed as:

$$\sigma_a^2(t) = (1-F)\sigma_a^2(0)t + d_i \quad [6]$$

where  $(1-\bar{F}_t)\sigma_a^2(0)$  is a reduced additive genetic variance due to inbreeding and  $d_i$  is reduction due to linkage disequilibrium by selection.

*Random genetic drift.* Random genetic drift is a dispersive process due to gene sampling. The genetic drift obtained from the simulated populations was considered as the realized genetic drift and was expressed in terms of standard deviation among genetic means from five simulated replicates of each population. For the deterministic equations, the genetic drift were estimated by the equation given by Hill (1974).

Hill's equation was established based on the assumption that variance and heritability stay constant. The drift variance ( $\sigma_D^2$ ) is a function of effective population size and selection intensity:

$$\sigma_D^2 = .25\sigma_a^2( [1-(1-C_m)h^2]/N_m + [1-(1-C_f)h^2]/N_f ) \quad [7]$$

where  $C_m$  and  $C_f$  are coefficients of order statistics for selected males and females;  $N_m$  and  $N_f$  are number of selected males and females. The equation is also unconditional on the selection differential but assumes a constant selection intensity, which means that selection intensity is constant from replication to replication but the selection differential varies from replication to replication. The equation [7] was also modified in this study to account for reduced  $\sigma_a^2$  and  $h^2$  due to both inbreeding and linkage disequilibrium simultaneously i.e., the reduced variance [6] was used in equation [7] for the estimation of

genetic drift variance.

#### 4.4 RESULTS

##### Estimated genetic responses

Unmodified RRE and GFM generally overestimated genetic responses, which was more apparent after six years in all three MOET populations.

The simulated small population with no restriction on F (MOET1 population) accumulated an average inbreeding coefficient of 22.5% at year 12. For this population, the equations modified only for reduced variance due to inbreeding obtained genetic responses (i.e., 2,209 kg from RRE(F) and 2,320 kg from GFM(F), respectively) closer to the realized genetic response (i.e., 2,191 kg for stochastic model) than the equations modified only for linkage disequilibrium. Values of 2,386 kg from RRE(LD) and 2,486 kg from GFM(LD), respectively, are in Figure 8 and 9. The difference between RRE and GFM equations, however, was not significant.

MOET2 population had the same population size as the MOET1 but with a strict restriction on F imposed. For MOET2, the estimated genetic responses from the modified deterministic equations for LD only, RRE(LD) and GFM(LD), were closer to the realized response than those from the modified deterministic equations for F only, RRE(F) and GFM(F) (Figure 10 and 11). This is due to the fact that a strict restriction on F lowered the cut off for selecting parents from year to year. Also, the reduction in variances were largely due to the effect of linkage disequilibrium rather than inbreeding.

Similar results to MOET2 were found in MOET3 population (Figure 12 and 13). However, the estimated genetic responses in MOET3 population were closer to the realized genetic response computed from the



stochastic simulation model than those in MOET2 population. The reason was that the strict restriction on inbreeding lowered cut off for selecting parents in MOET2 population more than in the MOET3 population. MOET3 had a larger population size.

After RRE and GFM were modified for reduced variance due to both inbreeding and linkage disequilibrium,  $RRE(F,LD)$  and  $GFM(F,LD)$ , the estimated genetic responses were, in general, very similar to the realized ones computed from the stochastic model for MOET1 and MOET3 populations.

The largest discrepancy between estimated and realized genetic responses occurred in MOET2 population (Figure 10 and 11). This was due to selection intensity used in the RRE and GFM equations. By definition of selection intensity, it results the top certain percent of animals selected as parents. In MOET2 population, strict restriction on inbreeding was imposed on the mating scheme. This resulted in selecting genetically inferior animals to avoid inbreeding. However, the selection intensity summarized in Table 2 was simply the proportion of selected animals over total number of animals available, not specifying a certain percent from the top. The MOET3 population, nevertheless, had less chance to select inferior animals even with the same mating scheme as MOET2 because of larger population size. This is one of the main difficulties in use of deterministic models to estimate genetic responses unless all the parameters in equations [3] and [8] remain constant throughout the time horizon of a breeding plan.

Overall, the estimated genetic responses from the modified deterministic models for both inbreeding and linkage disequilibrium

were similar to the realized responses from the stochastic simulation models. This, in part, is because the parameters used in the deterministic equations were from the summary of the stochastic simulation results, and reduction in variance was taken into account over time.

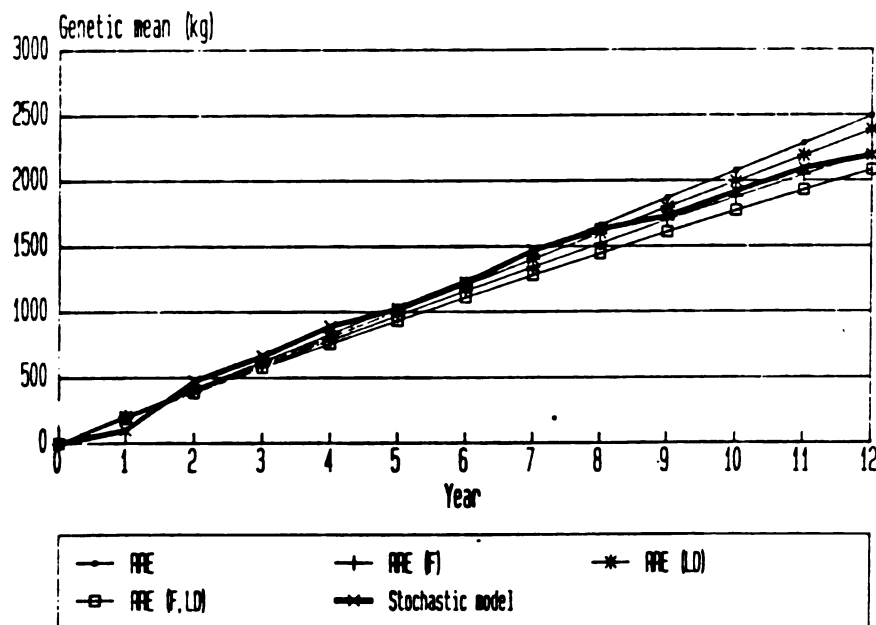


Figure 8. Estimated genetic responses by RRE in comparison to realized genetic responses in MOET1 population

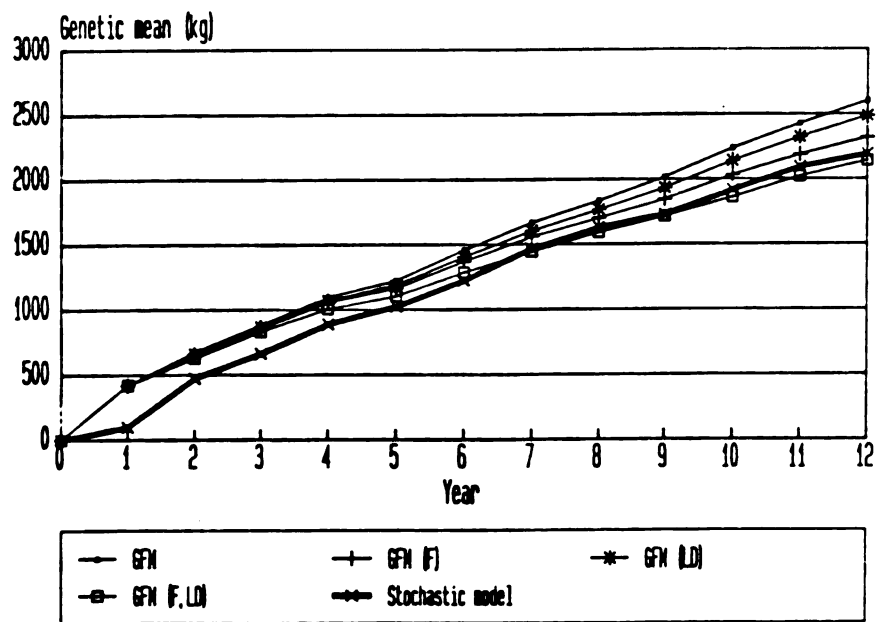


Figure 9. Estimated genetic responses by GFM in comparison to realized genetic responses in MOET1 population

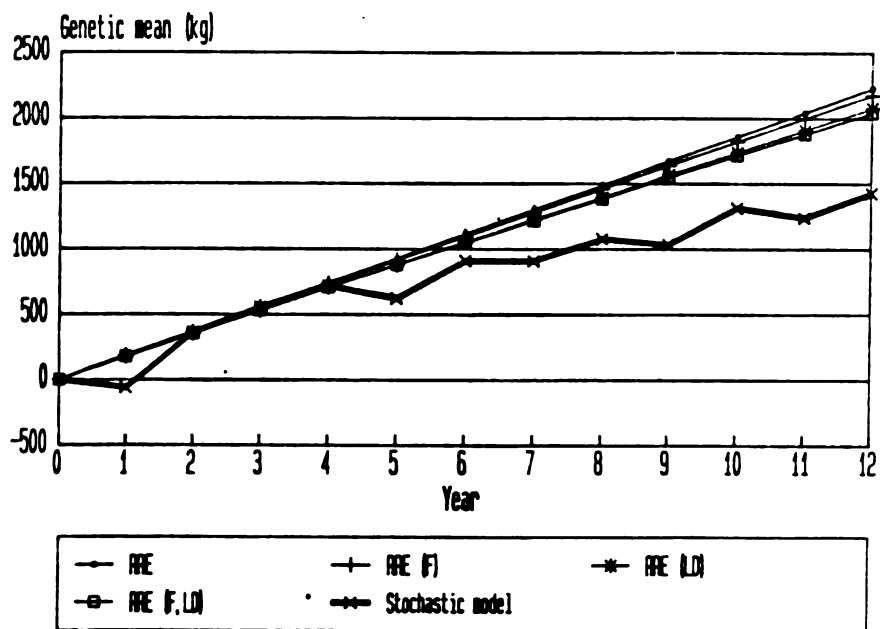


Figure 10. Estimated genetic responses by RRE in comparison to realized genetic responses in MOET2 population

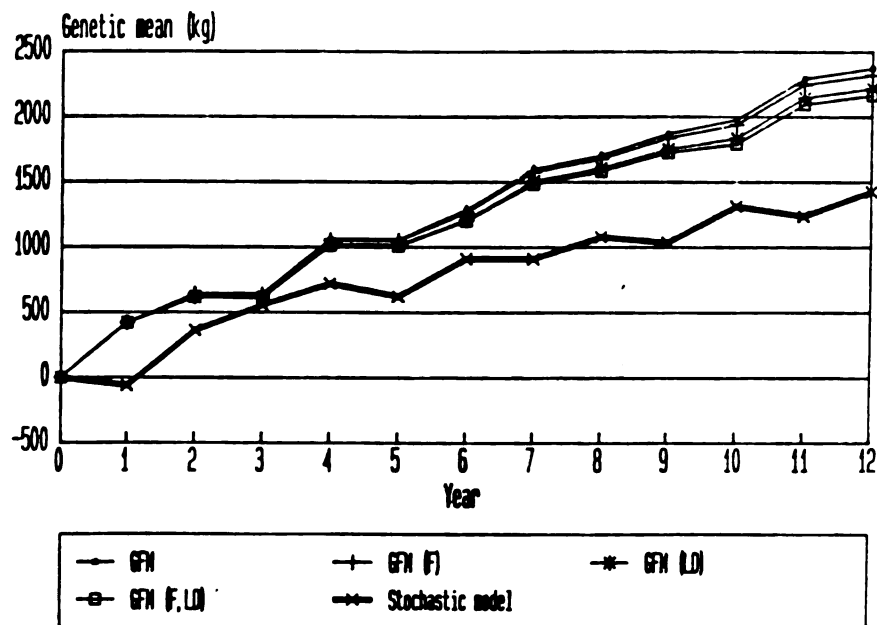


Figure 11. Estimated genetic responses by GFM in comparison to realized genetic responses in MOET2 population

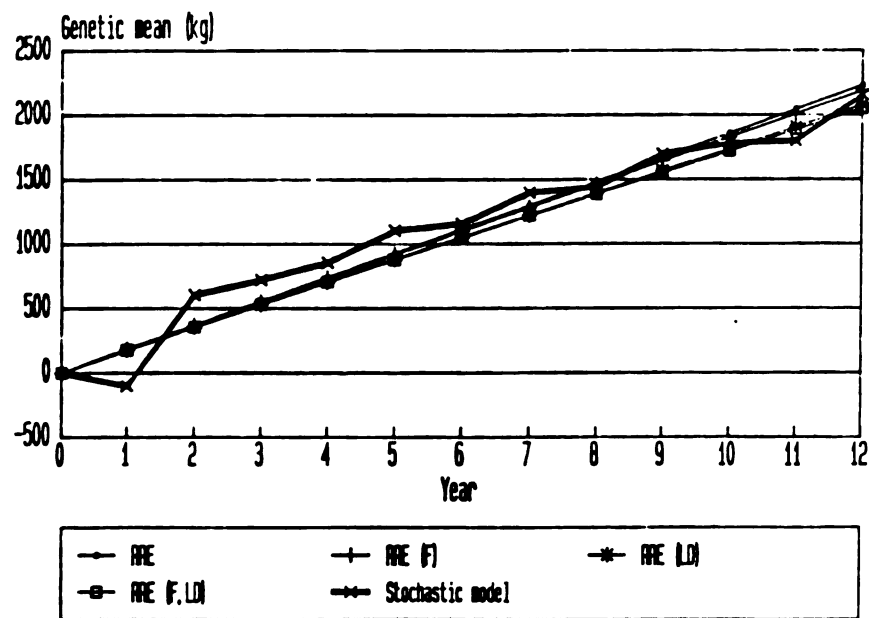


Figure 12. Estimated genetic responses by RRE in comparison to realized genetic responses in MOET3 population

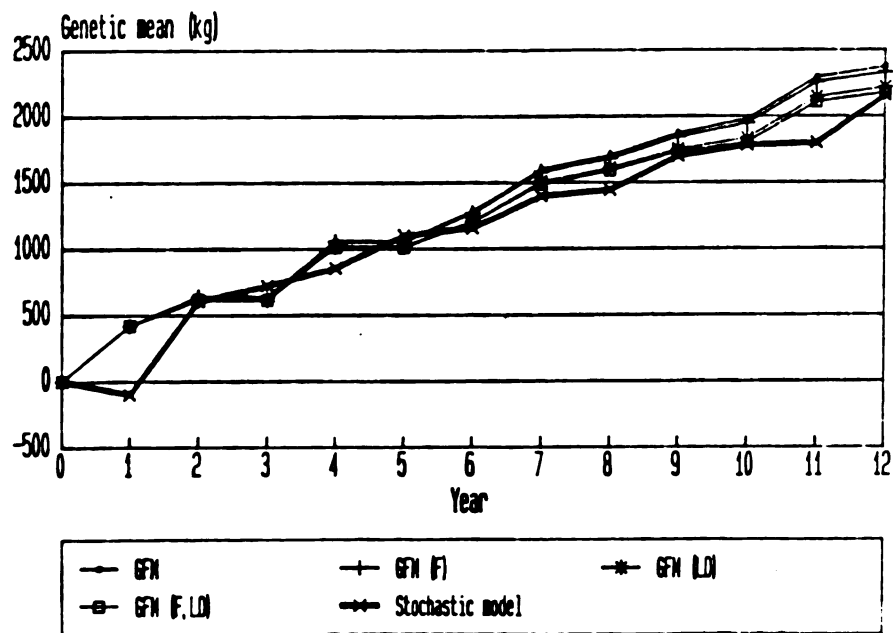


Figure 13. Estimated genetic responses by GFM in comparison to realized genetic responses in MOET3 population

### Estimated Random Genetic Drift

Along with estimated genetic responses, the estimated genetic drift variations from the modified deterministic equation [7] closely approximated the realized genetic drift variations in MOET1 and MOET3 populations (Figure 14 to 16).

In MOET2 population, the estimated genetic drift variation was much greater than the realized one mainly due to the same reasoning mentioned in previous section. That is, the strict restriction on inbreeding hindered the cut off for selecting parents.

Overall, the estimated genetic drift variation from the modified equation [7] was very similar to the realized ones from the stochastic simulation models.

### 4.5 CONCLUSIONS

Both the unmodified Rendel and Robertson's equation and gene flow model overestimated genetic responses. However, these deterministic equations can be used to predict the genetic responses and genetic drift accurately if the reduction in variance due to inbreeding and linkage disequilibrium over time is taken into account.

In a large population, inbreeding may not be important due to the large population size and a planned mating scheme used to avoid inbreeding. However, linkage disequilibrium created by selection can not be avoided and should be considered even in a large population.

One of the usual assumptions in the deterministic model calculations is that breeding events with parameters from year to year stay constant. However, the parameters such as selection intensity and generation interval might not be consistent throughout the period of



breeding plan because of some restrictions imposed such as inbreeding. This would create some large biases in estimation as occurred in MOET2. This was the main difficulty in the use of the deterministic equation used in this study. Nevertheless, with a moderate assumption such that all parameters stay constant from generation to generation, deterministic model can be an efficient alternative of stochastic model for estimation of genetic changes if reduced variances are considered.

If the parameters used in the deterministic models in this study had not been from stochastic results, the difference between the estimated and the realized responses from stochastic simulation would be much greater.

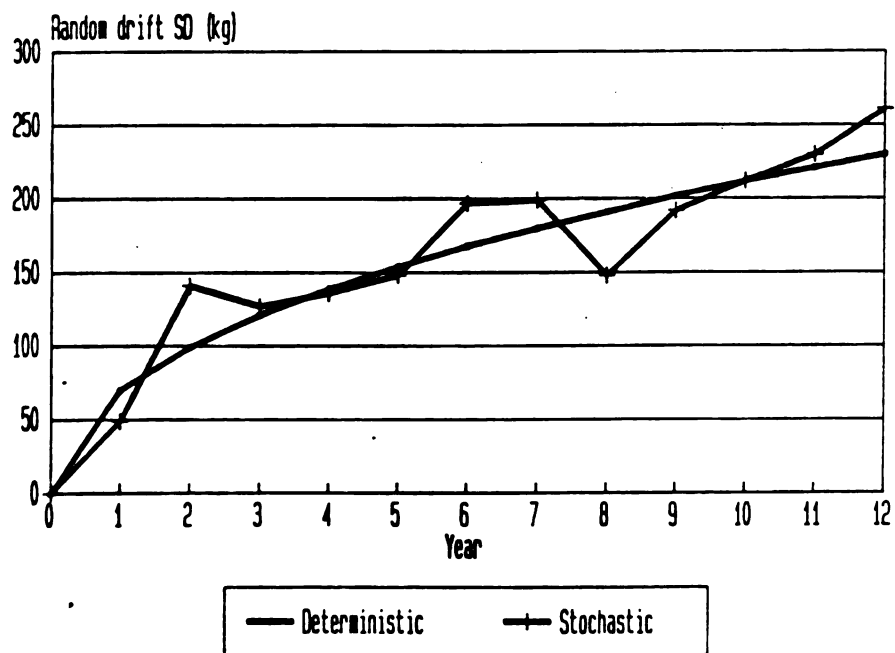


Figure 14. Estimated random genetic drift SD in comparison to realized random genetic drift SD in MOET1 population

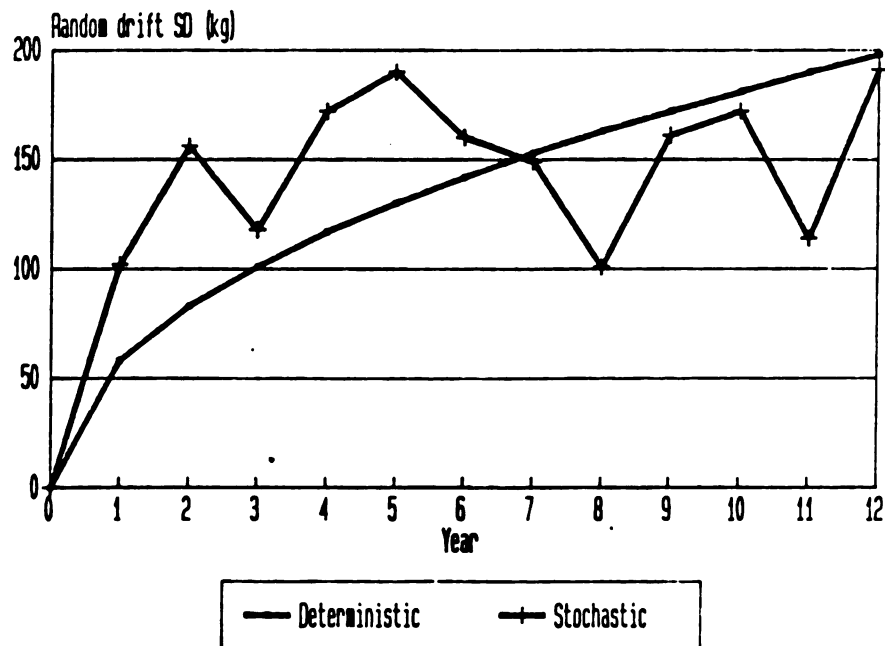


Figure 15. Estimated random genetic drift SD in comparison to realized random genetic drift SD in MOET2 population

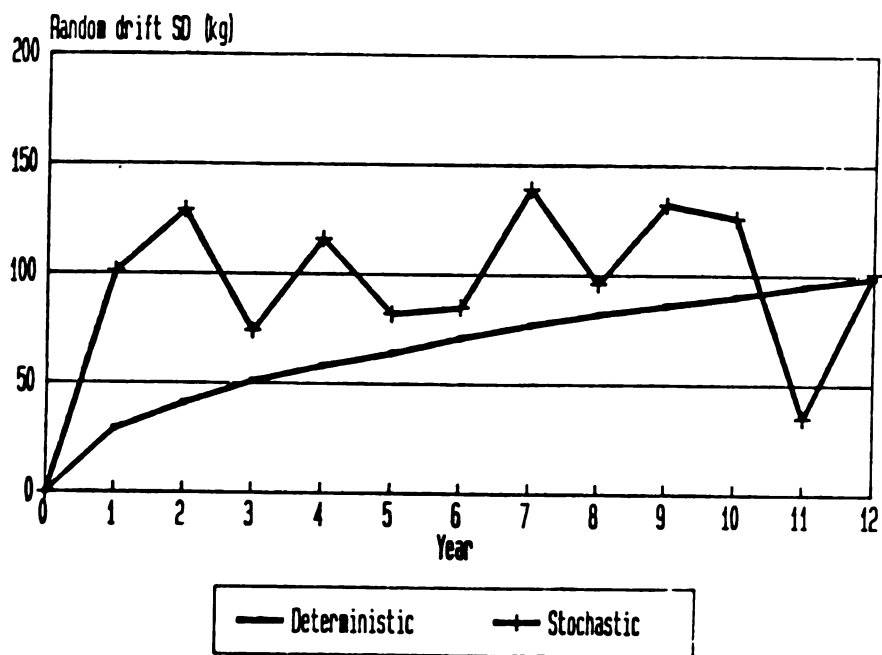


Figure 16. Estimated random genetic drift SD in comparison to realized random genetic drift SD in MOET3 population

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## 5. SUMMARY AND CONCLUSIONS

The use of artificial insemination in cattle populations has made it possible to improve genetic potential of production animals. New technology of multiple ovulation and embryo transfer has shown that it can add to the rate genetic improvement in current AI cattle populations.

This study examined the potential genetic improvement in three small closed dairy cattle populations using multiple ovulation and embryo transfer techniques and is composed of two investigations.

In the first investigation, the genetic changes such as the rate of inbreeding, linkage disequilibrium, and genetic response along with random genetic drift was studied by a stochastic modeling approach. The motivation of using a stochastic approach was that it could more accurately account for the random nature of populations. It was found that the MOET breeding scheme without restriction on inbreeding in consideration of mating design accumulated a rapid inbreeding coefficient even though considerable genetic response was achieved. Despite a larger response, this is not recommended in practical breeding design due to a high level of inbreeding. In the same small population structure using strict restriction on inbreeding in mating scheme, responses were not more efficient than conventional AI scheme as the obtained response was slightly less than the conventional AI progeny testing scheme. The remedy to improve the selection response with a strict restriction on inbreeding was found by increasing the population size.

Several factors influence the genetic progress, population size,

selection intensity, rate of inbreeding, and breeding scheme, and the variation among animals. Greater variation among animals makes the selection more efficient. However, this variation can be reduced depending on inbreeding and linkage disequilibrium. Linkage disequilibrium was as significant as inbreeding in reducing the variation among animals.

In the second investigation, the study was focused on improvement of the deterministic modeling approach for the prediction of genetic change. Even with a random nature of population, if deterministic models can predict the genetic change as close as stochastic models, then, it will save time, costs, and labor. The deterministic models of Rendel and Robertson's equation and gene flow model were examined. Both deterministic equations ignore the reduction in variances due to inbreeding and linkage disequilibrium in their original formulation. After reduced variances were taken into account in model calculations, the predicted genetic responses were similar to the results from the stochastic modeling approach. However, some difficulties are hard to overcome in the deterministic approach such as the estimation of level of inbreeding coefficients. The several estimation methods of inbreeding, however, were restricted to special cases. This might be, nevertheless, a smaller problem in a large population. Estimation of random genetic drift after adjusting for the reduced variances also gave similar results to stochastic models.

Extension of MOET techniques in open nucleus breeding schemes is feasible, which would increase selection intensity. Also, the problem of inbreeding can be reduced due to a large population size.

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