OPTIMIZATION OF DAIRY CATTLE BREEDING PLANS WITH INCREASED FEMALE REPRODUCTIVE RATES

T.H.E. Meuwissen

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VOORWOORD

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Theo

STELLINGEN

1. Alle fokprogramma's voor melkkoeien kunnen beschreven worden als nucleus programma's met een variabele mate van openheid.
     dit proefschrift

2. Verlaging van het aantal te selekteren dieren leidt niet altijd tot een hogere selektie-intensiteit.
     dit proefschrift

3. Het vooraf vastleggen van generatie-intervallen in fokprogramma's leidt tot suboptimale resultaten.
     James, J.W., 1987, J. Anim. Breed. Genet. 104: 23-27
     dit proefschrift

4. Hogere selektie-respons leidt vaak tot minder nauwkeurige selektie.
     dit proefschrift

5. Door voorkeursbehandeling van stiermoeders en het niet gebruiken van jonge stieren met hoge verwachte fokwaardes kunnen praktijkbedrijven zich uitsluiten van de veeverbetering.
     gedeeltelijk dit proefschrift

6. Voor optimale selektie over leeftijdsklassen heen is het essentieel dat de fokwaardeschattingen zuiver zijn.
     dit proefschrift

7. Moderne fokprogramma's met korte generatie-intervallen en kleine effektieve populatiegroottes zijn ondanks hun grotere spreiding van de selektie-respons toch te prefereren.
     dit proefschrift

8. Een mogelijke bijdrage van de voortplantingstechnologie aan de genetische vooruitgang is met name gelegen in verlaging van de aanvang van de reproduktieve leeftijd.

9. De konsument wil in de winkel een ander stuk vlees dan op het bord.

10. Het BST-onderzoek toont aan, dat veelomvattend onderzoek met eensluidend positieve resultaten niet hoeft te leiden tot maatschappelijke acceptatie van biotechnologische ontwikkelingen.

11. Modelonderzoekers maken eerst veelal grove aannames om praktische problemen om te zetten in theoretische en gaan daarna deze theoretische problemen heel secuur uitwerken.

12. De rechtvaardiging van de huidige methodes om variantie-componenten te schatten wordt volledig gevormd door hun eigenschappen in grote steekproeven, terwijl, vanwege de benodigde grote rekencapaciteit, slechts data-sets van beperkte omvang doorgerekend kunnen worden.

13. Op de lange termijn zal het aandeel van de dierlijke produktie aan de totale voedsel produktie dalen omdat de maatschappelijke aanvaardbaarheid van nieuwe technieken in de plantaardige sektor hoger is.

14. Doordat onderzoeksmanagers veel kijken naar wat er elders gebeurt, zijn onderzoeksthema's net zo trendgevoelig als de strandmode.

15. Met al die stoplichten lijkt Nederland een 'red light district'.

Proefschrift van T.H.E. Meuwissen,
Optimization of dairy cattle breeding plans with increased female
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CONTENTS

INTRODUCTION

Conventional progeny testing schemes are widely used to increase efficiency
in dairy cattle production. In these schemes, young bulls are obtained from
matings between bull sires, selected from progeny tested bulls, and bull dams,
selected from the commercial cow population. Young bulls are progeny tested
before being selected and used extensively. Generation intervals are long due
to progeny testing and usually bull dams have at least one individual record.
Increasing female selection differentials in progeny testing schemes by the
use of Multiple Ovulation and Embryo Transfer (MOET) increases genetic gain
only up to 10% (e.g. Foote and Millar, 1971; Cunningham, 1976; McDaniel and
Cassell, 1981; Van Vleck, 1981).

Nicholas (1979) was the first to propose the use of closed nucleus schemes
with short generation intervals to make optimal use of increased female
reproductive rate in dairy cattle breeding. These schemes were elaborated by
Nicholas and Smith (1983), which predicted 30 - 50 % higher response rates for
MOET nucleus schemes than for conventional progeny testing schemes. In their
adult schemes, selection was for family indexes containing full-, half-sib and
dam information and, in case of selection of females, individual performance
information. Generation intervals averaged 3.7 years. Juvenile schemes had
generation intervals of 1.8 years. Selection was for family indexes of the
sire and the dam. Alternatives to these original MOET schemes were proposed by
Colleau (1985) and Christensen and Liboriussen (1985) (see Ruane (1988) and
Colleau (1989) for reviews).

Both the conventional progeny testing and MOET nucleus schemes have
predefined generation intervals. However, James (1987) showed that generation
intervals can be optimized by selecting for high Best Linear Unbiased
Predicted (BLUP) breeding values estimates across all ages. This is because
BLUP breeding value estimates are corrected for genetic trend. Optimization of
breeding schemes is greatly simplified, since generation intervals do not have
to be predefined anymore.

Apart from differences in predefined generation intervals, closed nucleus
and progeny testing schemes differ with respect to the population from which

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elite females (nucleus dams and bull dams, respectively) are selected. Nucleus dams are selected from nucleus females, which have the same average genetic merit as contemporary bulls. On the other hand, bull dams are selected from the commercial cow population, which is of lower genetic merit. However, in progeny testing schemes, matings between bull sires and bull dams produce both male and female offspring. This female offspring is of equal genetic merit as the contemporary bulls and can be compared to the nucleus females in nucleus schemes. Their probability of selection as bull dam is higher than that of 'normal' commercial cows. From this it will be clear that progeny testing schemes actually are open nucleus schemes. Since BLUP corrects for pedigree information, selection across female offspring from bull sire and bull dam matings and 'normal' cows is optimized by selecting for high BLUP breeding value estimates.

Juga and Maki-Tanila (1987) simulated closed adult nucleus schemes. Predicted genetic gain was up to 124 % higher than simulated. Two factors probably caused an overestimation of the prediction model: i) neglection of reduction of genetic variance due to selection, which consists of reduction of genetic variance due to linkage disequilibrium (Bulmer, 1971) and reduction of variances of information sources which were previously under selection; ii) neglection of reduction of selection differentials due to finite population size and correlations between EBVs of relatives (Hill, 1976). Neglection of these factors might have caused that superior schemes had short generation intervals (Nicholas and Smith, 1983). Since large differences in genetic level between age classes, due to high response rates, favours selection from younger age classes having the highest genetic levels.

The aim of this study was to develop methods for the optimization of breeding plans and to investigate the effect of increased female reproduction rates on optimal breeding plans, genetic gain and variance of genetic gain. Prediction of genetic gain accounted for variance reduction due to selection and reduced selection differentials due to finite population size and correlations between relatives. An open nucleus breeding plan, including optimization of generation intervals and selection across tiers, i.e. the nucleus and the base, was modelled in a deterministic way. Progeny testing and closed nucleus plans were deducted from this concept. Generally, deterministic modelling provides more insight into the selection process and requires less

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computer time than Monte Carlo simulation (Brascamp, 1978). Monte Carlo simulation is usually more detailed and also provides an estimate of the variance of response, due to the variation of the results. In the present study, deterministic models are used, because insight into breeding plans helps to find the optimum strategy and because many plans may be evaluated at low computational costs. Also, variation of results of stochastic simulation may hinder optimization. Monte Carlo simulation was used to check deterministic models.

Chapter 2 describes the model for the prediction of selection response. All alternative breeding plans (a.o. progeny testing and MOET nucleus breeding schemes) are described as open nucleus breeding schemes. Reduction of variances due to selection is accounted for. Variance reduction due to inbreeding and inbreeding depression are ignored as is discussed in this Chapter. In Chapter 3 an approximation is derived for calculating reduced selection differentials in nested full-half sib populations. Chapter 4 gives optimized breeding schemes that differ in female reproductive rates. In Chapter 5, the effect of shortening generation intervals and of having a closed rather than an open nucleus on the variance of selection response is assessed. Aspects of the present study concerning prediction of genetic gain and its variance, optimization of breeding plans and practical limitations are discussed in Chapter 6.

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Chapter 2

A DETERMINISTIC MODEL FOR THE OPTIMIZATION OF DAIRY CATTLE
BREEDING BASED ON BLUP BREEDING VALUE ESTIMATES

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ABSTRACT

A deterministic model was developed to examine the optimization of open
nucleus breeding schemes in order to maximise the rate of genetic response in
dairy cattle. By changing the parameters, the model was able to simulate both
a closed nucleus and a progeny testing scheme. The model implicitly optimized
the generation interval and the selection across tiers by means of truncation
selection across age classes and tiers respectively. The effects of size of
the progeny test group and the nucleus size were assessed by comparing
alternative plans. It is possible to optimise a breeding plan given the
reproduction rates of the animals, the availability of different sources of
information, the age distribution of the animals (survival rates) and the
phenotypic and genetic parameters of the trait.

The steady state selection response was assessed by calculating the genetic
progress year after year until it stabilized. The genetic gain was corrected
for the effects of reduced variances due to previous selections and increased
variances due to genetic differences between parental age classes.

In an example the model was used to predict the improvement in milk yield in
a closed artificial insemination breeding scheme. The genetic gain of a
conventional progeny testing scheme was 34 % lower than the genetic gain of
the optimized breeding plan. The variance reduction due to selection decreased
the steady state genetic gain by 30%.

INTRODUCTION

The use of BLUP (Best Linear Unbiased Prediction) breeding value estimates
is common practice in dairy cattle breeding. The predicted breeding values of
animals of different ages can be compared directly, because the BLUP procedure
takes account of genetic trend. The generation interval is optimized, when the
animals with the highest breeding values are selected, irrespective of their
age or the accuracy of the predicted breeding value (James, 1987). If
selection is over several tiers (e.g. nucleus and base) it is optimal to
select the animals with the highest BLUP breeding values irrespective their
origin (provided there are genetic links between the tiers).

The gene flow model (e.g. Hill, 1974) is not suitable to predict the response to selection with optimal generation intervals, because the generation interval is a fixed input parameter of this model. The optimal generation interval depends on the genetic differences between the age classes (i.e. the genetic gain) (Brascamp, 1978) and the variances of the estimated breeding values (EBVs) within each age class. Both are influenced by previous selection rounds. Also optimal selection across tiers depends on the means and variances of the EBVs in the different tiers. The gene flow model is valuable to compare breeding plans, with different fixed generation intervals and selection across tiers, but the use of modern sire and dam evaluation methods make an optimized generation interval and optimal selection across tiers achievable.

The aim of this paper is to present a deterministic model for the prediction of the steady state selection response, with optimal generation intervals and selection across tiers. The steady state selection response is assessed by predicting annually the genetic merit and the reduced variances of the 'new born' age class until the genetic gain stabilizes. Every year the generation intervals and the selection across tiers are optimized. The steady state genetic gain is used as criterion to discriminate among breeding plans, because this criterion is not influenced by specific circumstances like the previous breeding plan or how the new breeding plan is implemented. This in contrast to criteria like the discounted returns, which take account of the selection response during the early years of selection.

The present model should describe dairy cattle breeding plans as open nucleus breeding plans, because this structure applies to many breeding schemes, e.g. the model should match a conventional progeny testing scheme, a nucleus breeding scheme (as proposed by Nicholas and Smith (1983)) and a sib testing scheme by varying the parameters that are to be optimized. There are three tiers: the male nucleus, the female nucleus and the base (i.e. the commercial cow population). The transfer rates between the tiers (the fraction to select from each tier) and the generation interval (i.e. the fraction to select from each age class) should be optimized by the model, because of the large number of parameters involved (i.e. the fraction to select from each age class within each tier), which renders a comparison between all possible combinations of values of these parameters impossible. The size of the nucleus

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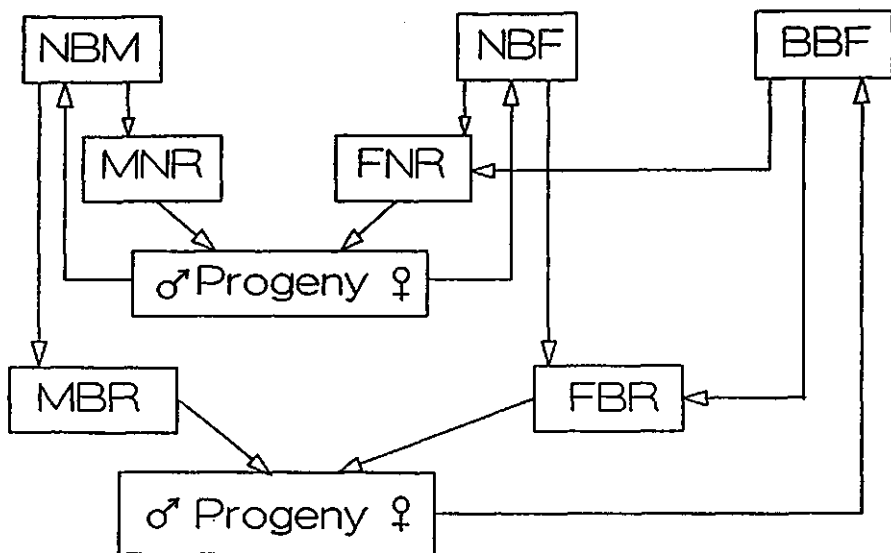
Figure 1. The open nucleus breeding system; MNR, males to breed nucleus
replacements; FNR, females to breed nucleus replacements; MBR, males to breed
base replacements; FBR, females to breed base replacements; NBM, nucleus born
males; NBF, nucleus born females; BBF, base born females.

and of the progeny test could be optimized by comparing alternatives for the
genetic response rate.

   First the model will be described followed by a demonstration of the model,
in which an artificial insemination (AI) breeding plan, without using MOET
(Multiple Ovulation and Embryo Transfer), is optimized. To make the model also
applicable to MOET plans, the possibility for animals to have full-sibs is
included.

                              THE MODEL

   In the model the population is divided into three tiers: the nucleus born
males (NBM), the nucleus born females (NBF) and the base born females (BBF).
Figure 1 shows the structure of the open nucleus breeding plan. Each tier is
subdivided into age classes and the age classes are subdivided into age
subclasses. Animals within an age subclass have a sire and a dam from the same

Table 1. The information sources.

	NBM	NBF	BBF
No. of progeny (bull was MBR as a 2-year-old)	$N(1000)^{1)}$		
No. of female full-sibs	m	$m^{2)}$	
No. of paternal half-sibs	1000	1000	1000
No. of full-sibs of sire	m	m	m
No. of half-sibs of sire	1000	1000	1000
No. of full-sibs of dam	m	m	
No. of half-sibs of dam	1000	1000	1000
Dam	1	1	1
No. of grand dams	2	2	2

No. of records considered is 1, 2 or 3, when the above mentioned animals
are 4, 5, or 6 years old (age at birth of selected offspring) respectively.
[1] Only one record per offspring is considered.
[2] m depends on the use of MOET on FNRs.

set of age classes and tiers. For example all the NBM of age 2 having a NBM
sire of age 4 and a BBF dam of age 5 are in the same age subclass. The age
classes are subdivided into age subclasses because the age of the sire and the
age of the dam of an animal influence the available amount of pedigree
information (e.g. compare a 4 year old untested sire with a 6-year-old progeny
tested sire). The animals within an age subclass are assumed to have an equal
amount of information available for the estimation of breeding values. In
practice, the amount of information will also differ within age subclasses,
but these differences are random, whereas the age of the sire and the dam is
determined by the model which optimizes the generation intervals.

The mean and the variance of the EBVs is calculated for every age subclass
using the selection index theory (Hazel, 1943). It is assumed here that the
variance of a selection index, including information of the animal itself, its
full-, half-sibs, its dam, its progeny, the full-, half-sibs of its sire and
of its dam and its granddam information, equals the variance of the BLUP-EBVs.
These information sources are only included in the index calculation when they
are available. Table 1 gives all the potential information sources and their
availability. The genetic correlation between different lactations of a cow is
taken as 1.0. Young bulls (2 year old) produce N female offspring (test bull)
and selected young bulls produce 1000 female offspring (selected bull). Thus,

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a 6-year-old bull will have N progeny records, when he was a test bull as a
two year old, and 1000 progeny records, when he was a selected bull as a two
year old. A selected bull produces more than 1000 female offspring, but the
additional offspring influence the accuracy and the variance of the EBVs only
marginally. The number of offspring of a test bull (N) is an input parameter
of the breeding programme. The variance of the EBVs of the 6-year-old bulls is
calculated by taking the mean of the variance of the EBVs of the bulls
weighted by the number of animals having 1000 or N progeny respectively.

The mean of the EBVs of an age class is calculated by taking the mean of the
genetic levels of the age subclasses weighted by the number of animals. The
variance of the EBVs of an age class is calculated by formula (1), which takes
account of the variance in EBV due to differences in mean between the age
subclasses (the second and third term in formula (1)).

$$\sigma^2_{EBVj} = \sum_{k=1}^{m} w_{jk}\sigma^2_{EBVjk} + \sum_{k=1}^{m} w_{jk}\mu^2_{jk} - (\sum_{k=1}^{m} w_{jk}\mu_{jk})^2 \qquad (1)$$

where: w_{jk}= relative number of animals in age subclass j k, where $\sum_{k=1}^{m} w_{jk}$=1
           for all ages j;

   m   = number of age subclasses within an age class;

   μ_{jk}= age subclass mean;

   σ_{EBVj}.= standard deviation of the EBVs of age class j.

The μ_{jk} and w_{jk} are calculated, when the age class is 'born' (as described
later).

There are four selection paths (see Figure 1): males to breed nucleus
replacements (MNR), males to breed base replacements (MBR), females to breed
nucleus replacements (FNR) and females to breed base replacements (FBR). Males
are selected from the male nucleus age classes by using the same truncation
point across the age classes. This maximizes the selection differential and
meanwhile optimizes the generation interval. Ducrocq and Quaas (1988)
described the algorithm used here to calculate this truncation point given the
number of animals that are to be selected. Females are selected from both the
NBF as well as the BBF age classes by using the same truncation point across
the NBF and the BBF age classes. This selection optimizes the generation

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interval within the NBF and within the BBF and optimizes the fractions
selected from the nucleus and from the base.

Besides the means and variances of the age classes, the number of animals
within each age class have to be specified, and these numbers depend on the
number of animals born and the rate of culling. Culling of cows is assumed to
have no effect on the rate of genetic progress for Korver and Renkema (1979)
found that the rate of genetic progress is hardly affected by culling for
production. The number of animals born and culled is fixed in the present
model and as a result the number of animals in each age class are constants
(input parameters).

By using normal distribution theory, the selected fraction and the
standardised selection differential are calculated for each age class within
each tier from the truncation points. In assuming random matings between the
selected males and females, the expected number of animals in the age
subclasses of the new born age class can be calculated (e.g. if one male is
selected from age class 2 and one from age class 3 and 10 females from age
class 2, then 10 animals will be born in age subclass 1 and 10 in age subclass
2, if 20 animals are born). This provides the w_{jk} for formula (1). The genetic
merit of the selected animals in an age class is calculated by:

$$S_j = \mu_{j.} + i_j \; \sigma_{EBVj}. \qquad (2)$$

where:

S_j = mean genetic merit of the selected animals in age class j;

i_j = standardised selection differential in age class j;

$\mu_{j.}$ = mean genetic level of age class j ($\mu_{j.} = \sum_{k=1}^{m} w_{jk} \; \mu_{jk}$)

The genetic merit (μ_{0k}) of the age subclasses of the new born age class equals
$\frac{1}{2}(S_j + S_{j'})$, where j and j' represent the age class of the sire and dam
respectively of age subclass 0k. The selection differentials used assume an
infinite population size and normal distributions. If the population is small,
order statistics should be used to calculate the selection differentials.

Thus, the model calculates the parameters of the new born age class (0) from
the parameters of the existing age classes. Now each age class becomes '1 year
older' (i.e. the parameters of age class 0 become those of age class 1, etc.).

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Then the parameters of age class 0 are calculated again. This procedure is repeated until the genetic gain per year is stable.

The input parameters of this model are the number of animals per age class in each tier (this includes the total size of the tier), the number of animals to select for each path (this includes the reproductive rates of the males and females), the size of the progeny test (N), the availability of the information sources (Table 1) and the genetic and phenotypic parameters of the trait under selection. The heritability of milk production is assumed to be 0.25 and the phenotypic standard deviation is set to 800 kg (this figure has only a scaling effect on the results). The phenotypic correlation between different records of a cow is assumed to be 0.4.

VARIANCE REDUCTION DUE TO SELECTION

The reduced (co)variances of the information sources of the selected animals in an age class are calculated by formula (3) (Cunningham, 1975), which is a generalization of Cochran's (1951) equation:

$$\sigma_{jk}{}^{*} = \sigma_{jk} - \sigma_{jI}\sigma_{kI}\ i_{\infty}(i_{\infty}-T)/\sigma_{II} \tag{3}$$

where: $\sigma_{jk}, \sigma_{jk}{}^{*}$ — covariance of j and k before and after selection respectively (if j=k the variance of j is indicated);

σ_{kI} (σ_{jI}) — covariance of index (selection criterion) and k(j) before selection;

σ_{II} — variance of selection index;

T — truncation point;

i_{∞} — standardised selection differential in a population of infinite size.

This formula is also used to calculate the reduced genetic variance and the covariances between the genotype for milk production and the information sources of the selected animals. The mean (co)variances of the selected animals (MNR's, FNR's, MBR's and FBR's) are calculated by taking the mean of the (co)variances within an age class weighted by the number of animals.

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The reduced (co)variances of age class 0 (the new born age class) are calculated from the reduced (co)variances of its sires and its dams (variance reduction due to inbreeding is neglected):

1. (Co)variances of pedigree information sources.

   These are obtained from the reduced (co)variances of the parents. The covariances between pedigree information of the sire and pedigree information of the dam is zero (neglection of inbreeding).

2. (Co)variances of own, full-, half sib and progeny information.

   The reduced variance of own performance information is $\frac{1}{4}\sigma^2_{gs}{}^* + \frac{1}{4}\sigma^2_{gd}{}^* + \frac{1}{2}\sigma^2_{g0} + \sigma^2_e$, where $\sigma^2_{gs}{}^*$, $\sigma^2_{gd}{}^*$, σ^2_{g0} and σ^2_e are the reduced genetic variances of the sires and dams, the unreduced genetic variance and the environmental variance respectively. The covariance of full-sibs is $\frac{1}{4}\sigma^2_{gs}{}^* + \frac{1}{4}\sigma^2_{gd}{}^*$. That of half-sibs is $\frac{1}{4}\sigma^2_{gs}{}^*$. The genetic variance in age class 0 is $\frac{1}{4}\sigma^2_{gs}{}^* + \frac{1}{4}\sigma^2_{gd}{}^* + \frac{1}{2}\sigma^2_{g0}$.

   The (co)variances of the progeny information is calculated in a similar way by using the genetic variances of the parents of the progeny.

3. Covariance between pedigree and non-pedigree (own, full- and half-sib information) information.

   The only link between, for instance, sire's pedigree information (P_{sp}) and own performance information (P_{own}), is the sires genotype (g_s). Thus the reduced covariance between P_{own} and P_{sp} equals $\frac{1}{2}\text{Cov}(P_{sp}, g_s)^*$ (i.e. the reduced covariance between P_{own} and g_s times the path correlation coefficient between the sire and the individual). Similarly, the covariances of P_{sp} with full-, half-sib and progeny information are $\frac{1}{2}\text{Cov}(P_{sp}, g_s)^*$, $\frac{1}{2}\text{Cov}(P_{sp}, g_s)^*$ and $\frac{1}{2}\text{Cov}(P_{sp}, g_s)^*$. The $\text{Cov}(P_{sp}, g_s)^*$ is obtained from equation (3). The covariances of dam's pedigree with own, full-, half-sib and progeny information are obtained in a similar way with all relationships vai the genotype of the dam. It should be noted that the path correlation coefficient between the dam and half-sibs is zero.

   This procedure of calculating the (co)variances of age class 0 gave the same results as formula (3) when this formula is used across generations. The use of formula (3) across generations requires the storage of the (co)variances of all the calculated generations and the covariances between these generations. This implies a practical limitation of the number of generations that can be calculated by using formula (3) across generations.

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AN EXAMPLE: OPTIMISING AN AI-BREEDING PLAN

This example is adapted to a dairy cattle industry with a closed population. It is assumed that MOET is not used and all progeny are born from AI-bulls. There are 1.5 million milk recorded cows and about 500 young bulls are progeny tested per year with about 100 heifer records per test bull. These numbers are only used to calculate the selected fractions. The selection differentials are not corrected for the finite population size. The Females to breed Nucleus Replacements (FNRs) are selected on their EBVs and on type, which is assumed to be uncorrelated to milk production. There are 10 dams selected per young bull on the EBVs and from these are 2 FNRs selected on type. Two FNRs produce on average one young bull (NBM) and one NBF per year. The FNRs are mated to the top 5 MNR bulls to produce nucleus replacements. There are 30 MBR bulls selected to sire the 70% best FBR cows to breed replacements for the cow population. It is assumed that 30% of the cows are replaced annually for reasons uncorrelated to the breeding goal. Selection for milk production is based on the EBVs of the animals irrespective of the accuracy of the EBV or the age of the animals. Table 2 shows the age distributions of the bulls and the cows.

Table 3 shows the steady state genetic response obtained, the genetic variance in the nucleus and base, the fraction of the FNR cows and of the FBR and FBR are fixed at 6, 6, 6 and 4 years respectively. Selection of the

Table 2. The age distribution of the bulls and cows due to unvoluntary culling.

Age class	percentage of cows	percentage of bulls
2	30.6	16.5
3	21.4	15.0
4	15.0	13.6
5	10.5	12.1
6	7.3	10.6
7	5.1	9.1
8	3.6	7.6
9	2.5	6.1
10	1.8	4.6
11	1.2	3.1
12	0.9	1.7

Table 3. The predicted results of the models A to E. The breeding plan and the models are described in the text and the abbreviations in Figure 1.

Models:	A.	B.	C.	D.	E.
Genetic gain (kg/yr)	116	110	166	115	77
Genetic standard deviation in nucleus (kg)	351	348	400	350	329
Gen. st. dev. in base (kg)	367	365	400	367	348
Fraction NBF of FNR (%)	4.04	4.79	4.31	0	0
Fraction NBF of FBR (%)	0.01	0.01	0.01	0	0
Generation interval MNR	4.26	4.56	2.38	4.32	6
Generation interval MBR	2.84	2.94	2.27	2.86	6
Generation interval FNR	2.83	2.97	2.41	2.84	6
Generation interval FBR	4.15	4.14	4.09	4.15	4

cows selected from the nucleus and the generation intervals of the MNRs, MBRs, FNRs and FBRs. These parameters were calculated using the following models:

A the full model as presented above,

B the same as A except that the extra variance due to differences in subclass mean are neglected (the 2nd and 3rd term of formula (1)),

C the same as A except that the variance reductions due to selection are

Table 4. The distribution of the use of selected animals over the age classes, for the 500 young bulls per year and 100 test records breeding plan.[1]

age classes:	% of MNRs	% of MBRs	% of FNRs from nucleus	% of FBRs from nucleus	% of FNRs from base	% of FBRs from base
2	42.0	72.9	2.4	0.0	54.5	23.6
3	4.8	7.7	0.7	0.0	15.0	23.1
4	3.3	3.4	0.5	0.0	17.4	17.9
5	0.1	0.2	0.2	0.0	6.6	14.1
6	37.7	11.7	0.1	0.0	1.9	10.1
7	9.4	3.2	0.0	0.0	0.3	6.6
8	2.1	0.8	0.0	0.0	0.0	3.7
9	0.4	0.2	0.0	0.0	0.0	1.8
10	0.1	0.0	0.0	0.0	0.0	0.7
11	0.0	0.0	0.0	0.0	0.0	0.2
12	0.0	0.0	0.0	0.0	0.0	0.0

[1]All individuals retained for possible use, if selected, unless forced to cull.

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neglected (the 2nd term of formula (3)),

D the same as A except that the female nucleus animals are neglected.

E the same as D except that the generation intervals of the MNR, MBR, FNR bull dams (FNR) is based on their first three lactation records. The FBR are selected at random, which gave an average generation interval of 4 years.

The response of the conventional progeny testing scheme (model E) with the fixed generation intervals was 34 % lower than the scheme with optimized generation intervals and selection across tiers (model A) (see Table 3). The response of model E was also predicted by formulas of Bulmer (1971) and Rendel and Robertson (1950) (see Appendix). The Appendix provides a test for the model, showing that the results of the model agree with the results of these calculations.

The predicted response increased by 43 % when the variance reduction due to selection was neglected (model C). This clearly demonstrates the impact of these variance reductions. Neglection of the female nucleus animals affects the response only marginally (model D). The required number of FNR cows decreases if MOET is used on these cows and as a result of their improved genetic merit the contribution of the nucleus females may become significant (Meuwissen and Ruane, 1989). Neglecting the extra variance due to the differences in subclass mean (model B) decreased the predicted genetic response by 5%. The majority of the MNRs, MBRs and FNRs were only selected from 2 or 3 age classes (see Table 4), which decreases the impact of the second and third terms of formula (1). The selection of mainly young animals (Table 4) is due to the high genetic gain, which decreases the probability of selecting older animals (since their genetic level is relatively low).

From Table 3 it appears that the generation interval is the major factor influencing the genetic variance by affecting selection accuracy. A shorter generation interval implies the selection of younger animals, which is less accurate. Thus, the genetic variance is less reduced. This reasoning does not apply to model C, where the variance reduction was neglected. Here the unreduced genetic variance in an increased genetic gain, which results in short generation intervals. Model E clearly shows that longer generation intervals result in a decreased genetic variance.

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The selection response in age class 1 of the base population from year 1 to 10 is on average 113 kg/year (the steady state response rate is 116 kg/year) when the breeding plan starts from an unselected population (which is unrealistic). During the first 10 years, the predicted genetic gain ranges from 0 to 255 kg/year, where a year with a low response is always followed by a year with a high response. Thus, although the starting situation is far from the equilibrium situation, the breeding plan approaches on average the steady state response very quickly. In a previously selected population with initial genetic differences between age classes, the genetic gain is expected to stabilize even faster, because the starting situation is closer to the equilibrium situation.

DISCUSSION

In the present model the standardised selection differentials were not corrected for finite population size. This correction is complex, if selection is across age classes and tiers. A conservative estimate of the selection differentials can be obtained by assuming that the predicted selected fractions of the age classes have to be realised (i.e. the selection differential across age classes is calculated as the weighted average of the selection differentials within age classes). This results in an underestimated selection differential, because selection across age classes implies optimal adaptation of the selected fractions to fluctuations of the age class means around their expectations. Hill (1976) provides formulas to correct the standardized selection differentials within age classes for the finite population size and the family structure, where the population is divided into unrelated families. If MOET is used, the population is divided into half-sib families which are subdivided into full-sib families. The next paper in this series will provide an approximation for this situation.

The conventional progeny testing scheme (model E) had a 34 % lower response rate than model A. This difference is mainly due to the optimization of generation intervals in model A, because the effect of selection across tiers is small (model A vs. model D) and the fraction of the genetic gain due to dams to breed dams is only 6 % (Everett, 1984). Thus, if BLUP EBVs are

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available, the selection of animals for their EBV, irrespective age, may lead to substantially increased response rates.

The variance reductions due to selection decreased the response rate by 30%. This suggests that the difference, between theoretical reponse rates and the reponses obtained in practice, might be mainly due to variance reduction due to selection and suboptimal generation intervals. According to Van Vleck (1987), the realised response rates are often 50 % less than predicted.

Differences in reponse rate between breeding schemes during the early years of selection were neglected. It was found that a breeding plan with annual optimization of the generation intervals approaches the steady state response rate very fast. Thus, the differences in financial returns from a breeding program due to differences in early response are probably negligible.

The present model can simulate many cattle breeding schemes that were described in the past, because these plans differed mainly in generation interval and/or selection across tiers. In essence, they are almost always open nucleus breeding schemes, with some fixed generation interval and selection across tiers (e.g. no selection across tiers gives a closed nucleus scheme). The optimization of this open nucleus breeding structure is greatly simplified by the use of BLUP sire and dam evaluation methods. By selecting the animals with the highest EBV across age classes and tiers, the generation interval and selection across tiers is optimized. The only parameters that still need optimization are the size of the nucleus and the size of the progeny test.

The present model neglects inbreeding, which occurs in finite populations. Inbreeding reduces the variance due to segregation of genes and may lead to inbreeding depression (due to dominant gene effects). If variance reduction due to inbreeding were included in the model, the genetic gain eventually declines to zero (Robertson, 1960). Thus, a time horizon has to be used to discriminate among breeding plans. Furthermore, the inbreeding rate has to be traded off against the costs of the breeding plan, because it is reduced by increasing the (effective) population size and by introducing foreign unrelated animals in the breeding stock.

Table 5. The effect of variance reduction due to inbreeding on the response to mass selection. The phenotypic variance, heritability and proportion selected in both sexes is 1, 0.6 and 0.1 respectively.

| Gene-ration | Effective population size | | | | |
| | 10 animals per generation | | | infinite[1] | |
	Genetic variance	Inbreeding coefficient	Genetic level	Genetic variance	Genetic level
0	0.60	0.00	0.00	0.60	0.00
1	0.44	0.05	1.05	0.45	1.05
2	0.39	0.10	1.89	0.43	1.91
3	0.37	0.14	2.67	0.42	2.73
4	0.36	0.19	3.41	0.42	3.55
5	0.34	0.23	4.13	0.42	4.37
6	0.32	0.26	4.82	0.42	5.18
7	0.31	0.30	5.50	0.42	6.00
8	0.30	0.34	6.14	0.42	6.81
9	0.29	0.37	6.77	0.42	7.63
10	0.27	0.40	7.37	0.42	8.44

[1] Inbreeding rate is zero.

Fortunately, in cattle breeding the time horizon is short relative to the generation interval. Thus, inbreeding will not affect the genetic progress very much before the time horizon is reached. Table 5 shows the effect of inbreeding on the selection response, when inbreeding depression is negligible. If the time horizon is 30 years and the generation interval is 6 years (i.e. the time horizon is five generations), the inbreeding coefficient of a plan with an effective population size of 10 animals per generation is 0.23 after 30 years. This inbreeding rate causes a 5 % reduction in genetic level. With a generation interval of 3 years (i.e. a time horizon of 10 generations) the inbreeding coefficient is 0.4 after 30 years and this causes a reduction in genetic level of 13 %. The genetic progress merit between the breeding schemes in Table 5 can be considered as maximum differences between breeding schemes caused by variance reduction due to inbreeding, because of the large difference in effective population size. Belonsky and Kennedy (1988) used Monte Carlo simulation to simulate pig breeding plans for 10 years of selection, which were 8-9 generations when selection and additional culling was based on BLUP breeding values. Although the inbreeding coefficients amounted up to 0.38, the response seemed to be unaffected by inbreeding (i.e. the genetic merit increased close to linearly over time). Thus, the effect of reduced genetic variances due to inbreeding on the response rate during a time

period of 9 generations is negligible. But inbreeding depression can also decrease the genetic gain and inbreeding increases the variance of the selection response.

Burrows (1984 a, b) predicted the inbreeding rate under selection for one generation and one sex. An extension of his approach to more (overlapping) generations and two sexes will be usefull. Trading off inbreeding rate against rate of gain remains subjective, but when breeding schemes are compared a correct predicted inbreeding rate will be informative to theoretical and practical breeders.

In the next paper in this series, an approximate formula will be developed, to account for the effect of a finite population of full- and half-sib families on the selection differentials. In a following paper the model will be used to optimize dairy cattle breeding schemes, with and without the use of MOET.

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APPENDIX

THE GENETIC GAIN OF A CONVENTIONAL BREEDING PLAN WITH FIXED GENERATION
INTERVALS.

Summary of the breeding plan:
- 500 young bulls progeny tested annually (they are 2 years old at birth of
100 female offspring)
- 5 MNR's and 30 MBR's are selected on 100 progeny records and have a
 generation interval of 6 years.
- 5000 FNR's are selected on 3 lactation records and have a generation
 interval of 6 years.
- FBR's are selected at random and have a generation interval of 4 years.
- the genetic, total environmental and permanent environmental variances are
160000, 480000 and 96000 respectively.

Calculations:
- number of bulls in age class 6 is 500 * 10.6 / 16.5 = 320 (see Table 2).
- number of cows in age class 6 is 1500000 * 0.073 = 110224.5 (see Table 2).
- fraction selected as MNR 5 / 320 = 0.015625
- fraction selected as MBR 30 / 320 = 0.09375
- fraction selected as FNR 5000 / 110224.5 = 0.04536
- the standardised selection differentials are 2.5102, 1.7852 and 2.1035 for
the MNR's, MBR's and FNR's respectively.
- fraction of BBF with young bull as sire (100*500)/(1500000*0.3)=0.1111
- when the response is stable over generations, the genetic variances are
  also stable over generations (Bulmer, 1971):

$$\sigma^2_{gs} = \tfrac{1}{4} \sigma^2_{gs} * R_{MNR} + \tfrac{1}{4} \sigma^2_{gd} * R_{FNR} + \tfrac{1}{2} \sigma^2_{g0} \qquad (A1)$$

$$\sigma^2_{gd} = \tfrac{1}{4} \sigma^2_{gs} * R_{MBR} + \tfrac{1}{4} \sigma^2_{gd} + \tfrac{1}{2} \sigma^2_{g0} \qquad (A2)$$

where:
$$R_{MNR} = 1 - r^2(EBV;g_s) \; i_{MNR}(i_{MNR}-T_{MNR}) \qquad (A3)$$
$$R_{MBR} = (1-r^2(EBV;g_s) \; i_{MBR}(i_{MBR}-T_{MBR})) * (1 - 0.11) + 0.11 \qquad (A4)$$
$$R_{FNR} = 1 - r^2(EBV;g_d) \; i_{FNR}(i_{FNR}-T_{FNR}) \qquad (A5)$$

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$$r^2(EBV; g_s) = 25\sigma^2_{gs}/(\tfrac{1}{4}\sigma^2_{gs}+\tfrac{1}{4}\sigma^2_{gd}+\tfrac{1}{2}\sigma^2_{g0}+480000+(99/4)\sigma^2_{gs}) \quad (A6)$$

$$r^2(EBV; g_d) = 3\sigma^2_{gd}/(\sigma^2_{gd}+480000+2(\sigma^2_{gd}+96000)) \quad (A7)$$

From (A2) follows $(3/4)\sigma^2_{gd} = \tfrac{1}{4} \sigma^2_{gs} * R_{MBR} + \tfrac{1}{2} \sigma^2_{g0}$ (A8)

Substitution of (A8) in (A1) provides after rearranging:

$$\sigma^2_{gs} = \sigma^2_{g0}(1/6\ R_{FNR} + \tfrac{1}{2})/(1 - \tfrac{1}{4}R_{MNR} - 1/12\ R_{FNR}\ R_{MBR}) \quad (A9)$$

Now formulas (A3) to (A9) are used iteratively to calculate σ^2_{gs} and σ^2_{gd}, with σ^2_{g0} as prior values. The iteration converged at 329.0 kg and 347.6 kg for σ_{gs} and σ_{gd} respectively. This implies that $r(EBV; g_s)$ and $r(EBV; g_d)$ are 0.9061 and 0.5919 respectively.

Substitution of these values in the formula of Rendel and Robertson (1950) gives:

$$\Delta G = \frac{(\Sigma\ I)}{(\Sigma\ L)} = \frac{(2.5102+1.7852(1-0.1111))*329*0.9061+2.1035*347.6*0.5919}{6 + 6(1-0.1111) + 2(0.1111) + 6 + 4}$$

= 76.7 kg/year (i.e. the same result as in Table 3).

where: ΔG the annual genetic gain

     Σ I is the sum of the selection differentials of the four paths
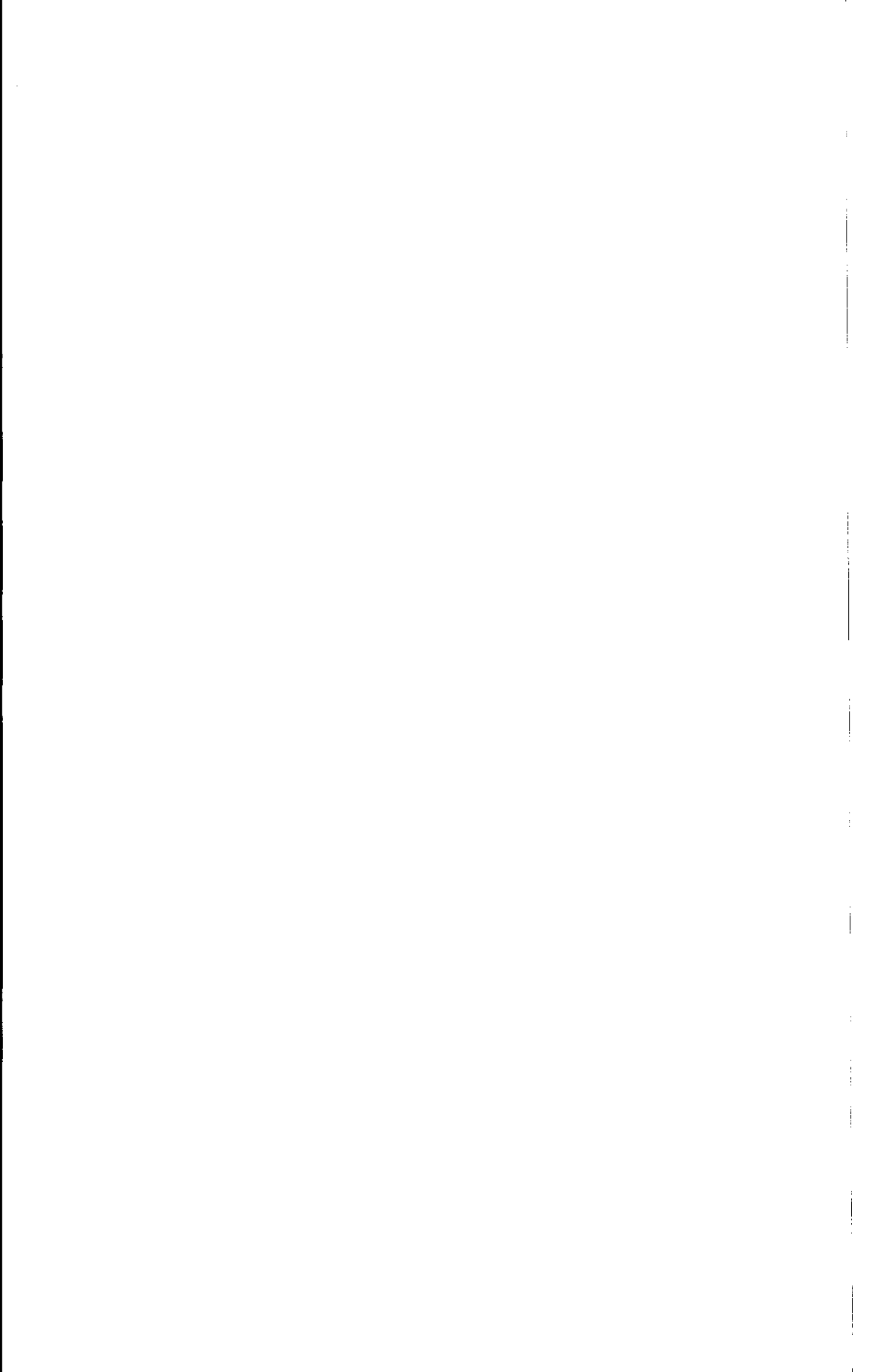
     Σ L is the sum of the generation interval of the four paths.

Chapter 3

REDUCTION OF SELECTION DIFFERENTIALS IN FINITE POPULATIONS
WITH A NESTED FULL-HALF SIB FAMILY STRUCTURE

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ABSTRACT

The effect of family structure is of increasing importance in modern
breeding schemes. Reasons are increased intra-class correlations between
relatives due to improved breeding value estimation methods which use all
family information, and increased family sizes possible with improved
reproduction rates. Also reduction of the generation intervals in modern
breeding schemes leads to increased intra-class (family) correlations, because
young animals have little information on individual or on progeny performance.

An approximation for the selection differential in a population divided into
families was derived. The result was then extended to an approximation for the
selection differentials in populations that are divided into full sib families
within paternal half sib families. The approximation was compared with Monte
Carlo results. It was concluded that the approximation was satisfactory (i.e.
rarely more than 5% in error). In some practical situations the approximation
was shown to be not more than 2% in error. With high intra-class correlations
and few animals selected, the reduction of the selection differentials is
maximal. When breeding values are based on family information and the family
structure is not accounted for, overestimation of the selection differentials
can be up to 61%.

INTRODUCTION

Modern sire and dam evaluation methods use all available information for the
prediction of breeding values. The use of more family information increases
the correlations between the estimated breeding values (EBVs) of family
members. The correlation between the EBVs of family members is called
intra-class correlation in this paper. Improved breeding schemes increase the
genetic gain. This results in the selection of more young animals, because
older animals tend to lag genetically (e.g. Hopkins and James, 1979). However,
young animals have little information on individual or on progeny performance.
Thus family information (on parents and collateral relatives - full sibs and
half sibs) dominates and the intra-class correlations of EBVs are high.

Increased correlations between EBVs in a finite population imply a reduction of the standardised selection differential (to be called selection differential) (Hill, 1976; Rawlings, 1976). Techniques such as AI (Artificial Insemination) and MOET (Multiple Ovulation and Embryo Transfer) increase the number of animals per family and decrease the number of families (with constant population size). This implies more family relationships and consequently more correlations between EBVs. Thus in modern breeding schemes the effect of the family structure on the selection differentials is increasing.

Hill (1976) and Rawlings (1976) provided exact formulas for the reduction of the selection differentials in finite populations of uniform families. Both authors also proposed approximate formulas. The exact formulas are difficult to use due to multiple numerical integrations. They also assume a population of uniform families. Whereas livestock populations usually consist of paternal half sib families, which are divided into full sib families (to be called a nested full-half sib family structure).

The aim of this paper is to provide an approximation for the calculation of the selection differential, when a finite population has a nested full- half sib family structure.

The approximation is found by first improving Rawlings' (1976) approximation. This approximation is poor if intra-class correlations are high. Next the formula was extended to match nested full-half sib family structures. The extended formula was compared with Monte Carlo simulation results.

A POPULATION CONSISTING OF UNIFORM FAMILIES

Rawlings' (1976) approximate formula is:

$$i_r(t) = \{1 - t(n_w-1)/(n_w n_f-1)\}^{\frac{1}{2}} i_r(0) \tag{1}$$

where: t = intra-class correlation between family members

$i_r(t)$ = reduced standardised selection differential with intra-class correlation t in a finite population

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n_w — number of animals within a family

n_f — number of families.

$i_r(0)$ is the reduced selection differential for uncorrelated EBVs (i.e. the family structure is neglected). The values for $i_r(0)$ are tabulated (e.g. Becker, 1975; Falconer, 1981) or approximated (Burrows, 1972). Formula (1) is an extension of the result by Owen and Steck (1962). Owen and Steck derived that $i_r(t)=(1-t)^{\frac{1}{2}}i_r(0)$, when all EBVs are equally correlated with correlation t. The term $t(n_w-1)/(n_w n_f-1)$ in formula (1) represents the mean intra-class correlation of all possible pairs of animals.

When t is high formula (1) overestimates the selection differential (Rawlings, 1976). To improve formula (1), the formula will be amended so as to give the correct selection differential at the extreme value of t=1. When t=1 all animals within a family have the same EBV. Thus the selection of the best animal out of $n_w n_f$ animals is equivalent to the selection of the best family out of n_f (uncorrelated) families, which can be approximated (Burrows, 1972) or obtained from standard tables (e.g. Becker, 1975; Falconer, 1981). In situations, where the number of animals selected is larger than n_w and not a multiple of n_w, the selection differentials have to be weighted (see Appendix). Formula (1) is forced to match $i_r(1)$ by varying the exponent (i.e. $\frac{1}{2}$ in formula (1)) with t:

$$i_r(t) = i_r(0) \ \{1-t(n_w-1)/(n_w n_f-1)\}^{w(t)} \qquad (2)$$

where:

$$w(t) = \tfrac{1}{2} \ (1-f(t)) + w(1)f(t) \quad \text{and} \quad 0<f(t)<1 \text{ for } 0<t<1 \qquad (3)$$

and: $\quad w(1) = \{\ln(i_r(1)) - \ln(i_r(0))\}/\ln\{1-(n_w-1)/(n_w n_f-1)\} \qquad (4)$

Thus exponent $w(t)$ is obtained by weighting the terms $\frac{1}{2}$ and $w(1)$ by the function $f(t)$. Formula (4) is obtained by solving equation (2) for $w(1)$ when t=1 (note that $i_r(1)$ is known).

Rawlings' approximation, which used $\frac{1}{2}$ as an exponent, performs well for small t. Thus the weighting function $f(t)$ has to be small for small values of t. When t approaches 1, $f(t)$ has to increase very quickly to make $f(1)=1$. The following function was found empirically to match the curve:

$$f(t) = a \ e^{b(t-1)} + (1-a) \ e^{c(t-1)} \qquad (5)$$

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where a,b and c are constants and b < c. Formula (5) is a weighted function of two exponential functions. In the first exponential term the b-factor is small so the function increases slowly. The second term has a large c-factor, which causes a rapid increase in function value when t approaches 1. The function was fitted to simulation data, which resulted in the following parameter estimates ($\pm$ s.d.):

$$a = 0.63 \ (\pm \ 0.005)$$
$$b = 3.36 \ (\pm \ 0.062)$$
$$c = 86 \quad (\pm \ 4.5).$$

The standard error of c is rather large, which means that the rapid increase in the function as t approaches one is not very well determined (for $0.95 < t < 1$). However, the correlation between EBVs of family members is usually not in this range: when own performance information is not available the correlation will be one, while if it is available the correlation will usually drop below 0.95. Since the second term in Formula (5) contributes only for $t > 0.95$ to f(t), it's only value is to make the approximation converge to $i_r(1)$. The second term can be omitted if this convergence is considered unimportant.

Hill's (1976) approximation is:

$$i_r(t) = i_\infty - (1-p)/\{2 \ i_\infty \ p(n_w n_f(1-t) + n_f t + 1)\} \qquad (6)$$

where: i_∞ = the selection differential for infinite populations

p = the selected fraction.

Formula (6) is an extension of Burrows' (1972) approximate formula for uncorrelated EBVs. The number of uncorrelated EBVs is weighted in formula (6) by the intra-class correlation (i.e. if t=0, there are $n_w n_f$ uncorrelated EBVs and if t=1 there are n_f uncorrelated EBVs). The results of the comparison of the formula (1), (2) and (6) are shown in Table 1. The subroutine SINTVI (Brascamp, 1978, pag. 93) is used in Tables 1 and 2 to approximate i_∞ and $i_r(0)$ (using Burrows' (1972) approximation for the latter). Approximations (1) and (6) were poor when the intra-class correlation was high, the number of families was small and these families consisted of many animals. The good performance of formula (2) in these situations is important, because this approximation will be used in the next section to approximate the selection

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Table 1. Approximated selection differentials for the selection of the best animal divided by the exact values as tabulated by Hill (1976) and Rawlings (1976). The approximations of Hill, Rawlings and Meuwissen correspond to Formula (6), (1) and (2) in the text respectively.

Population structure	Approxi-mation of	Intra-class correlation						
		0.0	.25	.50	.75	.90	.95	1.00
2 families	Hill	0.99	1.02	1.07	1.12	1.15	1.17	1.49
of 6 animals	Rawlings	0.99	1.00	1.03	1.13	1.31	1.44	2.11
	Meuwissen	0.99	0.99	1.00	0.99	0.99	1.02	1.04
6 families	Hill	0.99	0.99	0.99	0.98	0.98	0.98	1.08
of 4 animals	Rawlings	0.99	0.99	1.02	1.07	1.16	1.22	1.42
	Meuwissen	0.99	0.99	1.00	1.00	1.01	1.02	1.00
2 families	Hill	0.99	1.04	1.11	1.16	*)	0.57	negat.
of 24 animals	Rawlings	0.99	1.00	1.05	1.18	*)	1.63	2.80
	Meuwissen	0.99	0.99	1.00	0.99	*)	1.00	1.04

*)The exact values were not tabulated.

differential for the selection of full sib families, which are grouped into half sib families. Because of the use of AI, the number of half sib families is often small and the number of full sib families per half sib family can be large.

A POPULATION WITH A NESTED FULL-HALF SIB FAMILY STRUCTURE

The extension of Rawlings' (1976) approximation (1) to more complicated family structures is straightforward, since the term $t(n_w-1)/(n_w n_f-1)$ represents the mean intra-class correlation of all pairs of animals. For a nested full-half sib family structure the average intra-class correlation over all pairs of animals is:

$$t_{av}(t_{FS}, t_{HS}) = (t_{FS}(n_w-1) + t_{HS}n_w(n_{FS}-1)) / (n_w n_{FS} n_{HS}-1) \qquad (7)$$

where: t_{FS} = the intra-class correlation between full sibs

t_{HS} = the intra-class correlation between half sibs

n_{HS} = the number of half sib families

n_{FS} = the number of full sib families per half sib family

n_w — the number of animals within a full sib family.

Rawlings' approximation for a nested full-half sib family structure is now:

$$i_r(t_{FS},t_{HS}) = i_r(0,0) \{1-t_{av}(t_{FS},t_{HS})\}^{\frac{1}{2}} \qquad (8)$$

where: $i_r(t_{FS},t_{HS})$ — the reduced selection differential with intra-class correlations t_{FS} and t_{HS}.

The extension of formula (2) is less straightforward. In a nested full- half sib family structure there are three situations, in which the reduced selection intensities can be obtained from tables or formulas for uncorrelated variables:

A. $t_{HS}=t_{FS}=0$: there are $n_w n_{FS} n_{HS}$ unrelated animals,

B. $t_{HS}=0$ and $t_{FS}=1$: there are $n_{FS} n_{HS}$ unrelated full sib families,

C. $t_{HS}=t_{FS}=1$: there are n_{HS} unrelated half sib families.

Thus $i_r(0,0)$, $i_r(1,0)$ and $i_r(1,1)$ are known. Since $t_{FS}>t_{HS}$, all possible combinations of t_{FS} and t_{HS} form a triangle in a two dimensional space with the boundary points $(0,0)$, $(1,0)$ and $(1,1)$ (where for instance the point $(1,0)$ indicates the point where $t_{FS}=1$ and $t_{HS}=0$). Approximation (2) will be used three times here, to obtain $i_r(t_{FS},t_{HS})$. At first formula (2) will be used along the line between the points $(1,0)$ and $(1,1)$, using the known values of $i_r(1,0)$ and $i_r(1,1)$ to obtain $i_r(1,t_{HS})$. Secondly the line between the points $(0,0)$ and $(1,1)$ will be approximated using $i_r(0,0)$ and $i_r(1,1)$ to obtain $i_r(t_{HS},t_{HS})$. And thirdly the line between the points (t_{HS},t_{HS}) and $(1,t_{HS})$ will be approximated using $i_r(t_{HS},t_{HS})$ (from the second approximation) and $i_r(1,t_{HS})$ (from the first approximation) to obtain $i_r(t_{FS},t_{HS})$.

If $t_{FS}=1$ (i.e. along the line between $(1,0)$ and $(1,1)$), the EBVs of all animals within a full sib family are equal to the full sib family mean. Thus the population consists of n_{HS} half sib families and within each half sib family there are n_{FS} full sib family means. Using Formula (2), the first approximation along the line between $(1,0)$ and $(1,1)$ is:

$$i_r(1,t_{HS}) = i_r(1,0) \{1-t_{HS}(n_{FS}-1)/(n_{FS}n_{HS}-1)\}^{w(t_{HS})} \qquad (9)$$

where: $w(1) = \{\ln(i_r(1,1)) - \ln(i_r(1,0))\} / \ln\{1-(n_{FS}-1)/(n_{FS}n_{HS}-1)\}$ and the formulas (3) and (5) are required to calculate the weighed $w(t_{HS})$ from $w(1)$.

The second approximation along the line between $(0,0)$ and $(1,1)$ is:

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$$i_r(t_{HS}, t_{HS}) = i_r(0,0) \ \{1 - t_{HS}(n_w n_{FS} - 1)/(n_w n_{FS} n_{HS} - 1)\}^{w(t_{HS})} \tag{10}$$

where: $w(1) = \{\ln(i_r(1,1)) - \ln(i_r(0,0))\} \ / \ \ln\{1 - (n_w n_{FS} - 1)/(n_w n_{FS} n_{HS} - 1)\}$ and the formulas (3) and (5) are required to calculate the weighted $w(t_{HS})$ from $w(1)$.

Now $i_r(t_{FS}, t_{HS})$ is approximated along the line between (t_{HS}, t_{HS}) and $(1, t_{HS})$. Along this line the EBVs do not change from a set of independent EBVs at one end and another set of independent EBVs at the other end. Thus approximation (2) is somewhat modified:

$$i_r(t_{FS}, t_{HS}) = i_r(0,0) \ \{1 - t_{av}(t_{FS}, t_{HS})\}^{v(t_{FS}, t_{HS})} \tag{11}$$

where: $v(t_{FS}, t_{HS}) = v(0, t_{HS}) \ (1 - f(t_{FS})) + v(1, t_{HS}) \ f(t_{FS}) \tag{12}$

and: $v(1, t_{HS}) = \{\ln(i_r(1, t_{HS})) - \ln(i_r(0,0))\}/\ln(1 - t_{av}(1, t_{HS}))$

$$v(0, t_{HS}) = \{v(t_{HS}, t_{HS}) - v(1, t_{HS}) f(t_{HS})\}/(1 - f(t_{HS}))$$

$$v(t_{HS}, t_{HS}) = \{\ln(i_r(t_{HS}, t_{HS})) - \ln(i_r(0,0))\}/\ln(1 - t_{av}(t_{HS}, t_{HS}))$$

where $f(t_{FS})$ and $f(t_{HS})$ are from formula (5). Thus $v(1, t_{HS})$ and $v(t_{HS}, t_{HS})$ are chosen such that equation (11) equals $i_r(1, t_{HS})$ and $i_r(t_{HS}, t_{HS})$ respectively. $v(0, t_{HS})$ is chosen such that the weighed mean of $v(0, t_{HS})$ and $v(1, t_{HS})$ equals $v(t_{HS}, t_{HS})$, if t_{FS} equals t_{HS} in formula (12).

When only one sire is selected (i.e. only one half sib family) Formula (11) cannot be applied. If there is only one half sib family, $i_r(1,1)$ will be zero and the logarithm of $i_r(1,1)$ does not exist. However, this situation will not occur often because of inbreeding considerations.

Approximation (11) was compared with the mean selection differential in 2000 Monte Carlo simulations for various sets of intra-class correlations and family structures. The results were satisfactory in the sense that the approximation was rarely more than 5% in error, and was not found to be more than 10% in error. The largest deviations arose from large intra-class correlations ($t_{FS} = 1$ and $t_{HS} = 0.9$) and small numbers of half sib families ($n_{HS} = 2$).

Table 2 shows the reduced selection differentials of selected sires predicted by neglecting the family structure (i.e. the reduced selection

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Table 2. The selection differentials in the selection of sires in some breeding plans predicted by the selection differentials for uncorrelated variables (A), approximation (8) (see text) (B), approximation (11) (see text) (C), and by Monte Carlo simulation (2000 replicates) (D). The number of sires per full sib family is 5.

Breeding Plan	Trait (h^2)	Total no. of males (info-sources)		No. of sires per round of selection (n_{HS})	
			2	5	10
1 Bull sire selection in progeny testing*) scheme	Milkproduction (0.25)	200 bulls (100 daughter records)	t_{FS}/t_{HS} 0.43/0.22	0.43/0.22	0.43/0.22
			A 2.580	2.297	2.040
			B 2.423	2.242	2.014
			C 2.384	2.224	2.007
			D 2.390	2.218	2.008
2 Adult MOET nucleus breeding**) scheme	Milkproduction (0.25)	200 bulls (5 full sibs $(40/n_{HS}-1)*5$ HS's 1 dam)	t_{FS}/t_{HS} 1/0.64	1/0.56	1/0.45
			A 2.580	2.297	2.040
			B 2.110	2.157	1.984
			C 1.604	1.951	1.901
			D 1.603	1.931	1.908
3 Pig nucleus (littersize is 10 piglets)	Growth rate (0.25)	200 boars (own performance)	t_{FS}/t_{HS} 0.13/0.06	0.13/0.06	0.13/0.06
			A 2.580	2.297	2.040
			B 2.530	2.281	2.033
			C 2.525	2.297	2.032
			D 2.529	2.281	2.029
4 Pig nucleus (littersize is 10 piglets)	Growth rate (0.25)	200 boars (own performance 9 full sibs $(40/n_{HS}-1)*10$ HS's 1 dam)	t_{FS}/t_{HS} 0.78/0.50	0.76/0.42	0.73/0.33
			A 2.580	2.297	2.040
			B 2.224	2.193	2.000
			C 2.039	2.123	1.976
			D 2.060	2.100	1.971
5 Pig nucleus (littersize is 10 piglets)	Growth rate (0.25)	100 boars (own performance 9 full sibs $(20/n_{HS}-1)*10$ HS's 1 dam)	t_{FS}/t_{HS} 0.76/0.44	0.73/0.32	0.70/0.22
			A 2.328	2.018	1.730
			B 2.041	1.937	1.696
			C 1.886	1.894	1.684
			D 1.895	1.886	1.673

*) Bull dams have 10 offspring per year by using MOET (Multiple Ovulation and Embryo Transfer).
**) Like the breeding plans proposed by Nicholas and Smith (1983). Selection of full sib sires is allowed.

differential for uncorrelated breeding values), by formula (8), by formula (11) and by Monte Carlo simulation for a progeny testing scheme (scheme 1; selection for progeny information), an adult MOET scheme (scheme 2; selection on full- and half sib information) and three pig breeding schemes (scheme 3: selection on individual performance; schemes 4 and 5 : selection on individual performance and on full- and half sib information). In the schemes 1 to 4, the sires are selected from 200 selection candidates (40 full sib families with 5 full sibs per family). The number of half sib families is varied from 2 to 10. In scheme 5, the sires are selected from 100 candidates (20 full sib families and 5 full sibs per family). The reduced selection differentials for uncorrelated EBVs (A in Table 2) overestimate the Monte Carlo selection differentials. With high intra-class correlations (scheme 2) and few sires selected, the overestimation was 61% (or: the Monte Carlo selection differential was 38% lower than predicted from tables for uncorrelated EBVs). Rawlings' formula (8) provided a good approximation for the Monte Carlo selection differentials, when low intra-class correlations were present (schemes 1 and 3). Formula (8) overestimated the Monte Carlo selection differentials for scheme 2 considerably (by up to 32%). Under these practical circumstances the results of approximation (11) deviated less than 2 % from the Monte Carlo simulation results.

DISCUSSION

Finite numbers affect the variance of EBVs: when there are s families, the between family variance is reduced by a factor $1/s$. However, it is not correct to adjust both the selection differential and the variance for finite numbers. The reduced selection differential can be seen as the expected mean value of the m highest ranking of n animals, when the n animals are drawn at random from an infinite population of animals. Thus the variances for infinite populations should be used.

In this paper selection differentials are adjusted for correlations among EBVs of full- and half sibs. Apart from full- and half sibs, more distant relationships also occur (e.g. animals with the same grandsire). The influence of these other relationships on the selection differentials

probably is negligible, because of the low intra-class correlations involved.

The intra-class correlations are assumed to be the same among all full sibs and among all half sibs. Thus selection differentials can only be predicted for selection within categories of animals with uniform intra-class correlations (i.e. the EBVs are based on similar types of information). In deterministic models for the prediction of genetic gain, usually all animals within an age class are assumed to have the same kind of information, but an extension of the current results to non-uniform family size would extend the scope of the deterministic methods.

The reduction of the selection differential is larger in breeding schemes where much family information is used (i.e. scheme 2 and 4) and where the proportions selected are low (see Table 2). On the other hand using more family information increases the accuracy of selection (i.e. the correlation between the selection index, containing the information sources, and the breeding goal). For example, in the pig breeding schemes in Table 2 with selection of five boars per round of selection, the accuracy of selection in scheme 3 and 4 is 0.5 and 0.63 respectively. The product of the selection differential and the accuracy of selection is 1.14 and 1.32 respectively. Thus the superiority of scheme 4 over 3 is 16% instead of 26% as would be expected from the increased accuracy in scheme 4. It illustrates that inclusion of extra sources of information generally increases the rate of genetic gain, but the improvement is much lower than would be expected from the increase in accuracy alone.

Breeding schemes 4 and 5 differ in the number of selection candidates. In scheme 4 and in 5, the selection of 2 or 5 sires gave approximately the same reduced selection differentials and the selection of 10 sires gave a lower selection differential. The selection of 2, 5 or 10 sires corresponds to the selection of 1, 2.5 and 5 % respectively in scheme 4 and to 2, 5 and 10 % respectively in scheme 5. Thus the reduced selection differentials are more influenced by the number of sires selected than by the proportion selected.

Selection differentials, which are uncorrected for the correlations between EBVs, increase when the number of sires selected decreases (row A in Table 2). The reduced selection differentials for correlated EBVs increase less markedly or even decrease with a decreasing number of sires selected (row D in Table 2). The selection of a small number of sires

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implies the selection from a small number of half sib families in the next generation. Selection from fewer families decreases the selection differential. The number of sires selected is a trade-off between selection differential (calling for small numbers) versus inbreeding and genetic drift (calling for large numbers). The balance is shifted towards larger numbers of sires, when the effect of the family structure on the selection differential is taken into account.

Table 2 shows, that selection differentials should be corrected for family stucture, since the uncorrected differentials (A in Table 2) can overestimate the correct differentials by up to 61%. When the intra-class correlations are small (i.e. the EBVs do not contain much family information) or the number of selected sires is greater than 10, approximation (8) is probably satisfactory. It can be calculated on a pocket calculator, whereas for approximation (11) a computer subroutine is recommended. A computer subroutine using approximation (11) can be obtained from the author on request. Approximation (11) provided satisfactory results for a wide range of family structures and intra-class correlations; the predicted values were usually correct within a few percent and were rarely more than 5 % in error.

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APPENDIX

<u>The calculation of the reduced selection differential, when all animals within a family have the same estimated breeding value, from the reduced selection differentials of uncorrelated variates.</u>

The required selection differential is:

$$i = (n_w x_1 + \ldots + n_w x_a + n_r x_{a+1})/n_s$$

where: n_w = number of animals per family

x_i = expected value of ith ranking variate of n_f independent multi normal distributed variates

n_f = number of families

n_s = number of animals selected

n_r = number of animals selected from (a+1)th ranking family

a = number of families with all animals selected

The following selection differentials for uncorrelated variates are needed:

$$i_1 = (n_w x_1 + \ldots + n_w x_a)/(n_w a)$$

$$i_2 = (n_w x_1 + \ldots + n_w x_{a+1})/(n_w (a+1))$$

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i_1 and i_2 are the selection differentials for the selection of a and a+1 animals respectively from n_r unrelated animals. After some rearrangements :
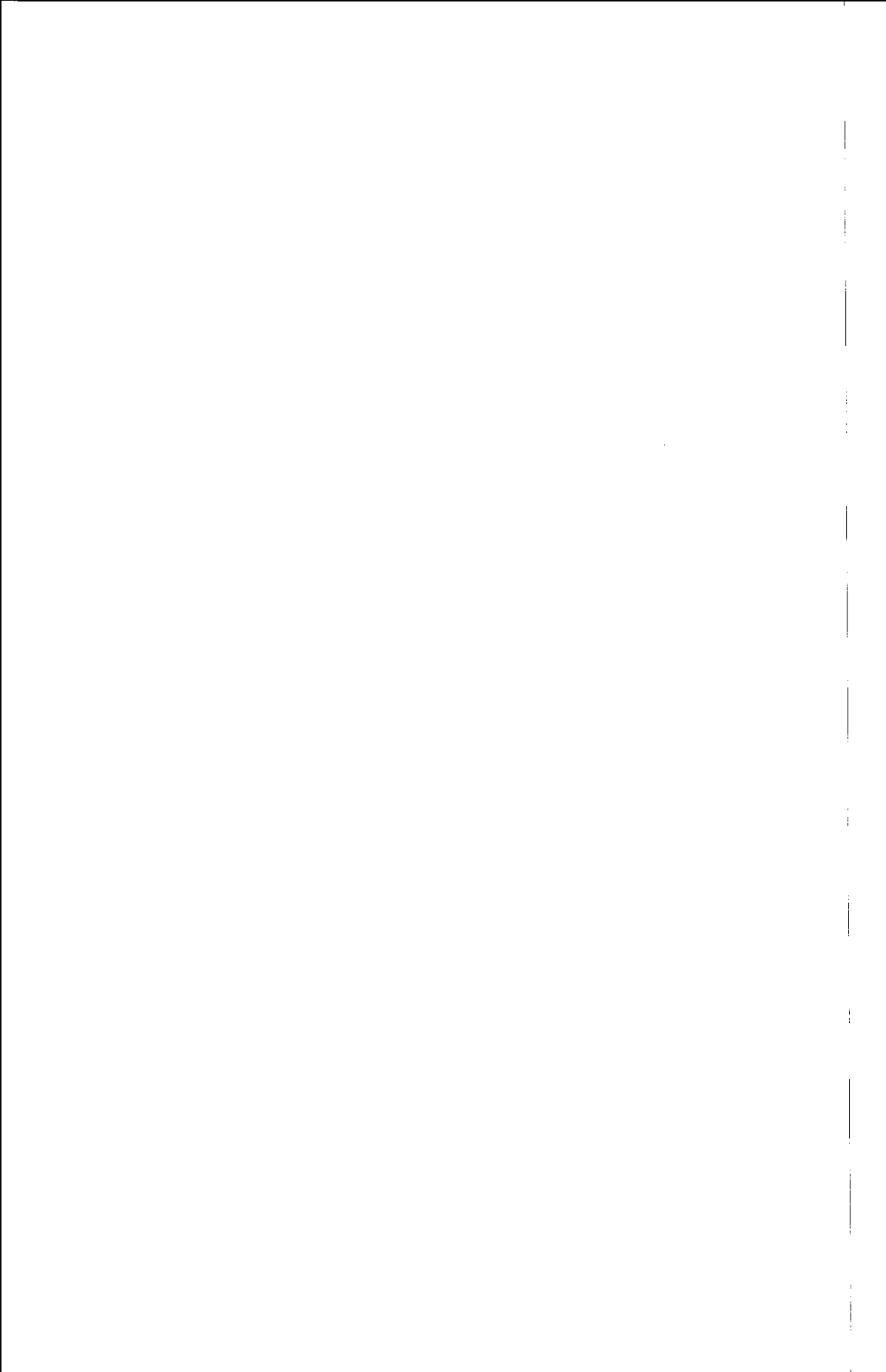
$$i = (i_1 \ a \ (n_w - n_r) + i_2 \ (a+1) \ n_r)/n_s$$

Chapter 4

THE USE OF INCREASED FEMALE REPRODUCTIVE RATES
IN DAIRY CATTLE BREEDING SCHEMES

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ABSTRACT

The effect of increased female reproductive rates on selection response,
on efficiency of progeny testing and on the openness of the nucleus was
investigated in open nucleus breeding plans. Conventional progeny testing
plans and closed nucleus plans are special classes of open nucleus plans.
In the open nucleus plans, generation intervals and selection across tiers
were optimised. The number of offspring per elite dam was varied from 1 to
41, progeny testing of young bulls in the female base population was varied
from 0 to 100 test records, and the size of the nucleus was varied from 250
to 2000 young bulls born per year. Also efficiency of selection was varied:
efficient selection in T(heoretical)-schemes and less efficient selection
in P(ractical)-schemes. Especially selection of base parents was less
efficient in P-schemes.

The deterministic prediction model took account of variance reduction due
to selection and reduction of selection differentials due to correlations
between estimated breeding values of relatives (order statistics). For
closed nucleus plans, the results of the model were verified with Monte
Carlo simulation results.

By increasing female reproductive rates, genetic gain increased by a
factor 0.08 and 0.16 for the T- and P-schemes respectively. The nuclei in
P-schemes were less open, due to the less efficient selection in the
female base population. Schemes that were less open benefited more from
increased female reproductive rates, because selection differentials in
small nuclei increased more than those in large base populations. The
optimal open nucleus plan became less open with increasing female
reproductive rates. Generally, progeny testing of bulls reduced genetic
gain (by up to a factor 0.1), but it also reduces inbreeding rates. Progeny
testing was more efficient in schemes that are less open: in P-schemes with
41 offspring per dam, progeny testing increased genetic gain. With many
offspring per dam there were fewer full sib families, causing lower
selection differentials due to order statistics effects. This effect could
be prevented by increasing the size of the nucleus.

INTRODUCTION

In dairy cattle breeding, MOET (Multiple Ovulation and Embryo Transfer) is increasingly used to improve reproductive rates of selected cows. The question arises how to make optimal use of techniques, that increase female reproductive rates, in dairy cattle breeding.

Nicholas and Smith (1983) proposed MOET nucleus breeding plans to make use of increased female reproductive rate. Characteristics are selection of sires and dams within a closed nucleus herd, short generation intervals and selection on family information (see Ruane, 1988, and Colleau, 1989, for reviews). Response rates predicted by Woolliams and Smith (1988), who corrected those of Nicholas and Smith, were up to twice the response rates of conventional progeny testing schemes. The responses were predicted by a deterministic model (i.e. theoretical predictions). Juga and Maki-Tanila (1987) used Monte Carlo simulation to estimate response rates of MOET schemes. The simulated genetic gains were about half the predicted genetic gains and in very small nucleus simulated were smaller than deterministic predictions of genetic gains of conventional large scale progeny testing schemes. This difference between deterministic and stochastic prediction of genetic gain occurred because the deterministic model did not account for reduction of variances due to selection nor for decreased selection differentials due to order statistics. The latter effect is enhanced by correlations among EBV (Estimated Breeding Values) of relatives (Hill, 1976).

The following modifications to the original Nicholas and Smith MOET plans have been proposed in the literature (see Ruane, 1988, and Colleau, 1989):
- young bulls are progeny tested;
- the nucleus is opened to superior animals outside the nucleus;
- nucleus females are spread over commercial herds.

When unbiassed comparison of lactation records across herds is feasible, the latter modification does not affect genetic gain. Figure 1 shows the structure of an open nucleus breeding plan. Open nucleus and conventional progeny testing schemes are similar: Nucleus Born Males (NBM) correspond to young bulls in progeny testing plans; Nucleus Born Females (NBF) correspond to daughters of bull dams; and Base Born Females (BBF) correspond to daughters of cow dams (i.e. the large majority of the commercial cow population). Essential factors are whether young bulls are progeny tested and whether the nucleus is open or closed.
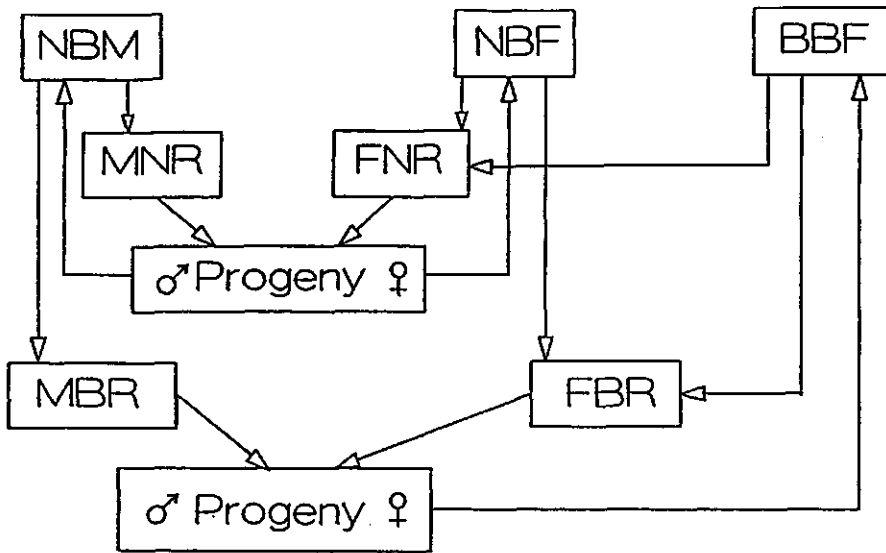
Figure 1. The open nucleus breeding system (Meuwissen, 1989); MNR, males to breed nucleus replacements; FNR, females to breed nucleus replacements; MBR, males to breed base replacements; FBR, females to breed base replacements; NBM, nucleus born males; NBF, nucleus born females; BBF, base born females.

Best Linear Unbiased Prediction (BLUP) EBV are corrected for genetic trend: EBV of animals of different age classes can be compared directly. Therefore, generation intervals will be optimised by selecting for high EBV across age classes (James, 1987). Consequently, predefining generation intervals for breeding plans is not necessary and will decrease (short term) genetic gain.

EBV also account for differences in pedigree between nucleus and base animals. In open nucleus plans, selection across nucleus and base is optimised by selecting for high EBV across tiers. Consequently, closing the nucleus will decrease genetic gain. However, in open nucleus plans selection across commercial herds might be biassed by preferential treatment. Selecting within a closed nucleus herd may overcome this problem.

This study investigates the effects of an increased reproductive rate of Females to breed Nucleus Replacements (FNR; see Figure 1) on the response rate, on the efficiency of progeny testing young bulls and on the 'openness' of the open nucleus plan. The size of the nucleus is varied. Because the efficiency of selection in all paths affects the genetic gain

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and structure of the optimized plan, the efficiency of the selections is
varied: efficient selection in T(heoretical)-schemes and less efficient
selection in P(ractical)-schemes. The deterministic model used here
accounts for variance reductions due to selection and reduced selection
differentials due to correlations between EBV of relatives (order
statistics).

Because of the large difference in predicted genetic gain between the
deterministic model of Nicholas and Smith (1983) and the stochastic model
of Juga and Maki-Tanila (1987), the deterministic model used here is tested
by Monte Carlo simulation. To save computer time, only a closed nucleus was
simulated.

METHODS

Breeding schemes

In Table 1 the parameters for the open nucleus breeding plans are
presented. Response rates can be predicted for theoretical breeding
schemes. Restrictions and inefficiencies that occur under practical
circumstances may hamper theoretical recommendations. The
T(heoretical)-schemes do not account for practical restrictions and
inefficiencies. In consultation with Dutch AI organisations some of these

Table 1. The parameters of the open nucleus breeding plans (see Figure 1
for the abbreviations).

	T(heoretical)	P(ractical)
No of pedigreed, milk recorded cows	1,500,000	1,500,000
No of NBM born/yr (= no. NBF born/yr)	M	M
No of MNR selected per year	5	10
No of MBR selected per year	30	30
No of FNR selected per year	$2M/n$	$5M/n$[*]
No of FBR selected per year	1,050,000	no selection
No of test records per young bull	N	N
Maximum no of progeny per bull per yr	35,000	35,000
Maximum no of progeny of 2 yr old bull	35,000	4,400
Involuntary culling of bulls in each age class (fraction of no of 2 yr old bulls)	0.05	0.05
Involuntary culling of cows in each age class (fraction of no of cows in age class)	0.30	0.30
Evaluation method of bulls and cows	Animal model	
Selection criterion	Estimated Breeding Value	
Generation interval	Optimised	

[*] n denotes the number of offspring per FNR per year

restrictions and inefficiencies are identified and modelled in the
P(ractical)-schemes: i) the number of FNR is 2.5 times as high in the P-
than in the T-schemes, to account for additional selection of FNR for
secondary traits (uncorrelated to milkproduction); ii) the selection
differentials of the FBR are assumed to be negligible low in the P-schemes
since selection of FBR is in commercial herds; and iii) the number of MNR
is twice as high in the P- compared to the T-schemes. Modification iii) was
introduced since the maximum number of offspring of a 2-year-old bull (age
at birth of offspring) is reduced because of low semen production of young
bulls and because young bulls can only produce semen after sexual maturity
is reached (i.e. when the bull is about 1 year old).

The number of NBM born per year (M), the number of test records per young
bull in the base population (N) and the number of progeny per FNR surviving
to two years of age (n) are varied:

    M = 250, 500, 1000 or 2000 NBM per year;
    N = 0, 50 or 100 test records per young bull;
    n = 1, 3, 11, 21 or 41 offspring per FNR.
The NBM and NBF have (n-1)/2 contemporary female full sibs, that complete
at least one lactation. A fraction 0.7 and 0.49 of these full sibs complete
a second and a third lactation respectively.

Model

The model described by Meuwissen (1989) will be used here to predict the
steady state genetic gain. The breeding plans are described as open nucleus
breeding plans. Progeny testing of young bulls in the base population is
optional. There is no progeny testing in the nucleus. The selection indices
allowed for own performance, full- and half sib information of the
selection candidate, of its sire and of its dam and progeny information.
(Provided that these sources of information are available.) This is
considered equivalent to selection for BLUP breeding values predicted by an
animal model. Selection is across age classes and tiers. When all FNR
(Figure 1) are selected from the nucleus, the optimum scheme is a closed
nucleus scheme as proposed by Nicholas and Smith (1983). The selection
indices in the model are adjusted for reductions of (co)variances due to
previous selections. Thus the model accounts for reduction in variance of
sources of information that were previously under selection and for

reduction in genetic variance due to linkage disequilibrium (Bulmer, 1971), but not due to inbreeding.

The approximation of Meuwissen (1990) is used to calculate the order statistics of the finite population accounting for the correlations between EBVs of full- and paternal half sibs. These were used to estimate selection differentials. The selection differentials across age classes are approximated by weighting the within age class selection differentials. The relative contributions of age classes to the total number of animals selected are used as weighing factors. These contributions were not corrected for order statistics.

Selection is for milk production (i.e. an aggregate trait, which might include milk, fat and protein yield). In the base population, i.e. prior to selection, the heritability, phenotypic standard deviation (σ_{p0}) and phenotypic and genetic correlations between lactations are assumed to be 0.25, 1, 0.4 and 1, respectively.

Simulation

A closed nucleus plan was simulated involving the annual selection of 5 sires and 100 dams to produce 4000 offspring a year (40 offspring per dam). No fixed effects were simulated. For the Monte Carlo simulations it was assumed that the 2-year-old bulls (180 bulls) are unvoluntary culled between age k and k+1 with probability 0.09, where k is 2,3,..,12. The probability that a cow is culled during a year is 0.3. The genotype of the animals were simulated by formula (1).

$$g_i = \tfrac{1}{2}g_s + \tfrac{1}{2}g_d + \sqrt{(\tfrac{1}{2})}\ h\ a_{1i0} \tag{1}$$

where g_i, g_s and g_d is the additive genetic value of the individual i, its
sire and its dam respectively;
h is the square root of the heritability in base population
($h^2 = 0.25$);
a_{ijk} is a random number from the distribution $N(0,1)$
($Cov(a_{ijk}, a_{i'j'k'}) = 0$, when $i \neq i'$, $j \neq j'$ and/or $k \neq k'$).
Both the deterministic and the Monte Carlo model do not account for variance reduction due to inbreeding nor inbreeding depression. The kth lactation of cow j was simulated by formula (2).

$$P_{jk} = g_j + E_{pj} + E_{tjk} \qquad (2)$$

and $\quad E_{pj} = \sqrt{(r_p - h^2)} \; a_{2j0}$

$\qquad E_{tjk} = \sqrt{(1 - r_p)} \; a_{3jk}$

where: P_{jk} is the kth lactation of the jth cow;

$\qquad E_{pj}$ is the permanent environmental effect of the jth cow;

$\qquad E_{tjk}$ is the temporary environmental effect of cow j in lactation k;

$\qquad r_p$ is the phenotypic correlation between lactations.

The breeding values of bulls and cows were evaluated by solving equations (3).

$$[Z'R^{-1}Z + A^{-1}/\sigma_{g0}^2] \; EBV = Z'R^{-1}y \qquad (3)$$

where: Z — incidence matrix of observations,

$\qquad$ A — matrix of additive genetic relationships among animals,

$\qquad$ EBV — vector of estimated breeding values,

$\qquad$ y — vector of average lactation records,

$\qquad$ R — variance-covariance matrix of environmental effects:

$\qquad\qquad$ diagonals: $(r_p - h^2) + (1 - r_p)/m_j$, where m_j is the number of

$\qquad\qquad\qquad$ lactations of cow j;

$\qquad\qquad$ off-diagonals: 0.

$\qquad \sigma_{g0}^2$ — genetic variance in base population (prior to selection).

The equations were solved by Jacobian iteration (e.g. Misztal and Gianola, 1987). Iteration was stopped when:

$$(EBV_{q-1} - EBV_q)'(EBV_{q-1} - EBV_q)/EBV_q'EBV_q \; < \; 10^{-10}$$

(subscript q denotes the qth iteration). The breeding plan was simulated for 25 years. The steady state genetic gain is estimated by linear regression of the mean genetic merit of the animals born during the years 16 to 25 on the year of birth. The steady state response rate predicted by the model of Meuwissen (1989) was $0.136 \; \sigma_{p0}$ per year.

Presentation

For clarification of the results, the relationship between the selection differentials, generation intervals and fraction selected from the nucleus, and the genetic gain is given by (see Appendix):

$$\Delta G = \frac{I_{MNR} + f_{NN}I_{FNR(NBF)} + (1-f_{NN})I_{FNR(BBF)} + (1-f_{NN})(I_{MBR} + I_{FBR(BBF)})}{L_{MNR} + f_{NN}L_{FNR(NBF)} + (1-f_{NN})L_{FNR(BBF)} + (1-f_{NN})(L_{MBR} + L_{FBR(BBF)})} \qquad (4)$$

where: ΔG is the steady state response rate,

I   is the average genetic selection differential within the category of animals denoted by the subscript,

L   is the average generation interval of the category of animals denoted by the subscript,

MNR, FNR(NBF), FNR(BBF), MBR and FBR(BBF) are Males to breed Nucleus Replacements, Females to breed Nucleus Replacements selected from the Nucleus Born Females, FNR selected from the Base Born Females, Males to breed Base Replacements and FBR selected from the Base Born Females (see Figure 1),

f_{NN} is the fraction of FNR selected from the NBF.

Formula (4) assumes that the fraction of FBR selected from the NBF (f_{NB}) is negligibly small. In the present study, this is reasonable since the number of FBR selected (1-1.5 million) is much larger than the number of NBF (250-2000), i.e. $f_{NB} \leq 0.002$. When the nucleus provides embryos to replace (a substantial amount of) the base animals, f_{NB} is not negligible small and Formula (A4) (see Appendix) should be used. Formula (4) reduces to the well known formula of Rendel and Robertson (1950) for progeny testing schemes when $f_{NN}=0$ (i.e. the contribution of NBF to the FNR is neglected).

Although the genetic lag between nucleus and base is canceled out of Formula (4), it affects the factors involved in this formula. Especially, f_{NN} is affected (and thus also female selection intensities in nucleus and base), since selection across nucleus and base is optimised. Genetic lags between nucleus and base are presented in $\sigma_{g\infty}$-units, where $\sigma_{g\infty}$ denotes the equilibrium genetic standard deviation in the nucleus of the selected population. This is because the probability of BBF animals having higher EBV than NBF animals, for which the lag is an indicator, depends also on $\sigma_{g\infty}$.

Simulation

Monte Carlo simulation of the closed nucleus plan was replicated 10 times. Linear regression of the genetic merit of the animals born during the years 16 to 25 on the year of birth resulted in a genetic gain of 0.134 σ_{p0} per year, with a standard error of 0.009 σ_{p0}/yr. This is in close agreement with the predicted genetic gain of 0.136 σ_{p0} per year.

T-schemes, n=1

Table 2 shows the genetic gain, selection differentials, generation intervals and fractions selected from the nucleus for the T-schemes, with one offspring per FNR. Progeny testing in T-schemes gives higher selection differentials of the selected MNR and MBR, increased lags between nucleus and base, less open nuclei (larger f_{NN}) and lower ΔG (see Table 2). The increased lag is due to the use of unselected young bulls as MBR. The decrease in ΔG is caused by the increased lag and by the decreased genetic variance in schemes with progeny testing. In schemes with progeny testing, the genetic variances are more reduced, because the accuracy of selection is higher than in schemes, where selection is based on family information. The fraction of the FNR selected from the nucleus (f_{NN}) is increased in schemes with progeny testing: the lag between nucleus and base is increased which makes the nucleus more competitive. The decreased genetic variance leads to reduced accuracies of selection: decreased variances of the EBV. Reduced variances of the EBV gives a lower probability of a BBF to have an higher EBV than the average NBF. Also this effect lowers the competitiveness of the base.

The $I_{FNR(BBF)}$ values in Table 2 are high. For example, in the scheme with 250 young bulls per year and no progeny testing, $I_{FNR(BBF)}$ is 0.885 σ_{p0}. Here, a fraction 0.42 of the FNR selected from the BBF are selected from age class 4 (results not shown). The accuracy of selection and the standardised selection differential in this age class are 0.66 and 3.26 respectively. The genetic selection differential within this age class is 0.66 * 3.26 * 0.455 = 0.979 σ_{p0}. The proportion selected within age class 4 is 0.0008. I_{MNR} is also large: 0.424 σ_{p0}. Eighty percent of all MNR come from age

Table 2. The genetic gain (ΔG; σ_{po}*)/yr), genetic standard deviation in nucleus (σ_g : σ_{po}), fraction of FNR selected from NBF (f_{NN}), genetic selection differentials (I; σ_{po}), generation intervals (L; yr) and lags for T-schemes with 1 offspring per FNR. Subscripts of selection differentials and generation intervals denote the class of animals selected (and their origin is between brackets) (see figure 1 for abbrevations).

No. of NBM/yr	250			500			1000			2000		
No. test rec./NBM	0	50	100	0	50	100	0	50	100	0	50	100
ΔG	.156	.153	.149	.160	.153	.146	.161	.151	.146	.163	.149	.149
σ_g **)	.455	.444	.434	.459	.441	.425	.460	.434	.419	.461	.426	.419
f_{NN}	.09	.09	.09	.10	.11	.12	.12	.15	.21	.14	.24	.40
I_{MNR}	.424	.605	.721	.459	.726	.923	.493	.901	1.103	.526	1.086	1.195
I_{MBR}	.334	.399	.414	.375	.445	.470	.411	.493	.528	.449	.534	.478
$I_{FNR(NBF)}$	.330	.304	.278	.323	.278	.229	.311	.235	.169	.296	.179	.123
$I_{FNR(BBF)}$	.885	.870	.859	.811	.791	.774	.744	.715	.690	.683	.643	.646
$I_{FBR(BBF)}$	.075	.071	.070	.075	.071	.068	.075	.069	.065	.075	.068	.065
L_{MNR}	2.3	3.5	4.2	2.3	4.0	5.4	2.4	5.0	6.2	2.5	6.0	6.3
L_{MBR}	2.3	2.8	3.1	2.3	3.0	3.4	2.3	3.3	3.9	2.4	3.7	3.8
$L_{FNR(NBF)}$	2.5	2.5	2.5	2.6	2.5	2.4	2.6	2.5	2.4	2.6	2.4	2.4
$L_{FNR(BBF)}$	3.4	3.5	3.6	3.1	3.2	3.4	2.9	3.1	3.2	2.8	3.0	3.0
$L_{FBR(BBF)}$	3.1	3.1	3.1	3.0	3.0	3.1	3.0	3.1	3.0	3.0	3.0	3.0
Lag***)	.95	.96	.98	.89	.93	.97	.84	.91	1.00	.78	.94	1.13

*) σ_{po} = base population phenotypic standard deviation units.

**) σ_g was 0.5 σ_{po}-units in the base population.

***)Genetic lag between nucleus and base in σ_g -units.

Table 3. The genetic gain (ΔG; σ_{p0}), fraction of FNR selected from NBF (f_{NN}) and the genetic lag (σ_{g0}-units) for the T-schemes according to the number of bulls tested (M), the number of records per bull (N) and the reproductive rate of the female (n).

		N=0			N=50			N=100		
		ΔG	f_{NN}	Lag	ΔG	f_{NN}	Lag	ΔG	f_{NN}	Lag
n	M									
1	250	.156	0.09	0.95	.151	0.09	0.96	.149	0.09	0.98
	500	.160	0.10	0.89	.153	0.11	0.93	.146	0.12	0.97
	1000	.161	0.12	0.84	.151	0.15	0.91	.146	0.21	1.00
	2000	.163	0.14	0.78	.149	0.24	0.94	.149	0.40	1.13
3	250	.161	0.18	1.01	.158	0.18	1.04	.155	0.18	1.02
	500	.165	0.21	0.96	.160	0.22	1.00	.155	0.24	1.04
	1000	.170	0.24	0.92	.160	0.28	0.99	.153	0.37	1.09
	2000	.171	0.27	0.87	.156	0.42	1.03	.156	0.69	1.25
11	250	.160	0.28	1.03	.158	0.28	1.05	.156	0.28	1.08
	500	.168	0.36	1.01	.163	0.37	1.04	.159	0.37	1.06
	1000	.173	0.43	0.98	.165	0.47	1.05	.158	0.52	1.16
	2000	.178	0.51	0.94	.164	0.64	1.12	.164	0.86	1.36
21	250	.155	0.29	1.01	.154	0.28	1.03	.153	0.28	1.06
	500	.164	0.40	1.00	.161	0.41	1.04	.159	0.41	1.10
	1000	.170	0.50	0.98	.165	0.55	1.04	.160	0.60	1.19
	2000	.176	0.59	0.59	.166	0.73	1.15	.166	0.90	1.41
41	250	.145	0.26	0.97	.145	0.26	1.01	.145	0.26	1.05
	500	.156	0.39	0.96	.155	0.41	1.02	.155	0.41	1.09
	1000	.165	0.53	0.96	.163	0.59	1.07	.160	0.64	1.21
	2000	.173	0.65	0.95	.168	0.79	1.18	.170	0.92	1.46

class 2. The accuracy of selection, the standardised selection differential, proportion selected and genetic selection differential in age class 2 are 0.40, 2.17, 0.016 (=0.8*5/250) and 0.395 σ_{p0}, respectively. The standardised selection differentials are high here, because selection is over all age classes, which results in many selection candidates and high selection intensities.

Increased female reproductive rate (n≥2)

Tables 3 and 4 show ΔG, f_{NN} and the lag between the nucleus and base for the T- and P-schemes, respectively. The maximum number of progeny per FNR (Female to breed Nucleus Replacement) (n) may not yield the maximum response rate for a particular scheme (see Table 3 and 4), but need to be optimised. When n is high, the number of full sib families is low and the EBV are correlated, which reduces the selection differentials. The number

Table 4. The genetic gain (ΔG; σ_{p0}), fraction of FNR selected from NBF (f_{NN}) and the genetic lag ($\sigma_{g\infty}$ units) for the P-schemes according to the number of bulls tested (M), the number of records per bull (N) and the reproductive rate of the female (n).

n	M	N=0			N=50			N=100		
		ΔG	f_{NN}	Lag	ΔG	f_{NN}	Lag	ΔG	f_{NN}	Lag
1	250	.129	0.09	1.24	.124	0.10	1.18	.120	0.11	1.18
	500	.131	0.10	1.17	.125	0.12	1.13	.123	0.15	1.14
	1000	.133	0.12	1.11	.126	0.16	1.10	.128	0.21	1.17
	2000	.134	0.14	1.04	.130	0.22	1.13	.131	0.29	1.32
3	250	.131	0.19	1.33	.128	0.21	1.28	.126	0.22	1.28
	500	.135	0.22	1.28	.130	0.26	1.23	.128	0.31	1.24
	1000	.138	0.26	1.22	.133	0.35	1.21	.133	0.46	1.29
	2000	.139	0.30	1.16	.135	0.49	1.25	.139	0.65	1.47
11	250	.134	0.36	1.39	.131	0.39	1.35	.130	0.42	1.36
	500	.140	0.45	1.37	.136	0.51	1.34	.134	0.58	1.36
	1000	.145	0.53	1.33	.140	0.66	1.34	.140	0.81	1.44
	2000	.149	0.62	1.30	.145	0.85	1.43	.149	0.95	1.67
21	250	.131	0.44	1.39	.131	0.49	1.37	.130	0.53	1.38
	500	.140	0.58	1.39	.138	0.67	1.39	.138	0.74	1.44
	1000	.148	0.71	1.39	.144	0.83	1.43	.145	0.92	1.54
	2000	.154	0.83	1.39	.151	0.95	1.54	.155	0.99	1.79
41	250	.121	0.42	1.34	.125	0.51	1.35	.125	0.54	1.37
	500	.135	0.65	1.39	.138	0.76	1.42	.139	0.84	1.48
	1000	.145	0.83	1.43	.148	0.92	1.51	.150	0.97	1.63
	2000	.156	0.93	1.47	.156	0.98	1.64	.160	0.99	1.87

of full sib families increases when the nucleus size increases. Thus the optimal n is higher for larger nucleus sizes (see Tables 3 and 4).

If EBVs were uncorrelated maximum n would be desirable if inbreeding is to be ignored. However EBVs of relatives are correlated and the more correlations and the greater the correlations the more the intended increase in selection intensity through increasing n is eroded. P-schemes have less problems with correlated EBVs through half sib relationships, therefore it may be expected that they have greater scope for increasing n than T schemes. EBVs are more correlated when selecting for sib information than for progeny test information. Consequently, the scope for increasing n is greater when young bulls are progeny tested.

When n is high, only few FNR have to be selected. They are predominantly selected from the nucleus, because this tier has the highest genetic level.

Thus, when n increases, the breeding plan becomes more closed (higher f_{NN}).
P-schemes are more closed than T-schemes, because the lag between nucleus
and base is larger in P-schemes.

Progeny testing is relatively more efficient in P- than in T-schemes (see
Tables 3 and 4). This is due to two effects. (1) The inefficient selection
of base parents (FBR are selected at random; 2-year-old bulls are almost
excluded from the MBR selection) increases the lag between nucleus and base
in P-schemes relative to T-schemes (see Table 3 and 4). A larger lag leads
to higher f_{NN}. Consequently, a further decrease in lag due to progeny
testing will have less effect on ΔG in P-schemes than in T-schemes. (2) In
P-schemes, without progeny testing, the lag is increased due to the
restriction on the use of 2-year-old bulls for MBR. This restriction has a
minor effect on the lag in schemes with progeny testing, because almost all
selected MBR are progeny tested. Thus the effect of progeny testing on the
lag is smaller in P-schemes.

DISCUSSION

Model

The results from the deterministic model used here, agreed well with
Monte Carlo simulations for closed nucleus schemes. However in practice
inefficiencies occur which are not modelled here. For example, fixed
effects need to be estimated and their estimates are subject to errors; the
number of offspring per FNR varies, which reduces accuracies of selection
and selection differentials (Keller and Teepker, 1990); selections are
often made within a subset of the population, because at a certain moment
not all animals are available for selection. In the P-schemes an attempt is
made to model some of these inefficiencies by selecting more animals than
is strictly required in view of the reproductive rate. This resulted in a
decreased genetic gain, an increased lag, an increased efficiency of
progeny testing and more closed breeding systems.

Variance reduction due to inbreeding decreases response rates as well.
However, in cattle breeding the generation interval is long compared to the
time horizon, i.e. only short term response is considered important. When
the effective population size is only 10 animals per generation (usually it
is larger), variance reduction due to inbreeding decreases the cumulative

selection response at year 30 by a factor 0.05 or 0.13, assuming generation intervals of 6 or 3 years respectively (Meuwissen, 1989). Differences between alternative breeding schemes due to different inbreeding rates will be even smaller. With dominant gene effects, inbreeding depression will reduce predicted response rates as well.

Although account was taken of the effect of the family structure on selection differentials, selection differentials were often high (up to 3.5 phenotypic s.d.). Selection across age classes implies that all fertile animals are selection candidates, which allows high selection intensities. Probably, selection differentials obtained here can be achieved in practice (cows producing 2800 kg milk above average are readily found). However, in the tail of the distribution the regression of genotype on phenotype might be non-linear (Robertson, 1977), i.e. genetic selection differentials might be lower than expected. Causes may be preferential treatment, a finite number of loci coding for milk production, and non-normality of genotype distributions after selection. Selection differentials were not restricted to a maximum, because the choice of the maximum, which is arbitrary, would affect the results very much (e.g. the optimum of n).

Genetic gains in Table 2 are higher than those in the example of Meuwissen (1989). After consultation of Dutch AI organisations, yearly involuntary culling of bulls is reduced from 0.09 in Meuwissen (1989) to 0.05 times the number of 2-year-old bulls in Tables 2, 3 and 4.

Progeny testing

High n also leads to an increased efficiency of progeny tests (see Table 3 and 4). This results from plans with high n being more closed: an increase in lag between nucleus and base due to progeny testing does not affect closed schemes. In Table 4, the schemes with n=41 and with progeny testing are more efficient than those without progeny testing. Apart from the generation intervals, which are optimised here, these schemes resemble the MOET hybrid schemes proposed by Colleau (1985): an (almost) closed nucleus with progeny testing of young bulls in the base. Generally, progeny testing did not increase or decrease genetic gain much (the maximum effect was an decrease in response by a factor 0.1). Schemes without progeny testing will have higher inbreeding rates, because the probability of selecting relatives is higher when selection is on family information (pedigree, full- and half sibs).

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<u>Increased female reproductive rate (n≥2)</u>

The extra genetic gain due to increasing the reproductive rate of females (n) is moderate in the T-schemes (a factor 0.08 or less) (see Table 3) and in agreement with results found for progeny testing schemes (e.g. Cunningham, 1976). In P-schemes increasing n is more effective: up to a factor 0.16 more response. It could be expected that increasing n does not increase the selection differential of the FNR much in conventional progeny testing schemes and in open nucleus schemes: selection differentials of the FNR are already high even if MOET is not used. Only in (almost) closed schemes, which have lower selection differentials for the FNR, an increase in n leads to a significant increase in selection differential of the FNR. Therefore, the effect of increasing n is higher in P-schemes, which are more closed.

When n increases, the optimised open nucleus plan becomes more closed (f_{NN} increases) (see Table 3 and 4). Thus, high n, makes a closed nucleus plan more competitive to an open nucleus plan. Selection within a closed nucleus herd may be preferred to open nucleus selection, when selection across commercial herds is difficult (e.g. due to preferential treatment).

Increasing n is more effective in P- than in T-schemes, because the P-schemes are more closed (f_{NN} is higher). In closed schemes, the selection differential of FNR is small when n is small and increases substantially when n increases. In open nucleus schemes, this selection differential is high even when n is small and increases only marginally when n increases. When in practice selection of base parents is not effective, selection within a closed nucleus herd will be relatively more efficient. Because the P-schemes are more closed than the T-schemes, a progeny test is more effective in P-schemes.

For a fixed nucleus size, there will be an optimal n (see Tables 3 and 4). When n is above the optimum (i.e. n is too high), the number of full sib families is too small, which decreases the selection differentials. Increasing the nucleus size increases the number of full sib families: the optimal n is larger for larger nucleus sizes. Therefore, increasing n calls for larger nucleus sizes.

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General

From Table 2 it is concluded that progeny testing young bulls decreases genetic gain. Literature on the optimisation of progeny testing schemes indicates, that each young bull must have about 50 test records (e.g. Skjervold and Langholz, 1964). However these studies used only progeny test results for the selection of bulls, which renders a progeny test essential. Here bulls might be selected on pedigree, sib, progeny and/or progeny test information. The optimisation of the generation interval resulted in short generation intervals and selection on pedigree and sib information, which gave higher response rates than selection for a progeny test.

From MOET nucleus scheme calculations (e.g. Nicholas and Smith,1983) and from the present results it can be concluded, that the generation intervals should be short in dairy cattle breeding. However, the optimal generation interval depends on the genetic gain achieved: if genetic gain is high, the average genetic merit of young animals is much superior to that of old animals, which are therefore less competitive. When genetic gain is low, the older animals are more competitive because their EBV are more accurate due to the accumulation of information during an animal's lifetime. The rate of gain in model calculations is usually not realised in practice because of inefficiencies that occur in practice (Van Vleck, 1988) and because of limitations in the prediction model (e.g. omission of variance reduction or order statistics effects). Thus, predicted optimal generation intervals may be underestimated.

Conclusions

Deterministic models, that account for variance reductions due to selection and reduction of selection differentials due to order statistics, predict similar response rates as Monte Carlo simulations, that neglect inbreeding and fixed effects, such as herd-year-season.

Increasing female reproductive rates cause increases in genetic gain of up to a factor 0.08 and up to a factor 0.16 for the T- and P-schemes respectively. The increase is larger for the P-schemes than for the T-schemes, because P-schemes use a higher proportion of females from the nucleus (i.e. less open schemes). Closed nucleus schemes benefit more from an increasing female reproductive rate, because selection differentials of FNR selected from the nucleus are low when female reproductive rate is low. In open nucleus breeding plans (e.g. conventional progeny testing plans),

the selection differential of FNR selected from the base is high even when female reproductive rate is low. Consequently, higher female reproductive rate makes closed nucleus plans more competitive to open nucleus plans. In situations, where selection across commercial herds is biased (e.g. by preferential treatment), selection within a closed nucleus herd might be preferred.

An increased female reproductive rate makes an optimal open nucleus plan more closed. This increases the efficiency of progeny testing, because an increased lag between nucleus and base due to progeny testing is less important in a more closed scheme. In P-schemes, which have larger lags due to inefficient selection of base parents, schemes with high female reproductive rates and progeny testing are even more efficient than similar schemes without progeny testing. These schemes are almost completely closed schemes. Generally, schemes with progeny testing are somewhat less efficient than schemes without progeny testing, but they will have lower inbreeding rates.

The number of offspring per FNR can be optimised, because a large number results in a small number of full sib families, which increases the effect of order statistics on selection differentials. An increasing number of offspring per FNR calls for increased nucleus sizes, because the number of full sib families is larger with larger nucleus sizes.

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APPENDIX

THE STEADY STATE GENETIC GAIN IN OPEN NUCLEUS BREEDING SCHEMES.

The derivation is analogous to that of Rendel and Robertson (1950). It is assumed that long before year 0 the genetic progress of the open nucleus plan (see Figure 1) is constant (i.e. the plan is in equilibrium). The average genetic merit of the nucleus animals born in year 0 is:

$$N_0 = \tfrac{1}{2}\{I_{MNR}+N_0-L_{MNR}\Delta G + f_{NN}(I_{FNR(NBF)}+N_0-L_{FNR(NBF)}\Delta G) + (1-f_{NN})(I_{FNR(BBF)}$$
$$+B_0-L_{FNR(BBF)}\Delta G)\} \qquad (A1)$$

where: ΔG is the steady state response rate,

N_0 is the average genetic merit of nucleus animals born in year 0,

B_0 is the average genetic merit of base animals born in year 0,

I   is the average selection differential of the category of animals denoted by the subscript,

L   is the average generation interval of the category of animals denoted by the subscript,

MNR, FNR(NBF) and FNR(BBF) are Males to breed Nucleus Replacements, Females to breed Nucleus Replacements selected from the Nucleus Born Females and FNR selected from the Base Born Females (see Figure 1), f_{NN} is the fraction of FNR selected from the NBF.

Similarly, the average genetic merit of the base animals born in year 0 is:

$$B_0 = \tfrac{1}{2}\{I_{MBR}+N_0-L_{MBR}\Delta G + f_{NB}(I_{FBR(NBF)}+N_0-L_{FBR(NBF)}\Delta G) + (1-f_{NB})(I_{FBR(BBF)}$$
$$+B_0-L_{FBR(BBF)}\Delta G)\} \qquad (A2)$$

where: MBR, FBR(NBF) and FBR(BBF) are Males to breed Base Replacements, Females to breed Base Replacements selected from the Nucleus Born Females and FBR selected from the Base Born Females (see Figure 1), f_{NB} is the fraction of FBR selected from the NBF,

Without loss of generality it is assumed that $N_0=0$. Now, from (A2):

$$B_0 = \{I_{MBR} - L_{MBR}\Delta G + f_{NB}(I_{FBR(NBF)} - L_{FBR(NBF)}\Delta G) + (1-f_{NB})(I_{FBR(BBF)}$$
$$-L_{FBR(BBF)}\Delta G)\}/(1+f_{NB}) \qquad (A3)$$

Substitution of (A3) in (A1) provides, after solving for ΔG:

$$\Delta G = \{(1+f_{NB})(I_{MNR} + f_{NN}I_{FNR(NBF)} + (1-f_{NN})I_{FNR(BBF)}) + (1-f_{NN})(I_{MBR} + f_{NB}I_{FBR(NBF)} +$$
$$(1-f_{NB})I_{FBR(BBF)})\} / \{(1+f_{NB})(L_{MNR} + f_{NN}L_{FNR(NBF)} + (1-f_{NN})L_{FNR(BBF)}) +$$
$$(1-f_{NN})(L_{MBR} + f_{NB}L_{FBR(NBF)} + (1-f_{NB})L_{FBR(BBF)})\} \qquad (A4)$$

In open nucleus breeding schemes, f_{NB} is usually negligible small, because the number of FBR selected is much larger than the number of NBF. Formula (A4) reduces to:

$$\Delta G = \{I_{MNR} + f_{NN}I_{FNR(NBF)} + (1-f_{NN})I_{FNR(BBF)} + (1-f_{NN})(I_{MBR} + I_{FBR(BBF)})\} /$$
$$\{L_{MNR} + f_{NN}L_{FNR(NBF)} + (1-f_{NN})L_{FNR(BBF)} + (1-f_{NN})(L_{MBR} + L_{FBR(BBF)})\} \qquad (A5)$$

Chapter 5

EXPECTATION AND VARIANCE OF GENETIC GAIN IN OPEN AND CLOSED NUCLEUS AND PROGENY TESTING SCHEMES

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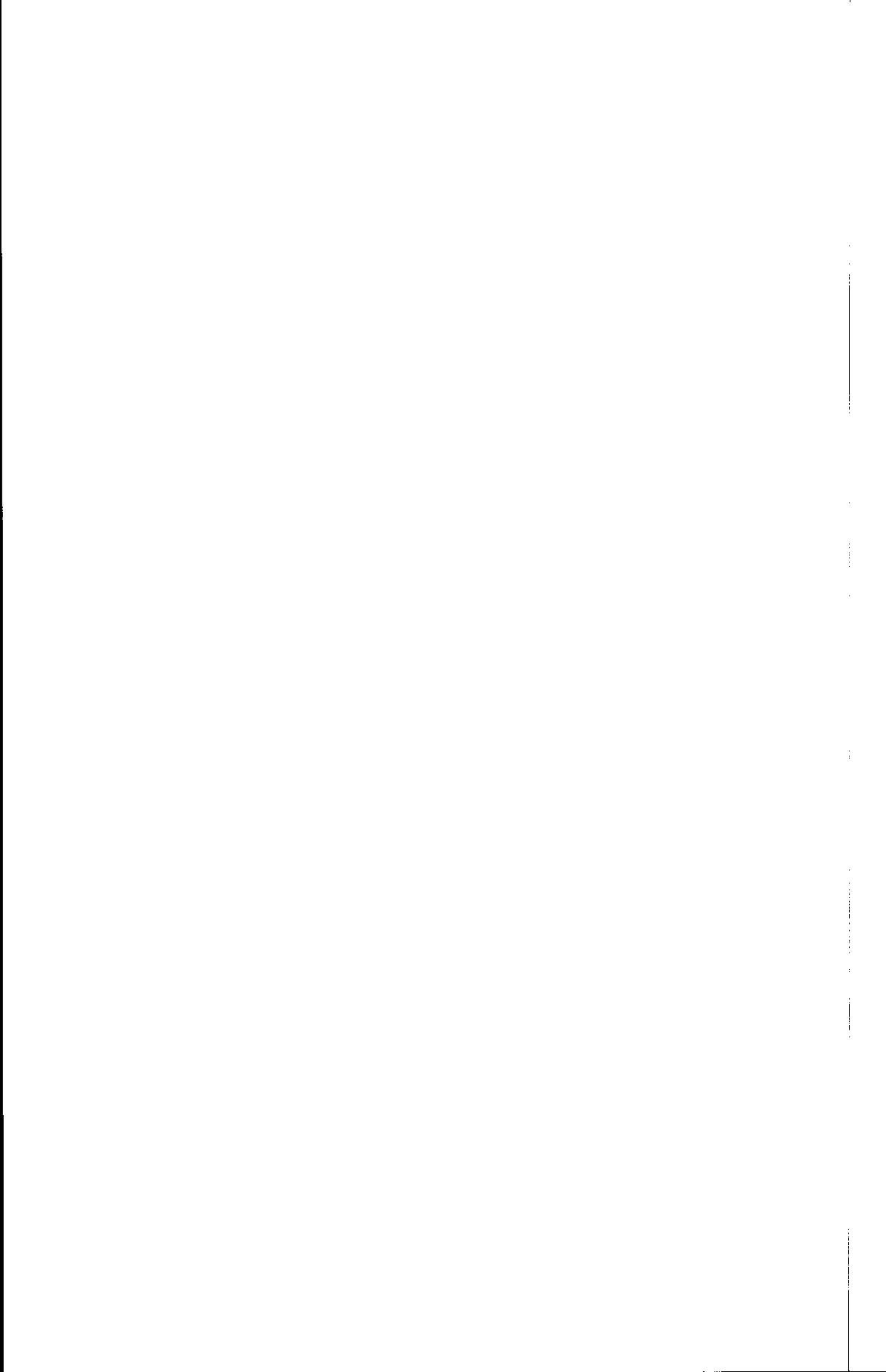
ABSTRACT

Open and closed nucleus and conventional and modern progeny testing
schemes were compared for the expectation and variance of the genetic gain.
Generation intervals were optimised, with minimum values of 2 and 6 years
(progeny test results available) for males in nucleus and progeny testing
schemes, respectively. Females had a minimum generation interval of 2
years, except in the conventional progeny testing schemes, which had a
minimum of 4 years (one individual record available). Apart from the
generation intervals and the progeny test, open nucleus and progeny testing
schemes were identical, since 'nucleus females' are also born in progeny
testing schemes, being full sibs of the young bulls and dispersed over
commercial herds. The number of nucleus sires (bull sires) selected was
varied between 4 and 32. Selection was for milk production.

A deterministic model was used, that accounted for variance reduction due
to selection and the effects of finite size and family structure on the
selection differentials. Prediction of the variance of the selection
response accounted for selection of full- and paternal half sibs.

Closed nucleus schemes gave 3, 13 and 19% higher response rates than open
nucleus and modern and conventional progeny testing schemes, respectively.
Reduction of genetic variance of open nucleus schemes was larger than that
of closed nucleus schemes, which caused the slightly higher response rates
of closed nucleus schemes. Standard deviations of selection responses of
closed nucleus schemes were 46, 79 and 86% higher, respectively.

Preference for the schemes was assessed using a quadratic utility
function expressing risk and inbreeding aversion. The increase in genetic
gain due to shortening of generation intervals more than compensated for
its increased variance. Whether the increased genetic gain due to closing
the nucleus compensated for its increased variance depended on the amount
of risk aversion. Selection of 4 sires and 8-16 sires had the highest
utility in progeny testing and nucleus schemes, respectively.

INTRODUCTION

Nicholas and Smith (1983) proposed the use of MOET (Multiple Ovulation
and Embryo Transfer) nucleus schemes to increase rate of gain in dairy
cattle breeding. In these schemes, selection is within a closed nucleus

herd, using short generation intervals, and selection is based on pedigree and sib information (see Ruane, 1988, and Colleau, 1989, for reviews). As alternatives to the original MOET nucleus schemes, among others, open nucleus schemes have been proposed, i.e. commercial as well as nucleus cows are considered for selection of nucleus dams. Due to the higher number of selection candidates, open nucleus schemes could have higher response rates than closed schemes, when Estimated Breeding Values (EBVs) are unbiassed and can be compared across herds (Meuwissen, 1989). However, with more offspring per donor cow, the fraction of the donor cows selected from the base decreases in open nucleus schemes (i.e. a 'more closed' nucleus) and the superiority of open over closed nucleus schemes decreases (Meuwissen, 1990b). Conventional progeny testing schemes are open nucleus schemes, where the nucleus females, the daughters of bull dams and bull sires, are dispersed among commercial herds.

MOET nucleus and conventional progeny testing schemes have predefined generation intervals. However, if EBVs are BLUP, generation intervals, which provide maximal response rates, are obtained by selection for high EBVs across all ages (James, 1987). Therefore, generation intervals should not be predefined, unless it is intended to reduce variances of selection responses or inbreeding rates by increasing generation intervals.

In a breeding scheme, expected genetic level of the population and variance of the genetic level increase over time. Here, a breeding scheme is called in steady state, when both expectation and variance of genetic level increase linearly over time (assuming variance reduction due to inbreeding is negligible). The steady state increment of both the expectation and the variance of the genetic level are called the expected genetic gain ($E(\Delta G)$) and the variance of the genetic gain ($V(\Delta G)$), respectively. The following example illucidates this concept and shows that genetic level increases significantly over time even when $E(\Delta G)$ is as high as $V(\Delta G)$: suppose in steady state $E(\Delta G)=V(\Delta G)=1$ unit per year, then after 25 years the expectation and standard deviation of the genetic level are 25 and 5 units, respectively (since $V(\Delta G)=25$ units^2).

Fast turn-over of generations, less accurate selection (both due to shorter generation intervals), selection of fewer dams from a small nucleus population (due to the use of MOET) all lead to an increase of the variance of the selection response. The variance of the selection response is an

indicator for the risk of the breeding plan. When considering mass selection, Hill (1977) suggested the following approximate relationship:

$$V(\Delta G) \approx 2 \ \Delta F \ V_a \tag{1}$$

where ΔF and V_a are the inbreeding rate and the additive genetic variance respectively. Equation (1) is exact when a trait, that is uncorrelated to the breeding goal is considered, i.e. $E(\Delta G) = 0$. If applied to the simulation results of MOET nucleus schemes of Ruane and Thompson (1989), Equation (1) overestimated $V(\Delta G)$ substantially. But, also the simulation results of Ruane and Thompson suggested a strong positive relationship between $V(\Delta G)$ and ΔF. Both risk and inbreeding are important for the selection of the best breeding plan.

The aim of this paper is to compare open and closed nucleus plans with optimised generation intervals and conventional progeny testing schemes, which have long generation intervals, for $E(\Delta G)$ and $V(\Delta G)$. To meet this goal, a model is built to predict $E(\Delta g)$ and $V(\Delta g)$. In the discussion it is tried to trade off $E(\Delta G)$ against $V(\Delta G)$.

MODEL

General

The model evaluates $E(\Delta G)$ and $V(\Delta G)$ until steady state is reached. In year 0 selection starts from an unselected base population. During evaluation, genetic variances and selection accuracies are corrected for ancestral selection. The generation intervals are optimised within each year of evaluation. When the yearly genetic gain and its variance have stabilized, evaluation stops.

The variance of the average breeding value of offspring of selected parents is approximately:

$$V(\tfrac{1}{2}\overline{TBV}_s + \tfrac{1}{2}\overline{TBV}_d) = V(\sum_{i=1}^{n_s} TBV_{s_i})/4n_s^2 + V(\sum_{i=1}^{n_d} TBV_{d_i})/4n_d^2 +$$
$$Cov(\sum_{i=1}^{n_s} TBV_{s_i}; \sum_{i=1}^{n_d} TBV_{d_i})/2n_s n_d \tag{2}$$

where $\overline{TBV}_s, \overline{TBV}_d$: average true breeding value of sires, dams (as deviation from that of the unselected base population)

TBV_{s_i}, TBV_{d_i} : TBV of sire i, dam i (as deviation from the base population)

n_s, n_d : number of sires, dams

In the following, components of Formula (2) will be derived. Define:

$$TBV_{s_i} = EBV_{s_i} + ERR_{s_i} \tag{3}$$

where EBV_{s_i} : estimated breeding value of sire i

ERR_{s_i} : error component of the EBV of sire i.

$V(EBV_{s_i})$ depends on accuracy of selection, numbers selected and population size and structure. When EBVs are BLUP, i.e. best predictors of the TBVs, $Cov(EBV_{s_i}; ERR_{s_i}) = 0$. Otherwise part of the ERR_{s_i} component could be predicted from the EBV_{s_i}, which implies that a better EBV could be obtained. Consequently, ERR_{s_i} is not affected by selection, and it follows that:

$$V(TBV_{s_i}) = V(EBV_{s_i}) + V(ERR_{s_i}) = V(EBV_{s_i}) + V_{TBV} - V_{EBV} \tag{4}$$

where V_{TBV}, V_{EBV}: variance of TBVs, EBVs in base population
(before selection).

When generations overlap, V_{TBV} and V_{EBV} depend on the age class, where the sire is selected from. V_{TBV} and V_{EBV} are obtained as the weighted average of the V_{TBV} and V_{EBV} within the age classes, respectively (weighting is by the contribution of the age class to the selected sires). In Formula (4), $V(TBV_{s_i})$, which is required for Formula (2), is derived from $V(EBV_{s_i})$ and base population parameters. Similarly,

$$Cov(TBV_{s_i}; TBV_{s_j}) = Cov(EBV_{s_i}; EBV_{s_j}) + R\ V_{TBV} - t\ V_{EBV} \tag{5}$$

where the additive genetic relationship between sire s_i and sire s_j is given by R; t is the intra-class correlation using base population parameters. The intra-class correlation is the correlation between EBVs of related animals. The model considers only full sib and paternal half sib relationships.

Analogously, $V(TBV_{d_i})$, $Cov(TBV_{d_i}; TBV_{d_j})$ and $Cov(TBV_{s_i}; TBV_{d_i})$ are derived from $V(EBV_{d_i})$, $Cov(EBV_{d_i}; EBV_{d_j})$ and $Cov(EBV_{s_i}; EBV_{d_i})$, respectively, and parameters from the base population.

Ranking of EBV and selection

Expectations and variances of the ranked EBVs should be obtained from
order statistics of unequally correlated multinormal variables (the
correlations are due to the family relationships between relatives).
Formulas for the expectations of ranked EBVs are available when the
population consists of uniform families (e.g. full - or half sib families)
(Hill, 1976). However, in the present situation the expectations and
variances are required for a nested full-half sib family structure. From
order statistics of uncorrelated normal variables, expectations and
variances of ranked half sib family means can be obtained. Similarly, those
of ranked full sib family means within a half sib family and those of
ranked EBVs of individual animals within a full sib family can be obtained.
The expected EBV of the k-th ranking animal within the j-th ranking full
sib family within the i-th ranking half sib family is:

$$E(EBV(i,j,k)) = E(x_{n_{HS}}(i)) \ \sqrt{(t_{HS}^* V_{EBV}^*)} + E(x_{n_{FS}}(j))$$

$$\sqrt{((t_{FS}^* - t_{HS}^*) V_{EBV}^*)} + E(x_{n_W}(k)) \ \sqrt{((1 - t_{FS}^*) V_{EBV}^*)} \tag{6}$$

where: n_{HS}, n_{FS} and n_W is the number of half sib families in the
population, full sib families per half sib family and full sibs per full
sib family respectively;
$x_n(i)$ is the i-th ranking variable of n uncorrelated normal distributed
variables with variance 1;
t_{FS} and t_{HS} are the intra-class correlations of full - and half sibs (the *
denotes that the values are corrected for ancestral selection).
In the present study all order statistics of normal deviates are
approximated applying David and Johnson (1954). Here, the assumption is
made that: $E(EBV(i,j,k)) = EBV(i,j,k)$, i.e. the expected value of the k-th
ranking animal in the j-th ranking full sib family in the i-th ranking half
sib family is assumed to be realised. This implies that those animals which
have the highest probability of selection are selected and selection of
animals with a lower probability of selection is neglected (assuming
symmetric distributions of ranked variables). Using (6), it is determined
which animals are selected (e.g. the first ranking animal in the first
ranking family, etc.).

Variances and covariances of ranked EBV

The variances and covariances of the EBVs of selected animals are:

$$V(EBV(i,j,k)) = V(x_{n_{HS}}(i))t_{HS}{}^*v_{EBV}{}^* +$$

$$V(x_{n_{FS}}(j))(t_{FS}{}^* - t_{HS}{}^*)v_{EBV}{}^* + V(x_{n_W}(k))(1-t_{FS}{}^*)v_{EBV}{}^* \qquad (7)$$

$$Cov(EBV(i,j,k);EBV(i,j,k')) = V(x_{n_{HS}}(i))t_{HS}{}^*v_{EBV}{}^* + V(x_{n_{FS}}(j))$$

$$(t_{FS}{}^* - t_{HS}{}^*)v_{EBV}{}^* + Cov(x_{n_W}(k);x_{n_W}(k'))(1-t_{FS}{}^*)v_{EBV}{}^*, \text{ where } k \neq k' \qquad (8)$$

$$Cov(EBV(i,j,k);EBV(i,j',k')) = V(x_{n_{HS}}(i))t_{HS}{}^*v_{EBV}{}^* +$$

$$Cov(x_{n_{FS}}(j);x_{n_{FS}}(j'))(t_{FS}{}^* - t_{HS}{}^*)v_{EBV}{}^*, \text{ where } j \neq j' \qquad (9)$$

$$Cov(EBV(i,j,k);EBV(i',j',k')) = Cov(x_{n_{HS}}(i);x_{n_{HS}}(i'))t_{HS}{}^*v_{EBV}{}^*$$

$$\text{where } i \neq i' \qquad (10)$$

$V(EBV_{s_i})$, $V(EBV_{d_i})$, $Cov(EBV_{s_i};EBV_{s_i'})$ and $Cov(EBV_{d_i};EBV_{d_i'})$, which are required for formula (4) and (5), are obtained from (7), (8), (9) and (10). The covariance between sires and dams is:

$$Cov(EBV(i,j,k);EBV(i',j',k')) = Cov(x_{n_{HS}}(i);x_{n_{HS}}(i'))$$

$$\sqrt{(t_{HS_m}{}^*t_{HS_f}{}^*v_{EBV_m}{}^*v_{EBV_f}{}^*)}, \text{ when } i \neq i' \qquad (11)$$

or:

$$Cov(EBV(i,j,k);EBV(i,j',k')) = V(x_{n_{HS}}(i))\sqrt{(t_{HS_m}{}^*t_{HS_f}{}^*v_{EBV_m}{}^*v_{EBV_f}{}^*)} +$$

$$Cov(x_{n_{FS}}(j);x_{n_{FS}}(j'))(\sqrt{(t_{FS_m}{}^*t_{FS_f}{}^*)} - \sqrt{(t_{HS_m}{}^*t_{HS_f}{}^*)})\sqrt{(v_{EBV_m}{}^*v_{EBV_f}{}^*)} \qquad (12)$$

where $t_{FS_m}{}^*, t_{HS_m}{}^* (t_{FS_f}{}^*, t_{HS_f}{}^*)$: $t_{FS}{}^*$, $t_{HS}{}^*$ of males (females),
$v_{EBV_m}{}^*, v_{EBV_f}{}^*$: $v_{EBV}{}^*$ of males, females.

Formulas (11) and (12) assume that the ranking of the family means of males and females is identical, which is correct when EBVs are estimated by an animal model (which is presumed here).

Predicted variances of EBVs assuming $E(EBV(i,j,k)) = EBV(i,j,k)$ were compared to Monte Carlo simulation results, which did not require this

Table 1. The standard deviation of the selection differential from 1000
Monte Carlo simulations compared to those predicted using the assumption
E(EBV(i,j))=EBV(i,j) (Estimated Breeding Value of the j-th ranking animal
in the i-th ranking family). Selection is from 5 families with 5 animals
per family. Intra-class correlation is 0.5 and variance of EBV is 1.

No. of animals selected	Monte Carlo simulation	E(EBV(i,j))= EBV(i,j)
3	0.48	0.51
4	0.46	0.51
5	0.44	0.46
6	0.43	0.44
7	0.42	0.45
8	0.40	0.42
9	0.40	0.41
10	0.39	0.40
15	0.36	0.37
25	0.35	0.35

assumption (Table 1). Due to this assumption, predicted were 3-11 % higher

than simulated standard deviations of selected EBV. The error is larger

when fewer animals are selected. Results are poor for selection of 1 and 2

animals (not shown). Selection of 1 or 2 animals does not occur in practice

due to inbreeding considerations.

Correction of variances for ancestral selection

First, variances of EBVs of sires selected for their EBV are obtained:

$$V_{EBV_s}{}^{**} = V_{EBV_s}{}^{*} (1 - I_{\infty_s}(I_{\infty_s}-X_{\infty_s})) \tag{13}$$

where: $V_{EBV_s}{}^{**}$ ($V_{EBV_d}{}^{**}$) is variance of EBVs of sires (dams) corrected for
ancestral selections and for selection based on the individual EBVs of the
sires (dams); I_{∞_s} is standardised selection differential of males for
infinite population sizes and X_{∞_s} is the standardised truncation point.
$V_{EBV_d}{}^{**}$ is obtained similarly.

Formula (13) requires the variance of EBV corrected for ancestral
selection ($V_{EBV_s}{}^{*}$). In the base population, Formula (13) can be applied
directly, because $V_{EBV_s}{}^{*}=V_{EBV_s}$. The first generation variances of EBV
corrected for ancestral selection are:

$$V_{EBV}{}^{*}= V_{EBV} - \tfrac{1}{2}(V_{EBV_s}-V_{EBV_s}{}^{**}) - \tfrac{1}{2}(V_{EBV_d}-V_{EBV_d}{}^{**}) \tag{14}$$

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By using Formulas (13) and (14) recurrently, variances of EBVs corrected for ancestral selection are obtained. Corrected variances of TBVs and intra-class correlations are obtained from:

$$V_{TBV}^* = V_{TBV} - \tfrac{1}{4}(V_{EBV_s} - V_{EBV_s}^{**}) - \tfrac{1}{4}(V_{EBV_d} - V_{EBV_d}^{**}) \tag{15}$$

$$t_{FS}^* = \{t_{FS}V_{EBV} - \tfrac{1}{4}(V_{EBV_s} - V_{EBV_s}^{**}) - \tfrac{1}{4}(V_{EBV_d} - V_{EBV_d}^{**})\}/V_{EBV}^* \tag{16}$$

$$t_{HS}^* = \{t_{HS}V_{EBV} - \tfrac{1}{4}(V_{EBV_s} - V_{EBV_s}^{**})\}/V_{EBV}^* \tag{17}$$

Overlapping generations

When generations overlap, covariances between the TBVs of animals of different age classes are required for calculating the variances and covariances of Formula (2). If generations are discrete, the covariance between the genetic merit in generations u and v is equal to the variance of the genetic merit in generation u, where u < v (Hill, 1977). For overlapping generations, this relation becomes:

$$\text{Cov}(TBV_{(0)};TBV_{(u)}) = \sum_v b_v \, \text{Cov}(TBV_{(v)};TBV_{(u)}) \tag{18}$$

where: $TBV_{(u)}$: TBV of animal in age class u,

b_v : relative contribution of age class v to age class 0 ($\sum_v b_v = 1$), and summation is over all contributing age classes.

Further, $\text{Cov}(TBV_{(v)};TBV_{(u)})$ is obtained in earlier years of evaluation as $\text{Cov}(TBV_{(v-u)};TBV_{(0)})$, where v > u. These covariances are identical to those obtained by the matrix method of Johnson (1977).

Genetic level

The genetic level of the new born age class is:

$$g_0 = \tfrac{1}{2}\sum_u c_{s_u}(g_u + I_{s_u}(V_{EBV_s}^*)^{\tfrac{1}{2}}) + \tfrac{1}{2}\sum_u c_{d_u}(g_u + I_{d_u}(V_{EBV_d}^*)^{\tfrac{1}{2}}) \tag{19}$$

where g_u: genetic level of age class u,

I_{s_u}, I_{d_u}: phenotypic selection differential of sires and dams of age class u, corrected for family structure and finite population size.

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Table 2. Parameters of the breeding schemes.

Nucleus size	512
Commercial cow population size	1,000,000
Test daughters/young bull (only in prog. testing scheme)	100
No. nucleus sires	varied : 4, 8, 16 and 32
No. nucleus dams	64
No. offspring/nucleus dam	8
No. base sires	30
Selection of base dams	random
Restrictions on optimised generation intervals:[*]	
open/closed nucleus schemes	2-10 yr
progeny testing schemes: sires	6-10 yr
dams: conventional	4-10 yr
modern	2-10 yr
Unvoluntary culling per year:	
bulls 5 % of no. of young bulls in each ageclass[**]	
cows probability of culling is 30 %	

[*] Age at birth of offspring.
[**] Unvoluntary culling of bulls is neglected for the path sires for nucleus animals due to storage of semen and the low demand for semen in this path.

c_{s_u}, c_{d_u}: fraction of sires, dams selected from age class u.

The phenotypic selection differentials within age classes are corrected for the finite population size and for correlations between EBVs of relatives using the approximation of Meuwissen (1990a).

BREEDING SCHEMES

Parameters of the open and closed nucleus and conventional and modern progeny testing schemes are presented in Table 2. The nucleus size is 512 animals (256 males and 256 females). In progeny testing schemes, nucleus females are female offspring of bull dam and bull sire matings (i.e. full sibs of young bulls) and are dispersed over commercial herds. Differences between open nucleus, modern and conventional progeny testing schemes are due to differences in generation intervals: minimum generation intervals are 2 (2), 6 (2) and 6 (4) years for the sires (dams), respectively. When sires are 6 years old, progeny test results are available and when dams are 4 years old, an individual record is available. Generations intervals are optimised within the limits imposed by the forementioned restrictions. In closed nucleus schemes commercial cows are not considered for selection of nucleus dams (in contrast to the other schemes). The commercial population consists of one million pedigree and milk recorded cows. Since nucleus

Table 3. Results of open and closed nucleus and conventional and modern progeny testing schemes.

No. of sires	$E(\Delta G)$ (σ_g/yr) [*]	s.d.(ΔG) [**] $(10^{-2}\ \sigma_g/yr)$	Gen. var. (σ_g^2) [***]	Fract. nucl. dams from nucl.	Gen. interv. sires	dams
Conventional progeny testing:						
4	0.246	2.27	0.67	0.19	6.1	4.3
8	0.240	1.73	0.67	0.09	6.1	4.3
16	0.231	1.41	0.67	0.03	6.2	4.3
32	0.223	1.25	0.68	0.02	6.3	4.4
Modern progeny testing:						
4	0.278	4.40	0.70	1.00	6.1	2.1
8	0.263	3.16	0.71	0.97	6.1	2.2
16	0.244	2.18	0.70	0.75	6.2	2.2
32	0.229	1.53	0.70	0.38	6.3	2.1
Open nucleus:						
4	0.281	9.83	0.85	0.32	2.0	3.4
8	0.284	8.05	0.85	0.31	2.0	3.3
16	0.284	5.72	0.84	0.32	2.3	3.3
32	0.277	4.36	0.83	0.16	2.4	3.6
Closed nucleus:						
4	0.299	19.6	0.89	1.00	2.0	2.3
8	0.297	14.7	0.89	1.00	2.0	2.3
16	0.290	10.3	0.88	1.00	2.3	2.3
32	0.281	7.5	0.88	1.00	2.4	2.6

[*] σ_g is genetic standard deviation in base population.
[**] Standard deviation of genetic gain.
[***] Steady state genetic variance in nucleus corrected for ancestral selection as a fraction of the base population genetic variance.

sires are also selected for service in the base, nucleus animals have many half sibs in commercial herds providing information for selection. Sires may be selected from the same full sib family.

Selection is for milk production, i.e. an aggregate trait which might include milk, fat and protein yield. The heritability is 0.25 and genetic and phenotypic correlations between lactations are 1 and 0.4 respectively.

RESULTS

Genetic gains of conventional and modern progeny testing and open nucleus schemes were about 19, 13 and 3 % lower than those of closed nucleus schemes, which had the highest response rates (Table 3). Meuwissen (1989) suggested that increasing the number of selection candidates by opening the

nucleus leads to a (slight) increase in genetic gain. However, intense
selection of base females as nucleus dam resulted in decreased genetic
variances in the nucleus (Table 3). This effect causes the slightly lower
genetic gains of open nucleus schemes compared to closed nucleus schemes.

Closed nucleus schemes had the highest standard deviations of genetic
gains: about 46, 79 and 86 % higher than those of open nucleus and
conventional progeny testing schemes respectively (Table 3).

In all schemes generation intervals were close to their minimum values
(Table 3). The closed nucleus schemes are similar to the juvenile MOET
nucleus schemes of Nicholas and Smith (1983). Reduction in genetic variance
was much higher for the conventional progeny testing schemes (Table 3), due
to the more accurate and more intense selection.

DISCUSSION

Figure 1 plots genetic gains of the breeding schemes taken from Table 3
against their standard deviations. When a low standard deviation of genetic
gain is wished, i.e. a low risk rate, say less than 0.02 σ_g-units, the
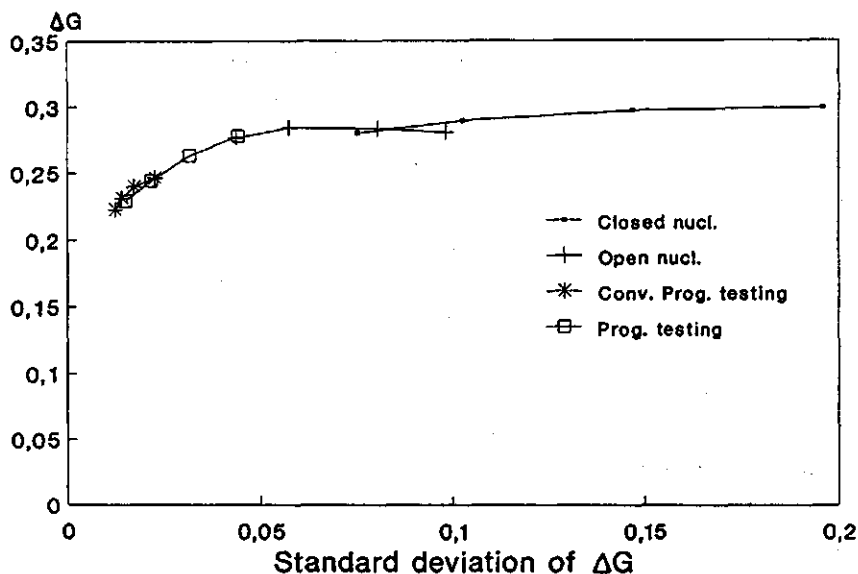
Figure 1. The selection response as a function of its standard deviation.

utility

risk preference

risk indifferent
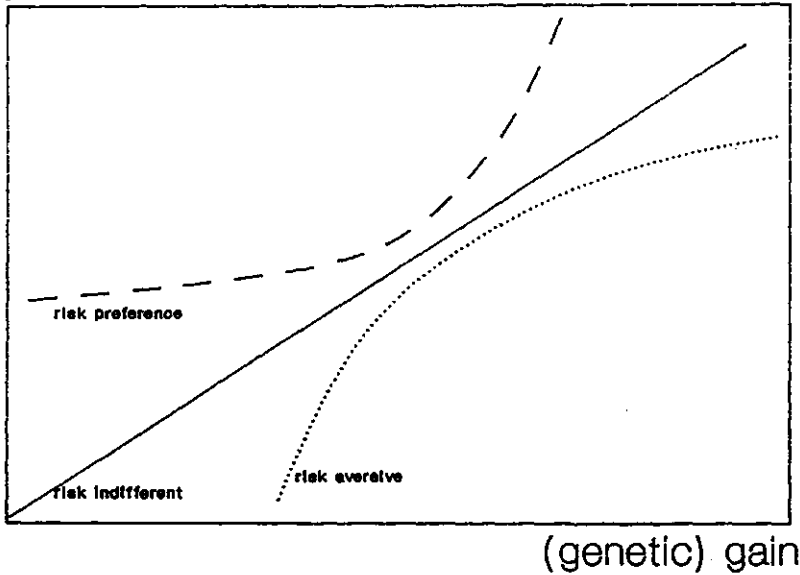
risk aversive

(genetic) gain

Figure 2. Examples of utility functions.

conventional progeny testing scheme will be chosen. Similarly, for every desired risk rate the optimal scheme will be found in Figure 1.

The preference of a decision maker is the subject of utility theory (see e.g. Anderson et al., 1977). Decision makers show risk preference, risk indifference or risk aversion. The majority of the decision makers is risk aversive. In the present situation, where an increase of risk (variance of the selection response) is accompanied by an increase of inbreeding, risk aversion is probably general. The utility function shows the use of (genetic) gain to the decision maker (see Figure 2). The utility function of an risk aversive decision maker increases at a decreasing rate. The decision maker chooses the alternative which has the highest expected utility. It seems reasonable to assume that higher moments than the variance do not affect the choice between breeding schemes significantly. Consequently, a second order approximation of the utility function over the relevant range will be adequate (the expectation of a third order function involves the third moment etc.). The quadratic approximation of the utility function is:

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Table 4. Expected utility of the breeding schemes from Formula (21).

No. of sires :	4	8	16	32
Risk aversion factor (a) is 0.72:				
Conv. prog. testing	0.202	0.198	0.192	0.187
Modern prog. testing	0.221	0.212	0.201	0.191
Open nucleus	0.217	0.221	0.224	0.220
Closed nucleus	0.207	0.218	0.222	0.220
Risk aversion factor (a) is 0.36:				
Conv. prog. testing	0.224	0.219	0.219	0.211
Modern prog. testing	0.260	0.247	0.230	0.217
Open nucleus	0.261	0.264	0.265	0.259
Closed nucleus	0.269	0.271	0.268	0.261

$$U(\Delta G) = \Delta G - a\ \Delta G^2 \qquad\qquad (20)$$

where : $U(\Delta G)$ is the utility of ΔG

a is a positive constant specifying risk aversion.

Only one constant a is required, because adding a constant to the utility function or multiplying the utility function by a constant does not affect the choice between breeding schemes. The relevant range of Formula (20) is from 0 to $1/(2a)$, i.e. beyond $1/(2a)$ function (20) deceases (a utility function can not decrease). Consequently, the probability of ΔG larger than $1/(2a)$ should be negligible small for all schemes considered. This is obtained by equating $1/(2a)$ to $0.299 + 2*0.196 = 0.69$ $(=\mu+2\sigma)$ (see Table 3). This gives a=0.72. Smaller values of a also will lead to small probabilities of ΔG being larger than $1/(2a)$ and are acceptable as well. By using the maximum a-value, also the aversion towards inbreeding will be partly accounted for. The expected utility is:

$$E(U(\Delta G)) = E(\Delta G) - a\ E(\Delta G^2) = E(\Delta G) - a\ V(\Delta G) - a\ (E(\Delta G))^2 \qquad (21)$$

Expected utilities are given in Table 4 for a=0.72 (maximum risk aversion) and a=0.36. Relative comparison of expected utilities is meaningless, since utility functions are indifferent towards addition of a constant. With maximum risk aversion, open nucleus schemes have the highest expected utilities and conventional progeny testing schemes the lowest. When a=0.36, closed nucleus schemes have the highest expected utility and conventional progeny testing schemes still have the lowest. It seems that the extra genetic gain due to shortening generation intervals more than compensates

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Table 5. Predicted and simulated (1000 replicates) results of two adult and a juvenile MOET schemes. In all schemes, 16 sires were mated to 64 dams.

Breeding scheme	Adult	Adult	Juvenile
Generation interval (yr)	4	4	2
No. of animals born / gener.	512	1024	512
Predicted results:			
$E(\Delta G)$ $(\sigma_g/yr)^{*)}$	0.171	0.211	0.242
s.d.(ΔG) (σ_g/yr)	0.122	0.137	0.176
$\sqrt{(2\ \Delta F\ V_{TBV}}^{*})^{**)}$ (σ_g/yr)	0.144	0.172	0.233
Simulated results:			
$E(\Delta G)$ (σ_g/yr)	0.189	0.228	0.221
s.d.(ΔG) (σ_g/yr)	0.091	0.101	0.177

*) σ_g is genetic standard deviation in base population.
**) the inbreeding rate (ΔF) was obtained from the simulations.

for the extra variance in genetic gain. The small increase in genetic gain due to closing the nucleus only compensates for the increased variance of genetic gain when risk aversion is not too strong. In the nucleus schemes, selection of 8 - 16 sires had the highest expected utilities, whereas in the progeny testing schemes selection of 4 sires had the highest expected utilities.

In order to check predicted variances of selection responses, two adult and one juvenile closed nucleus schemes were simulated by the simulation model described in Meuwissen (1990b). Generations were discrete, with generation intervals of 4 and 2 years, respectively. Sixteen sires were selected and mated to 64 selected dams. Male and female offspring were produced in equal numbers. Selection of sires and dams was for BLUP-EBV. In Table 5, predicted standard deviations of selection response were up to 36% higher than simulated. The predictor $\sqrt{(2\ \Delta F\ V_{TBV}}^{*})$ overestimated simulated standard deviations by up to 70%. The latter predictor gives correct standard deviations of traits, that are uncorrelated to the breeding goal. The standard deviation of the genetic level of traits, that are under selection, is lower than that of unselected traits (Table 5). The presented method for predicting variances of selection responses only accounted partly for the effects of selection, i.e. only covariances due to full- and half-sib relationships were accounted for. Probably, more distant relationships are important for predicting varainces of selection responses, similarly as for prediction of rates of inbreeding (Wray and

Thompson, 1990). The presented method for prediction of variances of
genetic gain must be seen as an first order approximation. For prediction
of utilities a first order approximation seems to be sufficient, since the
impact of variances of selection responses on utility is rather small.

The number of male and female offspring per donor cow was fixed. In
practice, numbers of offspring obtained by MOET are very variable. These
variances of family size cause extra differences in the contributions of
families to the next generation. The number of families that are
effectively forming the next generation is reduced and thus variance of
selection response is increased. Further, variance in family size leads to
variance in accuracy of selection, because the number of relatives that
provide information for the estimation of breeding values varies.

CONCLUSIONS

Closed nucleus schemes gave 3, 13 and 19% higher response rates than open
nucleus and modern and conventional progeny testing schemes respectively.
Standard deviations of the selection responses of closed nucleus schemes
were 46, 79 and 86% higher, respectively.

The breeding schemes with the shortest generation intervals had the
highest expected utilities. Whether closed nucleus schemes were prefered
above open nucleus schemes depended on the amount of risk aversion. In
progeny testing schemes, selection of 4 sires had the highest expected
utility and in nucleus schemes this was selection of 8 - 16 sires.

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Chapter 6

GENERAL DISCUSSION

INTRODUCTION

In Chapter 2 and 3 a model was derived for optimising animal breeding
plans for their steady state selection response. The model accounted for
variance reduction due to selection and reduction of selection
differentials due to correlations between estimated breeding values (EBVs)
of relatives in a finite population. These factors reduced predicted
genetic gains by 20 - 30% and by 0 - 30%, respectively. Dairy cattle
breeding schemes, e.g. conventional progeny testing and (closed) nucleus
schemes, were modelled as open nucleus schemes.

In Chapter 4, the model was used to optimize dairy cattle breeding
schemes with varying female reproductive rates. Optimal schemes had much
shorter generation intervals than conventional progeny testing schemes. The
'openess' of the nucleus schemes decreased with increasing female
reproductive rate. In Chapter 5, the increased risk of breeding plans with
short generation intervals was accounted for, which required prediction of
variances of selection responses. Even when maximum risk aversion was
assumed, breeding schemes with short generation intervals were preferred.

In this Chapter, effects, that were neglected in the prediction model,
optimization of breeding schemes and practical limitations are discussed.

MODEL

Variance reduction due to selection.

In the literature deterministically predicted response rates are often
higher than simulated, e.g. compare Nicholas and Smith (1983) to Juga and
Maki-Tanila (1987). Accounting for variance reductions due to selection,
which consists of reduction of genetic gain due to linkage disequilibrium
(Bulmer, 1971) and reduction of variance of information sources which were
previously selected for, reduced predicted response rates by 20 - 30%
(Chapter 2). When considering a wide variety of population structures, Wray

and Hill (1989) concluded that the ranking of breeding schemes was not greatly altered when accounting for variance reduction due to selection. If selection is for BLUP breeding value estimates the relative reduction in steady state genetic gain due to reduction in variance is (Dekkers, 1989):

$$\sqrt{(1/(1+I(I-x)))} \tag{1}$$

where I and x are the intensity of selection and the corresponding truncation point in an infinite population, respectively. Thus, reduction in genetic gain due to variance reduction depends on the intensity of selection, but not on the initial accuracy of selection.

Table 1. Reduced variances after selection: predicted by $1-I(I-x)^{*)}$ or by the average of 2000 Monte Carlo simulations (between brackets: the simulated as a percentage of the predicted values). Selection is from a population of 5 families of 5 animals each. Before selection variances were equal to 1.

| | | Simulated values: | |
| | Values predicted | Intra-class correlation | |
No. selected	by 1-I(I-x)	0.5	0.8
2	0.158	0.124 (78)	0.058 (37)
3	0.181	0.144 (80)	0.071 (39)
4	0.200	0.163 (82)	0.087 (44)
5	0.219	0.182 (83)	0.105 (48)
10	0.311	0.280 (90)	0.239 (77)
15	0.422	0.391 (93)	0.366 (87)

[*)] I is standardised selection differential; x is standardised truncation point for infinite population size.

In this thesis the expected variance reductions due to selection were predicted as $I(I-x)$, which is exact for infinite population sizes. In order to check the adequacy of this method for finite populations, 2000 populations of 5 families and 5 animals per family were simulated. Within each population the variance of n selected animals was estimated by:

$$(\Sigma EBV_i^2 - (\Sigma EBV_i)^2/n)/(n-1) \tag{2}$$

where EBV_i is the estimated breeding value of the i-th animal. In the denominator n-1 is used instead of n, because derivation of selection differentials was based on infinite population variances (see Chapter 3). The estimates of the variances were averaged and compared to $1-I(I-x)$ (Table 1). Predicted variances were up to 2.7 times as high as simulated

variances. Especially, when intra-class correlations between relatives were high, 1-I(I-x) was a poor predictor. The expectation of (2) is (Engel, 1990):

$$\Sigma V(EBV_i)/n -2\Sigma_{i<j}Cov(EBV_i,EBV_j)/(n(n-1)) + \{\Sigma E(EBV_i)^2 - (\Sigma E(EBV_i))^2/n\}/(n-1) \tag{3}$$

With random sampling, the expectation of (2) is $V(EBV_i)$ $(=V(EBV_j))$, where EBV_i denotes the i-th sampled EBV (and i≠j), i.e. Formula (2) is an unbiassed predictor of the variance of the EBVs. However, when EBVs are ranked, covariances between EBVs occur, for which the second term in Formula (3) accounts. The third term reflects the extra variance caused by the unequal expectations of the ranked EBVs. $E(EBV_i)$, $V(EBV_i)$ and $Cov(EBV_i,EBV_j)$ can be approximated as indicated in Chapter 5. However, prediction errors were large, because the difference between the variance and covariance terms is required, which are both affected by approximation errors.

The effect of underestimation of variance reduction on the predicted genetic gain can be assessed by calculating the steady state variance of BLUP breeding value estimates. When selection intensities and accuracies of males and females are equal, reduction of variance of EBV due to selection is given by the recurrent relations:

$$V(EBV)_t^{**} = (1-I(I-x)) \ V(EBV)_t^{*} \tag{4}$$

$$V(EBV)_{t+1}^{*} = \tfrac{1}{2}V(EBV)_0 + \tfrac{1}{2}V(EBV)_t^{**} \tag{5}$$

where * denotes correction for ancestral selection; ** denotes correction for ancestral selection and for selection on individual EBV; $V(EBV)_t$ denotes the variance of EBV in generation t. From (4) and (5), the steady state variance of EBV is:

$$V(EBV)_\infty^{*} = V(EBV)_0 \ / \ (1+I(I-x)) \tag{6}$$

Suppose the reduction in variance predicted by I(I-x) is 0.84, while the 'real' reduction in variance equals 0.94, which reflects the worst situation in Table 1. The remaining variance is a factor 2.7 smaller than expected. From (6), the predicted steady state variance is 0.54 $V(EBV)_0$,

and the 'real' value is 0.52 $V(EBV)_0$, i.e. a difference of 4%. Steady state genetic gain equals I $\sigma(EBV)_\infty^*$, i.e. steady state genetic gain is overestimated by about 2%. Thus, the effect of order statistics on variance reduction due to selection may be substantial, but this does not affect genetic gain substantially.

Formula (1) may be derived from (6), since the reduction in steady state genetic gain due to variance reduction due to selection equals $\sigma(EBV)_\infty^*/\sigma(EBV)_0$.

Reduced selection differentials due to finite population size and family structure.

Also reduction of selection differentials due to finite population size and family structures causes overestimation of selection response (Hill, 1976). This effect is negligible small in schemes with low intra-class correlations between estimated breeding values of relatives (say less than 0.5) and large population sizes (say larger than 100 selection candidates). When selection is mainly on sib and pedigree information, intra-class correlations exceed 0.5 and selection differential can be reduced up to 30%. This effect might cause major reranking of breeding schemes, since it is negligible in some breeding schemes while it reduces response substantially in schemes with high intra-class correlations between EBV of relatives. In chapter 3, an approximation was derived to account for these reductions in selection differential when selection candidates had a nested full-half sib family structure. Deterministic models that accounted for variance reduction due to selection and for reduction of selection differentials were in good agreement with Monte Carlo simulations that neglected variance reduction due to inbreeding (see Chapter 4).

Variance reduction due to inbreeding.

Variance reduction due to inbreeding was neglected in the model, that was derived in Chapter 2 and 3. As shown in Chapter 2, it affects short term genetic gains, up to 10 generations, only marginally (in view of the large differences in inbreeding rate considered in Chapter 2). In dairy cattle breeding, the time horizon is about 25 years, i.e. the time period beyond which returns are considered unimportant due to changes in production environment. In the context of inbreeding it is probably useful to define the time horizon as the period during which the breeding population will be

closed. This is usually shorter than 10 generations. When the evolution of genetic variance is to be predicted for 10 generations, the effect of inbreeding is not negligible (see Chapter 2). A poor predictor of the inbreeding rate is $\frac{1}{2}V(\Delta G)/V_a$ (see Chapter 5), where $V(\Delta G)$ and V_a are the variance of the selection response and the additive genetic variance, respectively. $V(\Delta G)$ is approximated in Chapter 5.

The infinitesimal model.

The genetic model used here was the infinitesimal model, i.e. the genetic value of an animal depends on a large number of additive unlinked genes of small effect each. However, the number of genes affecting a trait like milk production may be small, some will be linked and non-additive interactions of gene effects can be expected since biochemical pathways show many complex interactions. Thus, the infinitesimal model is a simplification of the true genetic mechanism. Even with very few loci (e.g. three), initial distributions of breeding values will be approximatly normal and thus regression of offspring on parents is almost linear, i.e. at least for one generation the infinitesimal model holds. Changes in gene frequencies due to selection will decrease or increase genetic variance. The size of the changes in gene frequencies per generation depends on the size of the gene effects, which on average are larger with smaller numbers of genes. Consequently, the number of generations, during which predictions by the infinitesimal model are satisfactory, depends on the number of loci and probably on other departures from infinitesimality. Beyond this period, knowledge about gene frequencies and effects are needed to predict genetic gain. Maki-Tanila and Kennedy (1986) showed that the infinitesimal model predicts response rates satisfactory up to three generations of selection except when a selection limit is reached and when dominant gene effects occur.

Variability in response to superovulation.

Variability in the number of offspring of parents was neglected here. However, responses of cows to superovulation are very variable: the number of eggs recovered varies from 0 to 40. Keller and Teepker (1989) and Ruane (1990) showed that especially cows not responding to superovulation cause decreased selection responses (up to 64% reduction of female selection differential), because they have to be replaced by cows with lower breeding

value estimates. When predicting response rates, this might be accounted for by including non-responding cows in the estimate of the average results of MOET. The number of families is reduced by non-responding cows. This should be accounted for when calculating selection differentials. By repeating superovulation treatment on non-responding cows until all cows respond, the problem of non-responding cows could be eliminated, but the generation interval will be increased. Also variances in family size cause increased variances of selection responses, because the effective number of families is decreased and because accuracy of selection will vary.

The repeatability model.

It was assumed that genetic correlations between milk production records of individual cows are 1, i.e. second and later lactations are repeated measurements of the first lactation record. In practice, genetic correlations between milk production records are somewhat lower than 1. Therefore, the genetic variance (or heritability) used here could be considered as the genetic variance common to all lactations and is lower than heritabilities found from lactation data. For instance, if the heritability of lactation records is 0.35 and genetic correlations between lactation records are 0.85, the 'common heritability' is about 0.25 ($\approx 0.35 * 0.85^2$).

Costs.

In order to keep calculations general, costs were not considered here. For instance, in this thesis no assumption was required about management of nucleus animals, i.e. in special herds or dispersed over commercial herds. Similarly, the results of MOET could be summarised in one figure: the number of offspring surviving till 2 years of age. Specification of the number of eggs recovered, the number of eggs successfully transfered, mortalility at birth etc. was not required. When accounting for costs, all these factors have to be specified as well and the general breeding plans considered here turn into special cases. In a competitive market like that of dairy cattle breeding, the effect of an increase in genetic improvement on the market share needs to be assessed in order to compare costs and returns. In a competitive market, Dekkers (1989) found that about 5 % more genetic gain would lead to $\pm$ 56 % increase in net present value of returns

over 20 years. Consequently, almost any costs are justified to obtain even
marginal increases of genetic gain. This argument applies to the part of
the costs-benefits curve that was covered by the competitive breeding plans
considered by Dekkers (1989). Since Dekkers' simulations were based on a
variety of present breeding schemes, the argument may be valid for all
present breeding schemes.

OPTIMIZATION OF BREEDING PLANS

Generation intervals.

A conventional progeny testing plan is a very robust method to obtain
genetic progress. Bulls have to prove themselves before they are
extensively used. In the male pathways selection response is almost
guaranteed. Due to recent developments in accuracy of breeding value
estimation procedures, EBVs (Estimated Breeding Values) of unproven bulls
and of cows have improved. Also availability and use of full sib
information, which is due to the use of MOET, leads to increased accuracies
of EBVs of unproven bulls. This made selection of unproven bulls
attractive, as was shown by Nicholas and Smith (1983). In dairy cattle
breeding plans, reduction of generation intervals more than compensates for
the accompanying reduced accuracy of selection.

The 'openess' of nucleus schemes.

In a progeny testing scheme, the number of bull dams required for the
production of young bulls decreased due to the use of MOET. Also selection
of bull dams that were themselves daughters of bull dams was increased
relative to the number of bull dams selected (Chapter 4). By housing the
daughters of bull dams in a special herd (nucleus herd) and selecting all
bull dams from this herd, closed nucleus schemes as proposed by Nicholas
and Smith (1983) are obtained. Expected steady state selection responses of
these schemes were competitive to those of open nucleus schemes, which
consider nucleus and (commercial) base animals as selection candidate (see
Chapter 5).

Secondary traits.

In this thesis selection was only for milk production, assuming that information on other traits, that are selected for, only marginally affect accuracies of selection for the overall breeding goal. The breeding goal is assumed to be dominated by milk production. When low heritable traits (e.g. fertility traits) have a substantial impact on the breeding goal, the value of progeny testing of bulls will increase (Teepker and Smith, 1990). Selection for traits, which are measured early in life, in both sexes and have an intermediate heritability (such as growth rate), will lead to shorter generation intervals. However, if these traits show considerable genotype * environment interactions, progeny testing will be favoured.

Random mating of selected parents.

In this study, optimization of breeding schemes for genetic gain was simplified by using the property of BLUP-EBV, that EBV can be compared across herds, age classes and tiers. Apart from numbers of animals to select and nucleus size, all other parameters were optimized just by selecting for high EBV. Selected sires and dams were mated at random. However, realised EBV depend on the breeding strategy used, i.e. the matrix of additive genetic relationships, which is used for EBV estimation, depends on breeding strategy. Assortative mating might increase genetic gain, because the variance of EBV will be increased (especially when EBV are mainly based on pedigree information). Smith and Hammond (1987) predicted increased selection responses of 5 - 6% when one generation of assortative mating based on mass selection was followed by one generation of index selection (proportions selected in both generations were 0.1 and $h^2 = 0.05 - 0.2$). It would be interesting to extend these results beyond two generations and to smaller proportions selected.

Factorial mating designs.

Woolliams (1989) suggested the use of a factorial mating design instead of the conventional nested full - half sib design. In a factorial mating structure, a donor cow is mated to several bulls, i.e. for each flush another bull is used. In MOET nucleus schemes, genetic gain was improved by up to 7%. This moderate improvement is easily obtained in practice, when donor cows are flushed more than once. A factorial mating design leads to less full sib relationships, whereas the number of (maternal) half sib relationships increases. Because half sibs have smaller intra-class

correlations of EBVs than full sibs, the reduction of selection differentials due to family structures is smaller for a factorial mating design. This could not be tested by the approximation for selection differentials in chapter 3, because this method was developed for a hierarchical mating design, i.e. only full- and paternal half sibs are considered. Extension of the method of Chapter 3, in order to account for maternal half sibs, will be tedious.

Value of half sib information from commercial herds.

The closed nucleus breeding schemes, considered in Chapter 5, used production records of base animals for breeding value estimation. Especially, half sib records of sires and dams were used. However, milk production records of commercial cows might not be available to the breeding organisation. Table 2 shows the effect of base animal records on the response rates and its standard deviations in closed nucleus schemes. Differences in response rates increased with an increasing number of sires selected. Selection of more sires caused smaller half sib families in the nucleus and thus the value of half sib information outside the nucleus increased. When information on relatives outside the nucleus is not available, accuracy of selection increases with selection of fewer sires. The effect of the use of base population records on the standard deviations of the response rates was neglegible (Table 2). Therefore, the consequences for inbreeding rates are expected to be neglegible as well. However, prediction of standard deviations did not account for variance in accuracy of EBVs. Variance in accuracy will be larger in schemes which use only records of nucleus animals.

Table 2. Genetic gain (ΔG) and its standard deviation (s.d.(ΔG)) (both in genetic standard deviation units per year) for closed nucleus schemes with (from Chapter 5) and without using base animal records for breeding value estimation.

No. of sires selected / yr	ΔG		s.d.(ΔG)	
Use of base animal records	No	Yes	No	Yes
4	0.294	0.299	0.197	0.196
8	0.287	0.297	0.146	0.147
16	0.272	0.290	0.106	0.103
32	0.254	0.281	0.078	0.075

Organizational aspects.

Open nucleus and conventional progeny testing schemes require the cooperation between the breeding organization and commercial farmers. A closed nucleus scheme might be managed by only one organization, which increases practical efficiency. Due to the small number of animals, that are to be tested in closed schemes, traits could be measured which are not measured in practice. Also, measuring juvenile predictors of milk production is often not feasible in commercial herds (Woolliams and Smith, 1988), especially when a challenge test is involved.

Heterogeneous variances within herds and preferential treatment.

Throughout this thesis it was assumed that generation intervals could be optimized by selecting for high EBVs across age classes. This assumes unbiasedness of EBVs. Wilhelm and Mao (1989) found that EBVs of young bulls are mostly overestimated. Consequently, it is not well possible to compare EBVs of young bulls to those of proven bulls in order to optimize generation intervals. EBVs of bull dams are potentially biased as well (Van Vleck, 1988). Heterogeneity of variances within herds and/or preferential treatment of bull dams might cause these biases.

Biasedness of EBVs should be reduced or eliminated before adapting breeding plans with selection on EBVs irrespective of age. Potential methods to achieve this are: log-transformation of milk production data, standardizing variances within herds, using only first lactation records, excluding extreme records, and housing all potential nucleus/bull dams in a special herd. The latter method implies a closed nucleus scheme. These schemes avoid selection across herds. Within nucleus herds, effects of heterogeneous variances are eliminated and preferential treatment within the herd does probably not interfere much with selection decisions. Preferential treatment also might occur within nucleus herds due to competition with other nucleus schemes.

In the future, scope for affecting milk production records and thus for preferential treatment will increase, due to the introduction of bovine somatotropin (Colleau, 1989) and other agents. This will hinder selection of elite females from commercial herds. This might lead to closed nucleus schemes.

Genotype * environment interactions.

There is not much evidence for genotype * environment interactions between commercial herds in milk production data (Meyer, 1987). Genotype * environment interactions between nucleus and commercial herds should be avoided by adjusting the nucleus herd management to that in 'the average commercial herd (of the future)'. Also, several nucleus herds could be used, reflecting different commercial conditions. Genotype * environment interactions could be enhanced, when nucleus breeding companies maximize production records by improving their management above that of commercial farms in order to stimulate semen and embryo sales.

Use of unproven bulls by commercial farmers.

In optimal breeding schemes, generation intervals of sires of base animals, i.e. sires to breed commercial cows, are short. The use of unproven bulls might not be accepted by commercial farmers, because of the risk involved. By using several unproven bulls (say 5-10), major fluctuations of the mean genetic level will be avoided. Performances of individual cows remain variable, which offers opportunities for selection. However, farmers might prefer a more homogeneous cow population, which is on average slightly inferior. If this notion is general, bulls have to be progeny tested before being used in practice. Due to the use of unproven bulls, the genetic level and -variance of the base animals will be too low for the best base animals to be competitive with nucleus animals. Consequently, a closed nucleus herd will be obtained, using short generation intervals within the nucleus and progeny tested bulls for commercial cows. The mechanism described leads to a clear distinction between nucleus and base herds in terms of genetic level, cows present and bulls used.

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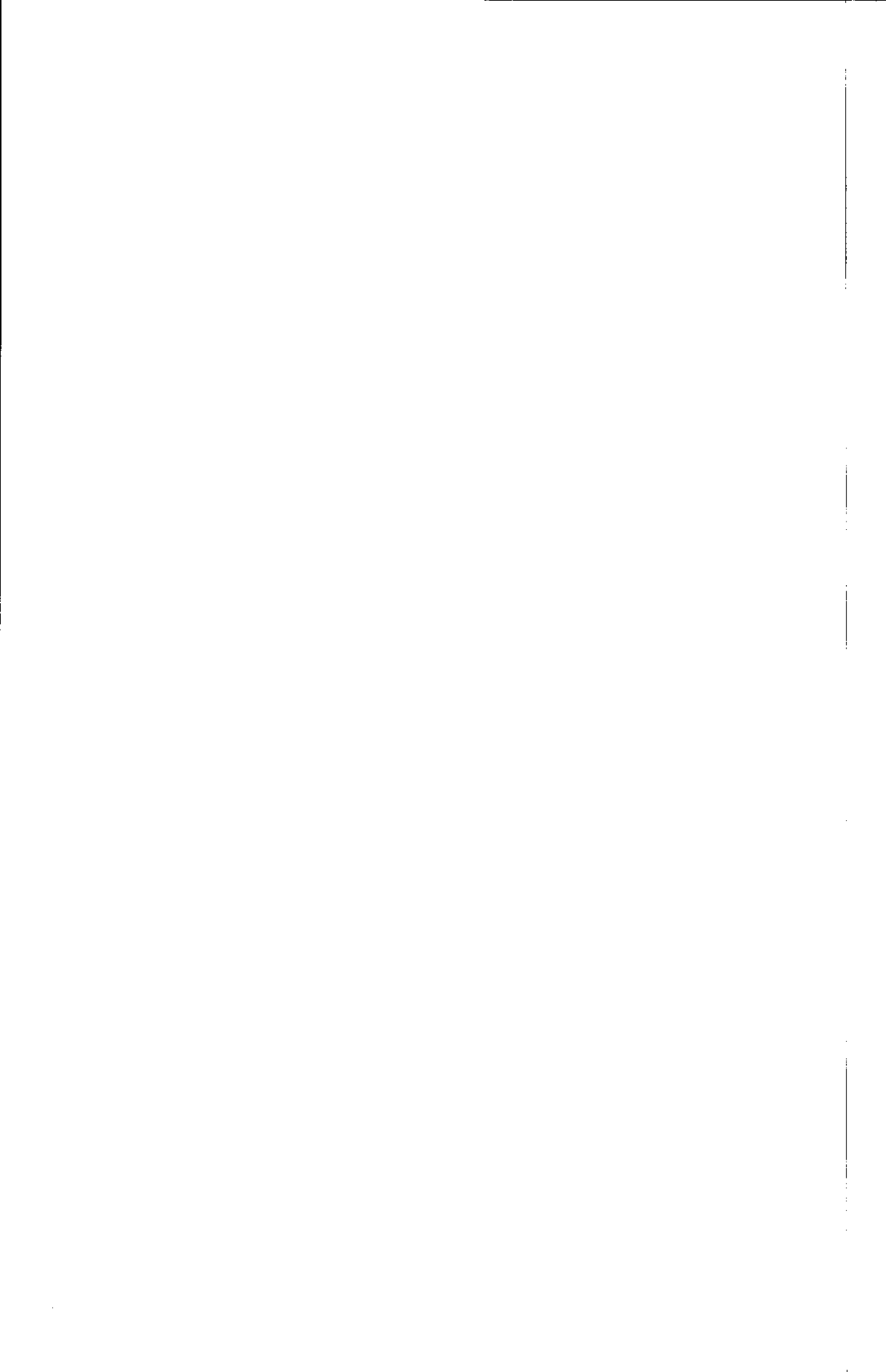
SUMMARY

Introduction

Nicholas and Smith (1983) proposed Multiple Ovulation and Embryo Transfer
(MOET) nucleus breeding schemes to increase reponse rates in dairy cattle
breeding. Predicted genetic gains were up to twice as high as those of
conventional progeny testing schemes. In the MOET nucleus breeding schemes,
selection was within a closed nucleus herd using short generation intervals
and mainly sib information. Juga and Maki-Tanila (1987) simulated MOET
nucleus schemes and found that predicted rates of gain were 124 % higher
than simulated. From this two questions arise: i) how to predict response
rates correctly; and ii) how to make optimal use of MOET in dairy cattle
breeding.

Prediction of response rates

Major factors decreasing response rates are:

1. Reduction of variances due to selection. This consists of reduction of
   variances of information sources, which were previously selected for,
   and reduction of genetic variance due to linkage disequilibrium between
   genes as described by Bulmer (1971). The effect of linkage
   disequilibrium could be accounted for by correcting the genetic variance
   for all selection on ancestral sources of information. This factor
   reduced response rates by 20-30%.

2. Reduction of selection differentials due to small numbers of selection
   candidates and small numbers of families (Hill, 1976). Selection
   differentials are often predicted assuming that breeding value estimates
   of selection candidates are uncorrelated. However, family relations
   between selection candidates cause correlations between breeding value
   estimates. Especially in schemes with short generation intervals, where
   breeding value estimates are mainly based on information of sibs,
   correlations between breeeding value estimates of sibs are high, since
   these are based on the same sources of information. An approximation for
   the reduced selection differentials in a nested full-half sib family
   structure was derived. Predicted response rates were reduced by up to
   another 30%.

3. Variance reduction due to inbreeding. Also, this factor reduces genetic
   variance and thus genetic gain substantially, when the inbreeding

coefficient is large. Even with an inbreeding rate of 5% per generation, i.e. effective population size is 10 animals per generation, it takes about 5 generations before the inbreeding coefficient is large enough to be of importance. Therefore, average selection response during the first five generations is not much reduced (6%). For 10 generations this figure is 13%. Thus, the impact of this factor depends on the time horizon (here: the time period during which the breeding population is expected to be closed to foreign breeding stocks). In view of the large difference in effective population size, i.e. 10 animals per generation vs. infinite (no inbreeding), it is concluded that up to 10 generations the impact of variance reduction due to inbreeding on the ranking of breeding schemes is not large.

The first and second factor were accounted for in this study. Variance reduction due to inbreeding was neglected.

Breeding schemes

In nucleus breeding schemes, nucleus dams are selected from the female nucleus population, which has the same genetic level as the bull stud. In progeny testing schemes, bull dams are selected from commercial herds. However, some cows born in commercial herds are daughters of bull sires and bull dams and are thus of equal genetic level as the bulls in the stud. These cows are comparable with the nucleus females in nucleus schemes and have an higher probability of being selected than 'normal' commercial cows. Thus, progeny testing schemes are open nucleus schemes, where daughters of bull sires and bull dams form the nucleus females and where 'normal' cows are the base population.

It was assumed here, that milk production records were not biased by housing of nucleus animals, i.e. in special nucleus herds or dispersed across commercial herds. There are only three differences between the nucleus schemes proposed by Nicholas and Smith (1983) and progeny testing schemes, that use MOET to increase reproductive rates of bull dams:

1. In the closed nucleus schemes of Nicholas and Smith, selection of dams is within the nucleus herd, whereas in open nucleus / progeny testing schemes nucleus and base population females serve as selection candidates. When, relative to the nucleus size, many bull dams have to be selected, this is advantageous for the open nucleus/progeny testing scheme. When the number of selected dams is small due to the use of

MOET, relatively many dams will be selected from the genetically superior nucleus population. This implies that the open and closed nucleus schemes become more similar, when female reproductive rates increase. With on average 8 offspring per donor cow per year, differences in genetic gain between open and closed nucleus breeding schemes were small.

2. Generation intervals are much longer in progeny testing schemes than in nucleus breeding schemes, which is partly due to progeny testing of bulls. James (1987) shows that generation intervals could be optimised in any schemes by selecting for BLUP breeding values across all age classes. The ad hoc nature of this optimization makes predefining generation intervals of breeding schemes redundant. Consequently, this difference between nucleus breeding and progeny testing schemes disappears. However, in practical progeny testing schemes, generation intervals are not optimised: only proven bulls (at least 5 years old) are considered for selection and usually cows without a milk production record are not considered for selection of bull dams. Selection response increases by about 15%, when these restrictions are abolished. Biasedness of breeding value estimates of young animals will reduce this improvement and selection response might be even reduced.

3. Progeny testing of young bulls in the base population. In open nucleus breeding schemes with optimised generation intervals, progeny testing reduces genetic gains by up to 10% depending on the number of sires used.

Variances of selection responses

Variance of the selection response is a measure for risk of the breeding plan. Further, variance of the selection response and inbreeding are positively related. Reduction of generation intervals due to the optimization procedure increased the standard deviation of the selection response by a factor 2 to 3. Utility theory was used to weigh selection response against its variance. A quadratic approximation of the utility function and maximum risk aversion were assumed. Schemes with optimised (short) generation intervals had the highest utility.

Closed nucleus schemes had a lower utility than open nucleus schemes, both with optimized generation intervals. This was due to the 80 % higher standard deviation of the selection response in closed nucleus schemes.

Differences in selection response were small: closed nucleus schemes had 3% more selection response than open nucleus schemes (8 offspring per donor cow). In these open nucleus schemes, selection of nucleus dams from the base was very intense, which resulted in less genetic variance in the nucleus offspring. This caused the small difference in genetic gain.

Main conclusions
- Variance reduction due to selection reduces predicted genetic gain by 20 - 30 %.
- Correlations between breeding value estimates of relatives reduce predicted selection differentials in breeding schemes by up to another 30%.
  - As reproduction rates of females increase, optimised open nucleus schemes (or progeny testing schemes) become more closed. With an average of 8 offspring per selected cow, open and closed nucleus schemes have almost euqual genetic gains.
- Variances of selection responses increase substantially, when generation intervals are reduced. However, when selection response and its variance were weighted, shorter generation intervals were still prefered.
- Variance of the selection response of closed nucleus schemes is higher than that of open nucleus schemes (both having optimised generation intervals). Therefore, under the assumption that field and nucleus herd milk production records both are unbiassed, open nucleus schemes were prefered.

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SAMENVATTING

DE OPTIMALISATIE VAN MELKVEE-FOKPROGRAMMA'S MET EEN VERHOOGD AANTAL
NAKOMELINGEN PER KOE.

Inleiding

Het Proef-Wacht-Fokstieren (PWF) programma wordt veel gebruikt om de
efficiëntie van de melkproduktie te verhogen. Mede als gevolg van het
nakomelingen onderzoek van de stiertjes zijn de generatie-intervallen lang.
Verhoging van het aantal nakomelingen per koe m.b.v. Meervoudige Ovulatie
en Embryo Transplantatie (MOET) kan tot een verhoogde selectie-intensiteit
van stiermoeders leiden, hetgeen de genetische vooruitgang met maximaal 10%
verhoogd (b.v. Cunningham, 1976).

Nicholas en Smith (1983) stelden het gebruik van MOET-nucleus-
fokprogramma's voor. In deze MOET-nucleus-fokprogramma's werden de
mannelijke en vrouwelijke dieren binnen een gesloten nucleus-bedrijf
geselecteerd, waarbij korte generatie-intervallen gehanteerd werden.
Selectie was op basis van afstammings en, indien voorhanden, volle en half
zuster en eigen informatie. De voorspelde genetische vooruitgang was twee
keer zo hoog als die van het PWF-programma.

Juga en Maki-Tanila (1987) simuleerden MOET-nucleus-fokprogramma's en
vonden dat de voorspelde genetische vooruitgang wel 124 % hoger dan de
gesimuleerde kan zijn. James (1987) liet zien hoe generatie-intervallen ge-
optimaliseerd kunnen worden, hetgeen het vooraf vastleggen van generatie-
intervallen overbodig maakte.

Uit het voorgaande vloeiden twee vragen voort: i) hoe wordt de genetische
vooruitgang correct voorspeld; en ii) hoe moeten fokprogramma's worden
aangepast om optimaal gebruik te maken van MOET.

Het voorspellen van de genetische vooruitgang

Er zijn drie factoren die de genetische vooruitgang aanmerkelijk
verlagen:
1. Reductie van varianties door selectie.
    Dit omvat de afname van de variantie van informatiebronnen, waarop reeds
    geselecteerd is, en de afname van de genetische variantie t.g.v. linkage
    disequilibrium van genen, zoals beschreven door Bulmer (1971). Door de

genetische variantie te corrigeren voor alle selectie op
voorouderinformatie, kon het effect van linkage disequilibrium berekend
worden. Variantie reductie door selectie reduceerde de voorspelde
genetische vooruitgang met 20 - 30 %.

2. De reductie van selectie-intensiteiten t.g.v. een klein aantal selectie-
kandidaten en een klein aantal families (Hill, 1976).
Voor het voorspellen van de selectie-intensiteiten wordt veelal
aangenomen, dat de fokwaardeschattingen ongecorreleerd zijn. De
familierelaties, die tussen de selectie-kandidaten bestaan, veroorzaken
echter correlaties tussen hun fokwaardeschattingen. Vooral in
fokprogramma's met korte generatie-intervallen zijn deze correlaties
hoog, omdat de fokwaardeschattingen dan voornamelijk gebaseerd zijn op
familie-informatie (lijsten van volle en halve zusters) en familieleden
hebben deels dezelfde familie-informatie. Er is een benadering afgeleid
voor het berekenen van de gereduceerde selectie-intensiteiten in
populaties met een geneste volle-half zuster/broer familie-structuur. De
voorspelde genetische vooruitgangen werden nog eens tot 30 % verlaagd
door dit effect.

3. Variantie reductie t.g.v. inteelt. Wanneer de inteeltcoëfficiënt hoog
is, verlaagt dit de genetische vooruitgang aanzienlijk. Zelfs bij een
inteelttoename van 5 % per generatie, oftewel een effectieve populatie-
grootte van 10 dieren per generatie, duurt het ongeveer 5 generaties
voordat de inteeltcoëfficiënt groot genoeg is om van belang te zijn.
Hierdoor wordt de gemiddelde genetische vooruitgang gedurende de eerste
5 generaties niet sterk verlaagd door variantie reductie t.g.v. inteelt
(6% verlaging). Gedurende de eerste 10 generaties is dit 13 %. Het
effect van deze factor hangt dus af van de tijdshorizon (hier: de
verwachte tijd dat de populatie gesloten is voor dieren uit andere
populaties). Wanneer het grote verschil in effectieve populatie-grootte,
10 dieren per generatie versus oneindig (geen inteelt), in aanmerking
wordt genomen, kan geconcludeert worden dat tot 10 generaties de invloed
van variantie reductie door inteelt op de rangorde van fokprogramma's
niet groot zal zijn.

In deze studie werd met de eerste twee factoren rekening gehouden. Variatie
reductie door inteelt werd verwaarloosd.

De fokprogramma's

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In nucleus-fokprogramma's worden de nucleus-moeders geselecteerd uit de nucleuskoeien, die hetzelfde genetisch nivo hebben als de (ongeselecteerde) KI-stieren. In het PWF-programma worden de stiermoeders in de praktijk geselecteerd. Sommige koeien in de praktijk zijn echter dochters uit paringen tussen stiervaders en stiermoeders. Deze hebben dus hetzelfde genetisch nivo als de stieren- populatie en zijn vergelijkbaar met de nucleuskoeien in nucleusfokprogramma's. Hun kans op selectie als stiermoeder is hoger dan die van 'normale' praktijk-koeien. Het PWF-programma is in feite een open nucleus-programma, waarbij de dochters uit de paringen van stiervaders en stiermoeders de nucleuskoeien en 'normale' koeien de basispopulatie vormen.

Er is hier aangenomen dat de melklijsten van koeien zuiver zijn ongeacht de huisvesting van de dieren: op nucleusbedrijven of verdeeld over praktijkbedrijven. Er zijn nu slechts drie verschillen tussen de door Nicholas en Smith (1983) voorgestelde nucleusprogramma's en PWF-programma's die gebruik maken van MOET om meer nakomelingen per stiermoeder te verkrijgen:

1. In de gesloten nucleusprogramma's van Nicholas en Smith worden de moederdieren binnen het nucleusbedrijf geselecteerd, terwijl in open nucleus/PWF-programma's de nucleus- en basispopulatie als selectiekandidaten fungeren. Dit is een voordeel voor het open nucleus/PWF-programma, wanneer, relatief t.o.v. de nucleusgrootte, veel stiermoeders geselecteerd moeten worden. Wanneer, door het gebruik van MOET, het aantal te selecteren moederdieren klein is, zullen relatief veel moederdieren geselecteerd worden uit de genetisch superieure nucleuspopulatie. Dit betekent dat open en gesloten nucleus-programma's meer op elkaar gaan lijken naarmate het aantal nakomelingen per donorkoe toeneemt. Bij 8 nakomelingen per koe per jaar, zijn de verschillen in genetische vooruitgang tussen open en gesloten fokprogramma's erg klein.

2. De generatie-intervallen zijn veel lager in PWF-programma's dan in nucleusprogramma's, hetgeen voor een deel komt door het nakomelingenonderzoek. James (1987) toonde aan dat de generatie-intervallen in elk fokprogramma geoptimaliseerd kunnen worden door over alle leeftijdsklassen heen op BLUP-fokwaardeschattingen te selecteren. Door deze ad hoc optimalisatie wordt het vooraf vastleggen van de generatie-intervallen in fokprogramma's overbodig. Hierdoor verdwijnt dit verschil tussen nucleus- en PWF-programma's. In de PWF-programma's

uit de praktijk worden de generatie-intervallen echter niet geoptimaliseerd: men selecteert alleen op nakomelingen ondezochte stieren (minstens 5 jaar oud) en meestal moeten stiermoeders een eigen lijst hebben. De selectie-response neemt met 15 % toe wanneer deze restricties opgeheven worden. De selectie-respons kan echter minder toenemen of zelfs afnemen door eventuele onzuivere fokwaardeschattingen van jonge dieren.

3. Het nakomelingen onderzoek van proefstieren in de basis. In open nucleusprogramma's met geoptimaliseerde generatie-intervallen verlaagt dit de genetische vooruitgang met maximaal 10 % afhankelijk van het aantal stieren dat gebruikt wordt.

De variantie van de genetische vooruitgang

De variantie van de genetische vooruitgang is een maat voor het risico van het fokprogramma. Verder is er een positief verband tussen de variantie van de genetische vooruitgang en de inteelt. De verkorting van de generatie-intervallen (ten gevolge van de optimalisatie) leidt tot een twee- tot drie-voudige toename van de spreiding van de selectie-respons. De selectie-respons en de spreiding van de selectie-respons werden tegen elkaar afgewogen met behulp van de 'utility' theorie. Er werd een kwadratische benadering voor de 'utility' functie en maximale risico vermijding verondersteld. De programma's met de geoptimaliseerde (korte) generatie-intervallen hadden de hoogste 'utility'.

De gesloten nucleus-programma's hadden een lagere 'utility' dan de open nucleus-programma's. Beiden met geoptimaliseerde generatie-intervallen. Dit kwam door de 80 % hogere spreiding van de genetische vooruitgang in de gesloten nucleus-programma's. De verschillen in selectie-respons waren klein: gesloten nucleus-programma's hadden 3 % meer respons dan open nucleus programma's (8 nakomelingen per donor koe). In deze open nucleus programma's leidde de erg intense selectie van nucleusmoeders uit de basispopulatie tot verminderde variatie van de nucleusdieren. Dit veroorzaakte het kleine verschil in genetische vooruitgang.

Belangrijkste conclusies:

- Variantiereductie door selectie verlaagt de voorspelde genetische vooruitgang met 20 - 30 %.

- De voorspelde selectie-intensiteit, en dus ook de voorspelde genetische
  vooruitgang, kan nog eens met 30 % afnemen door rekening te houden met
  de correlaties tussen familieleden.
- Wanneer het aantal nakomelingen per donor koe toeneemt, wordt een
  geoptimaliseerd open nucleus (of PWF) programma meer gesloten. Bij
  gemiddeld 8 nakomelingen per geselecteerde koe hebben open en gesloten
  fokprogramma's bijna dezelfde genetische vooruitgang.
- De variantie van de genetische vooruitgang neemt sterk toe, wanneer de
  generatie-intervallen korter worden. Na afweging van de genetische
  vooruitgang en zijn spreiding, kregen de programma's met korte
  generatie-intervallen nog steeds de voorkeur.
- De variantie van de genetische vooruitgang van gesloten
  nucleusprogramma's is hoger dan die van open nucleusprogramma's (beide
  met geoptimaliseerde generatie-intervallen). Hierdoor worden de open
  nucleus programma's geprefereerd, ervan uitgaande dat melklijsten op
  praktijk- en op nucleusbedrijven zuiver zijn.

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Curriculum Vitae

Theo Meuwissen werd op 24 juli 1963 geboren te Roermond (Limburg). In 1980 behaalde hij het HAVO diploma aan het Bisschoppelijk College te Echt. Na een jaar aan de Hogere Agrarische School te Den Bosch te hebben gestudeerd, begon hij in 1981 aan de studierichting Zoötechniek van de toenmalige Landbouwhogeschool te Wageningen. In 1987 studeerde hij met lof af met als hoofdvakken de Veeteelt en de Veevoeding en als bijvak de Agrarische Bedrijfseconomie. Sinds 1 februari 1987 is hij verbonden aan het Instituut voor Veeteeltkundig Onderzoek "Schoonoord" te Zeist, waar hij belast is met het modelmatig veefokkerij onderzoek.