

METHODS ON ECONOMIC OPTIMIZATION OF ANIMAL BREEDING PLANS

- notes for a Scandinavian post-graduate course in economic breeding planning, University of Helsinki, Department of Animal Breeding, Helsinki.
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ABSTRACT

This report contains notes on methods on economic optimization of animal breeding plans prepared for a Scandinavian post-graduate course in economic breeding planning at Helsinki, August 28 - September 8, 1978. The following subjects are covered. An introduction is given to deterministic models and Monte-Carlo procedures, secondly a comparison of methods to compute returns from breeding schemes as described by LINDHÉ (1968), PETERSEN et al. (1974), McCLINTOCK & CUNNINGHAM (1974), HILL (1974), NIEBEL (1974) and BRASCAMP (1973, 1974). The methods of McCLINTOCK & CUNNINGHAM and of HILL are shown to be identical, while the methods of LINDHÉ and PETERSEN et al., NIEBEL and BRASCAMP give different numerical results with the same basic assumption. The method of BRASCAMP (1975), based on HILL (1974), being most accurate. For the procedure of HILL a computer program (GFLOW) has been written and described dealing with various types of population structures. This program has been used for group work dealing with dairy cattle, pigs, sheep and poultry. Results are given.

Comparisons of costs and returns has been discussed in relation to inflation and risk. Some attention has been payed to recent work of JAMES & HOPKINS in relation to consistent definitions of generation intervals, selection differentials and the matrix of genetransmission described by HILL.

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1. INTRODUCTION

In optimizing breeding schemes different stages may be distinguished.

1. Definition of a breeding objective
2. Description of alternative breeding schemes
3. Estimation of economic and biological (including genetic) parameters needed
4. Derivation of selection indices
5. Quantitative comparison of the result of selection and selection efforts (costs) associated with alternative breeding schemes.

The theoretical basis for especially 4 and 5 originates from HAZEL (1943), introducing selection index theory in animal breeding, from DICKERSON & HAZEL (1944) and RENDEL & ROBERTSON (1950), developing formulae to predict annual genetic gain for given breeding plans. Here RENDEL & ROBERTSON (1950) themselves wrote: 'The application of the principles of problems arising in breeding farm animals for economical production are of comparatively recent origin. They are based on the theoretical considerations of WRIGHT, FISHER & HALDANE. The detailed application of their findings to animal breeding has been mostly due to LUSH and his co-workers. The general principles of this new approach are given by LUSH in his book Animal Breeding plans.'

In terms of volume of published literature the sequence of the 5 items mentioned above probably is - from much to few - 3 (especially genetic parameters), 4 (selection index theory and estimation of breeding values), 2 and 5 and finally 1. It is remarkable that the basic item for optimization of breeding schemes - definition of goals - is not touched very much. The goal, normally, is more or less taken for granted. Exceptions in this field are NIEBEL et al. (1972) and a large scale study of the Centre of Agricultural Strategy 'Strategy for the U.K. dairy industry' (CAS-1978). Another problem in this area is to define for which environment an objective, an aggregate genotype, is valid. For example in pigs aggregate genotypes generally are (implicitly) defined for test-station conditions. In recent years many authors show that the genetic relationships between comparable traits measured under station and field conditions deviate from unity and vary from trait to trait. Consequently relative weights

for traits in selection indices will depend on the environment for which the aggregate genotype is defined.

These notes are restricted entirely to item 5: Methods on economic optimization of breeding schemes.

The lines initiated by DICKERSON & HAZEL (1944) and RENDEL & ROBERTSON (1950) were extended by ROBERTSON & RENDEL (1950) and ROBERTSON (1958) dealing with progeny testing with A.I. The latter paper deals with the choice to test more bulls with smaller progeny groups or fewer bulls with larger progeny groups, considering test capacity fixed. This is a balancing of intensity of selection on the one hand and accuracy of selection on the other hand. SKJERVOLD (1963) and SKJERVOLD & LANGHOLZ (1964) extended this further to application in a co-operative A.I. breeding scheme for dairy cattle populations. The effect of variation in progeny group size and in the percentage of the population inseminated with semen of young bulls was studied. Still, resulting annual genetic gain was object of study.

The model of SKJERVOLD & LANGHOLZ (1964) was used in principle by LINDHE (1968) who introduced two additional elements, a) large variation in number of (deep frozen) doses of sperm stored per bull and b) another object of study: financial returns vs costs. In fact economic evaluation of cattle breeding schemes was introduced by POUTOUS & VISSAC 5 years earlier. After LINDHE's paper many studies followed on the topic economic optimization of breeding schemes, especially for dual purpose cattle. As indicated before, the object of study initially was (stable) annual genetic gain. Still in the approach of LINDHE financial returns are linearly related with annual genetic gain. BRASCAMP (1973) showed that deviation from this may be serious and the methods developed by McCLINTOCK & CUNNINGHAM (1974) and HILL (1974) offer the possibility to deal elegantly with the reason: selection only ultimately results in stable genetic gain, not in the early years. McCLINTOCK & CUNNINGHAM (1974) refer to their method as a discounted gene flow technique.

The set up of this notes is as follows.

Chapter 2 deals with a short introduction to 2 simulation methods used in the study of breeding plans. These are the so-called deterministic model (applied in most cases) and the Monte Carlo method (applied e.g. by RØNNINGEN (1969), in a study of two stage selection). In Chapter 3 the

3 methods of computation of financial returns from breeding schemes are described as applied by LINDHE (1968) and PETERSEN et al. (1974), by NIEBEL (1974) and by BRASCAMP (1973, 1975). Many authors developed different methods to compute financial returns. The methods described and compared in these notes are hoped to be representative. In Chapter 3, also the gene flow method of HILL (1974) is introduced. It will be discussed, however, referring to the original paper. The same is valid for BRASCAMP¹ (1975), in an application of HILL's method. Chapter 4 deals with criteria to assess optimum schemes and some attention has been paid to the contrast between 'national' and 'commercial' breeding schemes with respect to this. In Chapter 5 applications of 'discounted expressions' (introduced by McCLINTOCK & CUNNINGHAM (1974)) have been discussed, initiating with a comparison of the methods of McCLINTOCK & CUNNINGHAM (1974) and HILL (1974). For the method of HILL a matrix is needed to define transmission of genes from one generation to the next. In Chapter 6 this matrix is discussed more in detail, especially in relation with selection differentials and age structure. In Chapter 8 some FORTRAN computer subroutines and functions have been given which may be applicable in optimization work. In this chapter also a computer program (GFLOW) is described.

¹A summary of methods is given in 8.4, while in an appendix a part of BRASCAMP (1975) is reprinted.

2. DETERMINISTIC MODEL AND MONTE CARLO METHOD

Two types of approach will be illustrated with a simple example. Both approaches might be useful in optimization of breeding- or selection schemes.

The approach - which is called deterministic model here - involves a sequence of mathematical expressions which result in a criterion to maximize. This criterion will depend on some parameters which may vary freely. The objective is to find the combination of parameters which maximizes the objective.

The Monte Carlo method may be used if the approach above involves some assumptions which are not valid and cannot be fitted by mathematical function. In selection schemes the Monte Carlo method results in additive genetic values and phenotypic values for individuals. Selection is practised within the simulated set and selection response is calculated from the simulated values of selected individuals.

An example may clarify the methods.

Consider a case of two stage selection, where n_1 places are available for the first stage and n_2 places for the second. Suppose that $n_1 + 5n_2 = 1000$ (e.g. stage two is 5 times as expensive as stage 1, one place at stage 1 costs 1 money unit (stage 2 costs 5) and 1000 money units are available.) At stage 1 P_1 is measured ($r_{AP1} = .20$, A is additive genetic merit) and at stage 2 P_2 is measured ($r_{AP2} = .26$). At the end we need to select 10 individuals. The objective is to maximize the response to selection (that is average additive genetic merit of selected individuals). The parameters which are free to vary are n_1 and n_2 , given $n_1 + 5n_2 = 1000$. So $n_1 = 1000$, $n_2 = 0$ and $n_1 = 800$, $n_2 = 40$ etc.

2.1. Deterministic model

If $n_1 = 1000$ the situation is simple. The response to selection R can be calculated as

$$R = i_1 \cdot r_{AP1} \cdot \sigma_A,$$

where i_1 is the intensity of selection with a proportion selected $p_1 = 10/1000$. Also if $n_2 = 200$ the situation is simple.

We assume that in second stage only P_2 is used (not an index with P_1 and P_2) so

$$R = i_2 \cdot r_{AP2} \cdot \sigma_A$$

where i_2 is the intensity of selection with a proportion selected $p_2 = 10/200$.

All other cases are more complicated. For example if $n_1 = 600$, $n_2 = 80$. So $p_1 = n_2/n_1$ and $p_2 = 10/n_2$. For first stage again

$$R_1 = i_1 \cdot r_{AP1} \cdot \sigma_A$$

but in second stage the distributions of A and P_2 are no longer normal. To adjust for this the formulae of COCHRAN (1951) can be used, to correct variances and covariances for the selection at first stage. In general this adjustment is

$$\text{cov}(ab/c) = \text{cov}(ab) - \text{cov}(ac) \text{cov}(bc) \cdot C / \text{var}(c)$$

where $\text{cov}(ab/c)$ stands for the covariance between trait a and trait b after truncation selection for c, the other covariances and $\text{var}(c)$ are values without selection and $C = i(i-x)$. In the formula for C the i stands for the selection intensity for trait c and x stands for the absciss in a standard normal distribution at the point of truncation selection for trait c.

In our case, the response to the second stage selection is

$$R_2 = i_2 \cdot r_{AP2/P1} \cdot \sigma_{A/P1}$$

$$\text{or } R_2 = i_2 \cdot \text{cov}(AP2/P1) / \sigma_{P2/P1}$$

A sequence of mathematical expressions to calculate R may be:

$$n_1 = \text{variable}$$

$$n_2 = (1000 - n_1) / 5$$

$$i_1 = \text{selection intensity with fraction selected } n_2/n_1$$

$$i_2 = \text{selection intensity with fraction selected } 10/n_2$$

$$R_1 = i_1 \cdot r_{AP1} \cdot \sigma_A$$

$$x_1 = \text{truncation point with fraction selected } n_2/n_1$$

$$C = i_1(i_1 - x_1)$$

$$\text{cov}(AP2/P1) = \frac{\text{cov}(AP2) - \text{cov}(AP1) \cdot \text{cov}(PIP2) \cdot C}{\text{var}(P1)}$$

$$\sigma_{P2/P1} = \sqrt{\frac{\text{var}(P2) - \text{cov}^2(P1P2) \cdot C}{\text{var}(P1)}}$$

$$R_2 = i_2 \cdot \text{cov}(AP2/P1) / \sigma_{P2/P1}$$

$$R = R_1 + R_2$$

By trial and error we can find the optimal value for n_1 (and n_2).

2.2. Monte Carlo Method

We start with the general principle of the method.

First consider the situation where we wish to simulate a set of data for a trait with mean μ_1 and standard deviation σ_1 . This can be done by repeated calculation of

$$x_{1i} = \mu_1 + a_{1i}\sigma_1$$

where a_{1i} are 'normal deviates', independent drawings from a set of normal distributed random digits with mean zero and standard deviation 1.

This works, since $Ex_1 = E\mu_1 + \sigma_1 \cdot Ea_1 = \mu_1$ and

$$\text{var } x_1 = \text{var}\mu_1 + \sigma_1^2 \cdot \text{var } a_1 = \sigma_1^2, \text{ as we wish.}$$

Now we wish to simulate a variable x_2 , with mean μ_2 and standard deviation σ_2 , which has a correlation r_{12} with x_1 .

Look at

$$x_{2i} = \mu_2 + a_{1i}r_{12}\sigma_2 + a_{2i}\sqrt{1-r_{12}^2}\sigma_2$$

where a_{2i} again are normale deviates, uncorrelated with a_{1i} .

Now

$$\begin{aligned} Ex_2 &= \mu_2 \\ \text{var } x_2 &= r_{12}^2 \sigma_2^2 + \sqrt{1-r_{12}^2}^2 \sigma_2^2 = \sigma_2^2 \\ \text{cov } x_1 x_2 &= r_{12} \sigma_1 \sigma_2 \quad \text{since } \text{cov } a_1 a_1 = 1 \text{ and } \text{cov } a_1 a_2 = 0 \end{aligned}$$

The result is satisfactory.

The term $\sqrt{1-r_{12}^2}$ can be found as follows.

First we know $\text{cov } x_1 x_2$ has to be $r_{12} \sigma_1 \sigma_2$. To get this result we need

$$x_{2i} = \mu_2 + a_{1i}r_{12}\sigma_2 + a_{2i}d_{2i}\sigma_2$$

where a_{2i} are normal deviates, uncorrelated with a_{1i} and d_{2i} remains to be solved.

But $\text{var } x_{2i}$ has to be equal σ_2^2 , and so

$$\begin{aligned} \text{var } x_2 &= r_{12}^2 \sigma_2^2 + d_{21}^2 \sigma_2^2 \\ \text{and } d_{21}^2 &= (1 - r_{12}^2) \\ \text{or } d_{21} &= \sqrt{1 - r_{12}^2} \end{aligned}$$

This principle can be extended to many traits.

Take x_3 , mean μ_3 , standard deviation σ_3 and correlations with the previous trait r_{13} and r_{23} .

First $\text{cov } x_1 x_3 = r_{13} \sigma_1 \sigma_3$

This gives:

$$x_{3i} = \mu_3 + a_{1i} r_{13} \sigma_3 + a_{2i} d_{32} \sigma_3 + a_{3i} d_{33} \sigma_3,$$

d_{32} and d_{33} remain to be solved.

Now,

$$\text{cov } x_2 x_3 = r_{23} \sigma_2 \sigma_3 = r_{12} r_{13} \sigma_2 \sigma_3 + d_{32} \sqrt{1 - r_{12}^2} \sigma_2 \sigma_3$$

So

$$d_{32} = (r_{23} - r_{12} r_{13}) / \sqrt{1 - r_{12}^2}$$

Finally

$$\text{var } x_3 = (r_{13}^2 + (r_{23} - r_{12} r_{13})^2 / (1 - r_{12}^2) + d_{33}^2) \sigma_3^2$$

Or

$$d_{33} = \sqrt{1 - r_{13}^2 - (r_{23} - r_{12} r_{13})^2 / (1 - r_{12}^2)}.$$

With more traits the d_{ij} 's become more and more complicated. With a computer, however, the system is fairly easy to handle. The procedure to transform a correlation matrix into a triangle matrix with d_{ij} 's, $j \leq i$ is called Choleski-procedure (see e.g. BEDALL AND ZIMMERMANN, 1978), and may be written as the transformation of

$$C = \begin{pmatrix} c_{11} & c_{12} & \dots & c_{1n} \\ c_{22} & c_{22} & & \\ \vdots & \vdots & & \\ c_{n1} & c_{n2} & \dots & c_{nn} \end{pmatrix} \quad \text{to } D = \begin{pmatrix} d_{11} & & & 0 \\ d_{21} & d_{22} & & \\ \vdots & \vdots & \ddots & \\ d_{n1} & \dots & \dots & d_{nn} \end{pmatrix}$$

where C is a correlation matrix and D is a triangular matrix such that $C = DD'$

The algebra to solve d_{ij} , $j \leq i$ is as follows:

$$d_{ii} = c_{ii} - \sum_{k=1}^{i-1} d_{ki}^2 \quad d_{ij} = 0 \quad \text{if } i > j$$

$$d_{ij} = (c_{ij} - \sum_{k=1}^{i-1} d_{ki} d_{kj}) / d_{ii} \quad \text{if } i < j$$

Returning to our example. Putting x_1 , x_2 and x_3 as P_1 , A and P_2 respectively, we could simulate 1000 'individuals' using the appropriate parameters ($\sigma_1 = \sigma_{P_1}$, $\sigma_2 = \sigma_A$, $\sigma_3 = \sigma_{P_2}$, $r_{12} = r_{AP_1}$, $r_{13} = r_{P_1P_2}$ and $r_{23} = r_{AP_2}$). Dependent on the combination of n_1 and n_2 we draw randomly n_1 individuals from 1000, representing the n_1 individuals tested at first stage. Then we pick the best n_2 individuals with respect to P_1 and the best 10 out of n_2 individuals with respect to P_2 . The average A-value of these 10 individuals equals the response to selection.

2.3. Merits of both methods

The selection responses calculated with the deterministic model are expectations. So only one sequence of calculations is needed to get the expected response for a particular combination of n_1 and n_2 . For the Monte Carlo procedure this is not so: An outcome for a particular set of 1000 animals is an unbiased estimate of the expected response to selection (R), but the standard deviation of this estimate is not zero. Consequently repeated calculation with different sets of 1000 animals are needed to get an estimation of R with a low enough standard deviation. So a disadvantage of the Monte Carlo procedure is that, in general, it is far more time consuming. On the other hand, to get a standard deviation for R may be an advantage.

For the Monte Carlo procedure we did not make any assumption for selection intensities. Two comments should be made with respect to this.

1. Implicitly, I assumed that $i = z/p$, where p is the proportion selected and z is the ordinate in a standard normal distribution at the truncation point x . If selection is from small numbers this gives an

- overestimate of i . Adjustment for this is possible (see chapter 8).
2. The relation $i = z/p$ is valid for a standard normal distribution and adjustment for small numbers also assumes a standard normal distribution. In the second stage distributions are no longer normal, so the formula given for the response to selection in the second stage is theoretically not correct. If one expects the bias in result to be too large, one may choose a Monte Carlo approach instead of a deterministic model.

Summarizing:

1. Monte Carlo methods generally are more time consuming than deterministic models.
2. Deterministic models generally need more complicated theoretical knowledge than Monte Carlo methods.
3. With Monte Carlo methods it is easy to get standard deviations of results, with deterministic models it is not.
4. Sometimes deterministic models are not appropriate because theoretical problems are not solved where Monte Carlo methods get around these problems.

3. METHODS TO COMPUTE RETURNS FROM BREEDING SCHEMES

3.1. Introduction

Some different approaches to compute financial returns from breeding schemes will be discussed in this chapter.

These methods have been used by LINDHE (1968), BRASCAMP (1973), NIEBEL (1974), PETERSEN et al. (1974) and BRASCAMP (1975) for breeding schemes in dual purpose cattle.

The discussion in this chapter will be limited to the returns from genetic improvement in dairy characters.

The problem involved may be illustrated by Fig. 3.1, which shows a schematic relation between costs for different breeding schemes and annual genetic gain resulting from these schemes. Increasing costs may be thought to result from the purchase and progenytesting of more young bulls, the preparation and storage of more doses deepfrozen semen. Increasing annual genetic gain results from higher selection intensities, a higher accuracy of progeny testing.

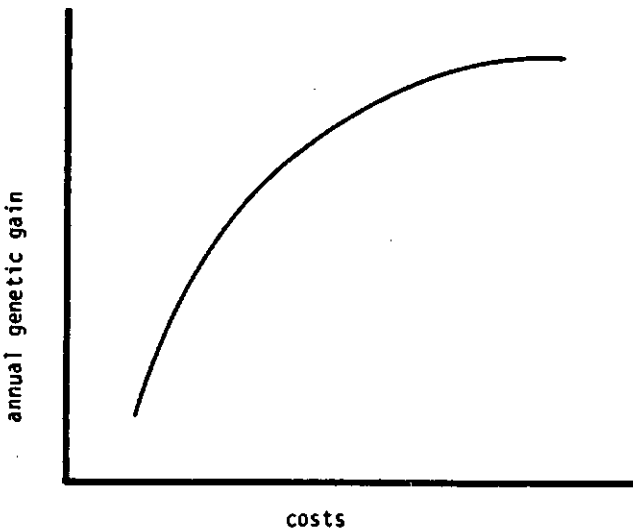


Fig. 3.1 Schematic relation between costs for a breeding scheme and annual genetic gain.

Fig. 3.1 shows that with increasing costs put into a breeding scheme also the annual genetic gain increases. However, the increase of the annual genetic gain slows down at higher costlevels. Consequently, investments above a certain costlevel will not be worthwhile because the additional annual genetic gain resulting from it is considered to be too small. The obvious question now is above which costlevel the additional increase in annual genetic gain is considered to be too small to justify additional investments. Computation of returns from breeding schemes (which can be seen as a translation of annual genetic gain in the same units as costs: money) is considered to solve the question stated above.

The question stated above involves two aspects:

1. How to compute returns.
2. According to what criteria can we measure justification of further investments.

This chapter deals with the first aspect. The second aspect will be discussed in chapter 4.

Before discussing general differences between methods (3.3.) we will describe the principle of discounting (3.2.). After that the methods will be described in more detail (3.4.).

3.2. The principle of discounting

The base of discounting is as follows.

Suppose that the rate of interest is r . This may be 5 %, 8 %, 10 % etc. ($r = .05, .08, .10$) and may be the annual rate of interest received putting money in a bank or the annual rate of interest to pay borrowing money. There are several other possible meanings of r , but we will leave that to chapter 4.

Receiving 1 money unit today may be seen to be equivalent to receiving $1 + r$ money units one year after today. The additional r money units today are necessary to cover the difference of one year, because this r money units could be received otherwise by putting the one money unit in a bank for one year or has to be paid if one money unit has to be borrowed because the receipt is delayed by one year.

In a breeding programme costs have to be made in different years and returns from this (i.e. production from improved animals) will be received in later years. Looking at one round of selection in a dual purpose breeding scheme, for example, the picture may be as follows. In the first year costs for buying young bulls and for performance testing for growth, in the second year costs for test inseminations, collection and storage of deepfrozen semen, maintenance of bulls (feeding, housing), some continuing in third and later years up to the selection of bulls through progeny test results. Returns are attained from year 2 from slaughter-progeny of performance tested young bulls and from year 9 or so from improved milk yield expressed in progeny of selected bulls.

By discounting costs and returns are put on a same comparable basis. Suppose that the base year is the birth of a batch of young bulls, then costs in year 3 are multiplied by $1/(1+r)^3$ to discount these costs to the common basis and returns attained in year 10 are multiplied by $1/(1+r)^{10}$. It is obvious that especially with high r , returns attained far in future have a very small discounted value and that from an economic viewpoint (when returns are calculated by discounting) short generation intervals are even more important than from a viewpoint of annual genetic gain.

The choice of the base year varies somewhat with authors. With breeding schemes for dual purpose cattle commonly the year of birth of young bulls is taken or the year of selection of proven bulls. This choice generally will not affect the ranking of different breeding schemes in terms of economic evaluation because both costs and returns are affected to the same extent (both divided by a same factor, $(1+r)^n$, where n is the number of years between birth of young bulls and selection among young bulls based on progeny test results).

Some algebra in relation to discounting will be given here:

$$\sum_{i=1}^n \left(\frac{1}{1+r}\right)^i = \left(1 - \frac{1}{(1+r)^n}\right) / r \quad (3.1)$$

$$\sum_{i=1}^{\infty} \left(\frac{1}{1+r}\right)^i = 1/r \quad (3.2)$$

3.3. General differences in methods

The approaches worked out by LINDHE (1968) and PETERSEN et al. (1974) are identical in principle. Returns computed by these authors are linearly related with the annual genetic improvement (ΔG).

In the notation of PETERSEN et al. (page 250)

$$R_{BF} = N \cdot \Delta G_{BF} \cdot V_{BF} / r \quad (3.3)$$

In this formula R_{BF} stands for financial returns from breeding scheme, N = population size, ΔG_{BF} = annual genetic gain in butterfat, V_{BF} = the monetary value of an improvement of one kg butterfat and r = rate of interest. This formula will be discussed in more detail in 3.4. At this stage it is important to note that V_{BF} is independent of the breeding scheme (but is determined by economic and biological factors) and independent of ΔG_{BF} . So in Fig. 3.1 we simply can put R_{BF} on the vertical axes and we end up with a relation between money and money, input and output. The annual genetic gain is computed by the formula of SKJERVOLD and LANGHOLZ (1964)

$$\Delta G = \frac{I_{SS} + (1-y)I_{PB} + I_{DS} + I_{DD}}{L_{SS} + (1-y)L_{PB} + yL_{YB} + L_{DS} + L_{DD}} \quad (3.4)$$

where I stands for the genetic superiorities for the pathways SS (sire to son), PB (proven bulls), DS (dam to son) and DD (dam to daughter) and L for the respective generation intervals, YB for young bulls (test bulls) and y for the proportion of inseminations with semen of young bulls.

The method of LINDHE differs from PETERSEN's in some assumptions and at first sight in the criterion to assess an optimum scheme. One difference will be mentioned in 3.4., the other in chapter 4.

The method of NIEBEL (1974) is different from the previous one described. This difference may be illustrated in two ways:

1. Comparing with (3.3), the method of NIEBEL (1974) amounts to a V_{BF} which is not constant (as with PETERSEN and LINDHE) but depends on the breeding scheme.

2. Combining (3.3) and (3.4), R_{BF} equals:

$$R_{BF} = b_1 I_{SS} + b_2 I_{PB} + b_3 I_{DS} \quad (3.5)$$

where for PETERSEN et al. $b_1 = b_3 = V_{BF}/r \cdot \Sigma L$ and $b_2 = (1-y) \cdot V_{BF}/r \cdot \Sigma L$ (ignoring N and path DD).

These weighing factors have been computed by NIEBEL differently and result in other values for R_{BF} . In principle b_1 and b_3 will be low compared with b_2 because these factors are adjusted for the fact that female dairy offspring of bull sires and bull dams will be born much later than dairy offspring of proven bulls. Consequently discounted returns from these genetic superiorities (i.e. from improved milk yield) have less financial value. The methods of BRASCAMP¹(1973, 1975) are characterized by the same basic idea as the method of NIEBEL. The weighing of the genetic superiorities of paths should depend on the time it takes for these genetic superiorities to be expressed in improved milk yield. Compared with NIEBEL, the weighing factors in (3.5) are derived by evaluation of the flow of genes of selected parents in time through the population; NIEBEL's weighing factors can be seen as approximations.

The 1973 method is based on the financial value of the genetic superiorities for the different pathways expressed in subsequent generations of offspring of selected parents. This method was based on the ideas of McCLINTOCK and CUNNINGHAM (1974).

The 1975 method is based on the financial value of the genetic superiorities for the different pathways expressed in subsequent years. This method is entirely based on the paper of HILL (1974), dealing with the flow of selected genes in time through a population.

BRASCAMP (1975) concludes the 1975 method to be superior to the 1973 method. Nevertheless, in the context of discussion of general differences between methods, it is worthwhile to describe one aspect of the 1973 paper. Let's denote financial returns, evaluated with the 1973 method as RT. Analogous to (3.3) RT may be written as

$$RT = N \cdot \Delta G \cdot DF \cdot p/r \quad (3.6)$$

In comparison DF.p replaces V_{BF} in (3.3) and DF was called the discount

¹Appendix

factor for the time lag between the starting point of a breeding scheme (the birth of a batch of young bulls) and the expression of resulting genetic superiority in the population. It should be mentioned that V_{BF} also consists of the product of two parts: p (the net income per kg butterfat, NI_{BF} , according to the notation of PETERSEN) and a part similar to DF , say DF_c , a constant discount factor for the time lag.

So $DF = RT.r/(\Delta G, p.N)$, and in the 1973 paper it was analysed how DF depended on the breeding scheme. In Fig. 3.2 (BRASCAMP, 1973) the relation is given between DF and two factors describing a breeding scheme: the proportion of the inseminations with semen of young bulls and the number of deepfrozen semen stored per young bull. It can be seen that DF varies from .33 to about .40.

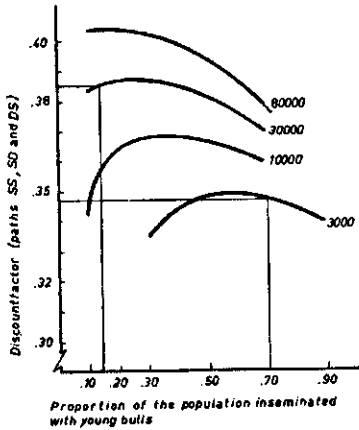


Fig 3.2 The relation between the discount-factor of the timelag and the proportion of the population inseminated with young bulls for different doses-alternatives

(BRASCAMP, 1973)

3.4. The methods of PETERSEN et al. and LINDHE

The returns R_{BF} , according to Petersen et al. (1974) are computed as given in formula (3.3)

$$R_{BF} = N \cdot \Delta G_{BF} \cdot V_{BF} / r \quad (3.3)$$

$$= N \cdot \Delta G_{BF} \cdot V_{BF} \cdot \sum_{i=1}^{\infty} \left(\frac{1}{1+r} \right)^i \quad (\text{see } 3.2)$$

In this formula ΔG_{BF} has to be interpreted as the stable annual genetic gain, achieved by a continuous breeding programme and V_{BF} the value of one unit annual genetic gain from one year to another.

The summing (and discounting) over an infinite number of years indicates that

- a) genetic gain, once created is assumed to be maintained infinitely
- b) as discussed in 3.1, financial returns are computed over an infinite number of years.

I will not discuss assumption a) here. Assumption b) will be discussed in chapter 4, where the choice of time period for evaluation of returns will be discussed. It can be mentioned here, however, that when $r = .1$ (as PETERSEN assumes) for $n = 10, 15, 20, \infty$ respectively $\sum_{i=1}^n \frac{1}{(1+r)^i}$ equals 6.1, 7.6, 8.5 and 10. So most returns are attained in early years and consequently the assumptions are less dramatic as it looks at first sight.

The stable annual genetic gain is used by PETERSEN et al. as the increase in genetic superiority expressed in heifers from one year to another. The heifers in one year represent a fraction p_1 of all cows in a herd. A fraction $p_2 = p_1 (1-p_1)$ survives to a second lactation and will express the increase in genetic superiority one year later. In general, a fraction $p_1 (1-p_1)^{i-1}$ survives to the i -th lactation and will express the increase in genetic superiority $i-1$ years later. So the value of one unit increase in genetic superiority in heifers in year 1 discounted to year 1 has a total value (over 15 lactations) of

$$V_{BF} = N I_{BF} \cdot \sum_{i=1}^{15} p_1 (1-p_1)^{i-1} \cdot \frac{1}{(i-1) \cdot CI} \cdot \frac{1}{(1+r)} \quad (3.7)$$

where NI_{BF} is the net income per kg butterfat and CI is the calving interval. Putting $p_1 = .33$ and $r = .1$, and $CI = 1$, $V_{BF} = .839NI_{BF}$

In PETERSEN's paper costs have been discounted to the base year = year of first lactation of heifers born from proven bulls in the scheme. So the birth of young bulls from which these proven bulls are selected takes place in year -9.

The value for DF in Fig. 3.2 assumes as base year the year of birth of young bulls.

So using PETERSEN's figure .839 for $\sum_{i=1}^{15} p_1 (1-p_1)^{i-1} \frac{1}{(1+r)^{(i-1)CI}}$

amounts to an average comparable value for

DF of $.839 \cdot \left(\frac{1}{1+r}\right)^9 = .356$, which is well in the range of Fig. 3.2.

Summarizing the method of PETERSEN et al. (1974):

1. A breeding program is assumed which is in operation long enough to produce a stable annual genetic gain.
2. The returns expressed in improved dairy progeny from one round of selection are assumed to start 9 years after the birth of a year batch of young bulls.
3. Improvement expressed in heifers of year 9 are evaluated for subsequent lactations and discounted to year 9.
4. This discounted value is maintained from year 9 to infinity and discounted in turn to the base year 9.

A similar procedure has been developed for expression of genetic gain in growth rate. This will not be discussed here.

The method adopted by LINDHE (1968) is similar to the method described above. As base year LINDHE adopts the year of birth of heifers born from proven bulls. At page 35 of his paper LINDHE calculates the value of 1 % improvement in milk yield as 3.36 millions Skr. This figure may be attained as follows.

The net value of 1 % in milk yield values 10.6 Skr. (equivalent to NI_{BF}). The value of one unit improvement in the first lactation of a heifer values $.83 \left(\frac{1}{1+r}\right)^2$, second lactation .78, third .71 and one third of a fourth lactation $.69/3$ (LINDHE assumes an average of $3\frac{1}{3}$ lactations per cow). This adds up to $.83 + .78 + .71 + .23 = 2.65$.

Now, $2.65 \cdot 10.6 = 28$ Skr. is the value of 1 % improvement in milk yield applicable at birth of a calf. Since heifers represent 30 % of all cows, at population level this values $400000 \cdot 28 \cdot .3 = 3.36$ millions. The only difference with PETERSEN (except choice of base year) is the approximation of $3\frac{1}{3}$ lactations by 3 whole and $\frac{1}{3}$ of a fourth lactation instead of evaluating them over 15 lactations.

3.5. The method of NIEBEL

To calculate returns from a breeding scheme basically the following formula¹⁾ is used (changed to notation used here)

$$R = \frac{1}{\Sigma L} \sum_j I_j \cdot b_j \quad (3.8)$$

In this formula R stands for discounted returns, ΣL and I_j for sum of generation intervals and for genetic superiority as before, b_j is a weighing factor, different for each pathway.

This factor b_j depends on the time it takes from the birth of selected parents to birth of offspring and the time over which returns are to be evaluated. Suppose t_j is the time between birth of selected parents and birth of offspring and d is the time interval between birth of selected parents and the end of the period over which returns are to be evaluated.

$$\text{Then } b_j = \sum_{k=t_j}^d \frac{1}{(1+r)^k} \quad , \quad (\text{NIEBEL, page 122}) \quad (3.9)$$

the sum of constant amounts of money received between birth of offspring and end of evaluation period, discounted to the birth of selected parents.

For path SS $t_j = L_{SS} + yL_{YB} + (1-y)L_{PB}$, for dairy offspring is born from young bulls and proven bulls, being sons of the bull sires SS.

For path PB $t_j = L_{PB}$, for path DS $t_j = L_{DS} + yL_{YB} + (1-y)L_{PB}$.

It can be shown that by adopting (3.1)

$$b_j = \left[\frac{1}{(1+r)^{t_j}} - \frac{1}{(1+r)^d} \right] / r \quad (3.10) \quad (\text{Equivalent to NIEBEL (1974) page 118-119})$$

¹⁾In fact NIEBEL divides not by $1/\Sigma L$ but by $1/C\Sigma L$, where C is the "Nutzungsdauer" = average number of lactations per cow.

So the weighings for the genetic superiorities of paths SS, PB and DS are b_{SS} , $b_{PB} \cdot (1-y)$ and b_{DS}

3.6. The methods of BRASCAMP. See Appendix.

In 3.7. the term "discounted expression per cow" will be discussed and in 3.8. the numerical values of discounted expressions implicitly or explicitly adopted by PETERSEN (1974), NIEBEL (1974) and BRASCAMP (1973, 1975) will be compared. The term originates from McCLINTOCK and CUNNINGHAM (1974).

3.7. Discounted expressions per cow

As discussed in 3.3. the financial returns (R) from a breeding scheme can be written as:

$$R = (b_1 I_{SS} + b_2 I_{PB} + b_3 I_{DS}) \cdot p \cdot N$$

These returns are evaluated over a certain time period (PETERSEN, ∞ years, NIEBEL 25 years, BRASCAMP (1973) 4 generations of offspring, BRASCAMP (1975) 25 years) and are the results from one round of selection.

Now, the weighing factors b_i may be called "discounted expressions per cow" or "per first insemination". They represent the discounted financial value of one unit genetic superiority.

This discounted financial value is the result of the expression of (a part of) the genetic superiorities of the selected parents by offspring which show these superiorities during many years (and generations) after the original act of selection.

Further this discounted value is thought to be accumulated in one imaginary cow in the base year. So multiplication with p and N gives the financial value discounted to the base year for the whole population.

3.8. Numerical comparison of discounted expressions

Discounted expressions per cow have been calculated by PETERSEN et al. (1974) and NIEBEL (1974) as follows.

PETERSEN: For SS and DS the discounted expressions are equal and are calculated as $.356/\Sigma L.r$. The figure .356 has been calculated before (see 3.4). For PB the discounted expressions are those for SS (and DS) multiplied by $(1-y)$, the proportion of inseminations with proven bulls.

NIEBEL: For SS and DS the discounted expressions are calculated according to (3.10) divided by ΣL , while for PB an extra multiplication with $(1-y)$ is needed.

In Table 3.1 results have been given. Assumptions:

$$L_{SS}=L_{PB}=6.75, L_{YB}=2.75, L_{DS}=6, L_{DD}=4.5, r = .10.$$

Table 3.1 Discounted expressions per cow for 4 methods discussed in the text.

Path	Proportion of inseminations with young bulls		
SS	.20	.50	.70
Petersen (1974)	.153	.162	.168
Niebel (1976)	.089	.110	.127
Brascamp (1973)	.079	.088	.095
Brascamp (1975)	.068	.081	.091
PB			
Petersen (1974)	.122	.081	.050
Niebel (1974)	.150	.099	.061
Brascamp (1973)	.195	.133	.087
Brascamp (1975)	.191	.132	.086
DS			
Petersen (1974)	.153	.162	.168
Niebel (1974)	.098	.119	.139
Brascamp (1973)	.165	.185	.201
Brascamp (1973)	.158	.183	.203

Comparison of discounted expressions calculated for PETERSEN and NIEBEL clearly illustrates the point that for paths SS and DS it takes much longer time to attain the first returns (from granddaughters!) than for PB (from daughters). This fact is accounted for by NIEBEL, not by PETERSEN. A further interesting point is the difference for DS between NIEBEL and BRASCAMP. This can be clarified looking at Fig. 1 (Thesis page 6). In this Fig. 1 DS are considered to be the dams of the batch of young bulls. So the base year for this path is the birth of their sons and first returns are attained from testdaughters of these young bulls (year 3). In NIEBEL's approach the base year for DS is the birth of the dams themselves. Again the first returns are from testdaughters of their sons, but this happens in year 9 approximately. This difference would account for a factor $1/(1+r)^6 = .56$, which is rather close to the difference in Table 3.1. The logic of this type of problems (choice of base year) will be discussed in chapter 4.

The differences between BRASCAMP (1973) and (1975) have been discussed in the thesis (1975). It was concluded that the 1973-method contained some deviations caused by the approximation of 25 years by 4 full generations of offspring. Within 25 years for some pathways in Fig. 1 (appendix) later than 4th generation females are lactating, while most generations are not completed within 25 years.

3.9. Numerical example to BRASCAMP (1975)

In this part some more detailed results will be given of the application of the method of HILL (1974) to a particular dairy cattle example (BRASCAMP, 1975) to illustrate the flow of genes of selected parents in a population.

Table 3.2 gives the genetic make up (associated with path SS) of males and females in different age classes and years.

There are 7 male age classes (males of age 6 and 7 are bull sires and contribute 1/4 or 3/4 to their offspring in the respective years: generation interval = $6\frac{1}{2}$ years).

Further there are 13 female age classes, contributing 0, .25, .22, .15, .10, .08, .06, .05, .03, .02, .02, .01 and .01 respectively to female replacements and

0, 0, .22, .18, .14, .11, .08, .07, .05, .04, .04, .04 and .03 respectively

to male replacements ($L_{DD} = 4.5$ and $L_{DS} = 6$).

The contribution of males to females is as follows:

age class 2 and 3 (young bulls) approximately $\frac{1}{2}y$ and $\frac{1}{2}y$ and age class 6 and 7 (proven bulls) approximately $\frac{1}{2}(1-y)$ and $\frac{1}{2}(1-y)$, resulting in $L_{yB} = 2\frac{1}{2}$ and $L_{PB} = 6\frac{1}{2}$. These values are approximate where the probabilities for female offspring of young and proven bulls to enter the herd are assumed to be slightly different (Appendix 1, thesis).

The 1's in year 1 age class 1, in year 6 age class 6 and in year 7 age class 7 represent ageing of the young bulls, containing 100 % of their own genes. The males in year 6, age class 6 are bull sires and contribute $\frac{1}{2} \cdot \frac{1}{2} = .125$ of their genes to all bulls of age 1 in year 7 (because .375 comes from bull sires a year older and the other half from females).

Table 3.2 Genetic make up (relative to path SS) in males en females in different years and age classes (1-7 males, 1-13 females) ($y = .10$)

age class	years												
	1	6	7	8	9	10	11	12	13	14	15	25	50
1	1	0	.125	.375	0	0	0	0	.017	.096	.142	.037	.042
2	0	0	0	.125	.375	0	0	0	0	.017	.096	.029	.043
3	0	0	0	0	.125	.375	0	0	0	0	.017	.021	.043
4	0	0	0	0	0	.125	.375	0	0	0	0	.071	.043
5	0	0	0	0	0	0	.125	.375	0	0	0	.073	.043
6	0	1	0	0	0	0	0	.125	.375	0	0	.039	.042
7	0	0	1	0	0	0	0	0	.125	.375	0	.024	.040
1	0	0	0	0	.001	.008	.012	.001	.017	.088	.133	.037	.042
2	0	0	0	0	0	.001	.008	.012	.001	.017	.088	.036	.043
3	0	0	0	0	0	0	.001	.008	.012	.001	.017	.027	.043
4	0	0	0	0	0	0	0	.001	.008	.012	.001	.067	.042
5	0	0	0	0	0	0	0	0	.001	.008	.012	.068	.042
6	0	0	0	0	0	0	0	0	0	.001	.008	.023	.042
7	0	0	0	0	0	0	0	0	0	0	.001	.029	.041
8	0	0	0	0	0	0	0	0	0	0	0	.033	.042
9	0	0	0	0	0	0	0	0	0	0	0	.015	.044
10	0	0	0	0	0	0	0	0	0	0	0	.133	.044
11	0	0	0	0	0	0	0	0	0	0	0	.088	.042
12	0	0	0	0	0	0	0	0	0	0	0	.017	.042
13	0	0	0	0	0	0	0	0	0	0	0	.001	.041

These bulls (with .125 of SS genes) are young bulls in year 8, age class 2 and contribute $.125 \cdot \frac{1}{2} \cdot \frac{1}{2} \cdot .10 = .001$ to all females in age class 1, year 9. (Other genes from proven bulls, young bulls of 1 year older and females).

Another example will be illustrated: .133 (year 15, age class 1 females).

These females get their genes from parents in year 16.

Parents are: young bulls of age class 2: $.017 \cdot \frac{1}{2} \cdot \frac{1}{2} \cdot .10 = .000$

proven bulls of age class 7: $.375 \cdot \frac{3}{4} \cdot \frac{1}{2} \cdot .90 = .127$

and females in age classes 2, 3, 4, 5 and 6

age class 2 $.017 \cdot \frac{1}{2} \cdot .25 = .002$

3 $.001 \cdot \frac{1}{2} \cdot .22 = .000$

4 $.012 \cdot \frac{1}{2} \cdot .15 = .001$

5 $.008 \cdot \frac{1}{2} \cdot .10 = .000$

6 $.001 \cdot \frac{1}{2} \cdot .08 = .000$

Together this gives .130

So most genes originating from SS to this group of females is transmitted by sons of the bull sires, which are 7 year old proven bulls at that time. Following the pattern in Table 3.2 we see

1. The first lactating females appear in year 10, expressing only .1 % of bull sires' genetic superiority.
2. Even up to year 25 the pattern is very irregular.
3. In year 50 all animals in all age classes contain about the same fraction of bull sires' genetic superiority: 4.2 %. This equals $1/EL=1/23.8$, the weighing factor for I_{SS} to calculate stable annual genetic gain. This stable value is about 3.8% for $SD(=.9 \cdot 4.2)$ and 4.2 % for DS.

From Table 3.2 discounted expressions for SS can be derived. Heifers in age class 2 express .1 % of sires genetic superiority and heifers represent a fraction f_2 of all lactating cows in that year. So per cow the value of this .1 % is $.001 \cdot f_2 / (1+r)^{10}$, since the lactation occurs in year 10.

The value of improvement by SS expressed in year 15 is:

$$(.088 \cdot f_2 + .017 \cdot f_3 + .001 \cdot f_4 + .012 \cdot f_5 + .008 \cdot f_6 + .001 \cdot f_7) / (1+r)^{15}$$

So the discounted expression per cow as discussed in 3.7 are the sum of the values calculated as above in subsequent years. The numerical values of f_i are given in Appendix 2 (thesis).

The discounted expressions will depend on the genetic make up of females in different years and age classes (a function of y , and generation intervals as caused by definition of gene transmission), on the number of years considered and on the interest rate.

Some results of the effects of number of years and interest rate are given in Table 3.3.

Table 3.3 Effects of number of years considered and interest rate (r) on discounted expressions per cow ($y = .20$).

Path	SS	r				SD	r			
		.0	.05	.10	.15		.0	.05	.10	.15
Years	5	0	0	0	0	0	0	0	0	
	10	.001	0	0	0	.187	.116	.074	.048	
	15	.056	.028	.015	.008	.437	.248	.146	.089	
	25	.434	.166	.068	.030	.751	.363	.191	.107	
	50	1.341	.313	.097	.037	1.510	.486	.215	.113	

Table 3.3 shows that the relative contribution of SS and SD to returns depends on the number of years considered. If the time period over which returns are to be evaluated is only 10 years, returns through SS simply have not occurred yet. The relative contribution of SS to SD increases as the number of years considered increases. Further consider the case $r = .0$, where no discounting has been adopted. Also in that case, the contribution of SS and SD to return is not equal. If gene flow is considered pathways contribute differently to returns, even if discounting is not adopted, caused by different 'speed' of expressing the genetic superiority of the paths in improved yield.

4. COMPARISON OF RETURNS AND COSTS; INFLATION AND RISK

In this chapter some methods to compare returns and costs will be summarized (4.1.). Secondly we will discuss the effect on this comparison of inflation and risk (4.2.). Finally some remarks will be made how to come to a decision which breeding scheme should be adopted (4.3.).

4.1. Methods of comparison of costs and returns

Various methods have been described by NIEBEL (1974).

Chapter 3 started with a schematic relationship between costs and annual genetic gain. We saw that putting more money (costs) into a breeding scheme results in higher annual genetic gain. However, the increase in annual genetic gain slows down at higher cost levels, so the question is: which cost level is optimum. It was suggested then that translating annual genetic gain into money would provide a solution and chapter 3 dealt with this translation.

Here, three methods of comparison of costs and returns will be described.

4.1.1. Net returns (*Kapital Wert*)

This method has generally been applied in economic optimization of breeding schemes. It works as follows: For a breeding scheme costs associated with one round of selection (e.g. one batch of young bulls) are calculated and discounted to a base year. Returns resulting from this round of selection are calculated over a certain period ahead and are discounted to the same base year. (It is clear that the interest rate and number of future years to be considered have to be chosen beforehand).

The difference between discounted returns and discounted costs is called net returns. The optimum breeding scheme is the scheme with highest net returns. Net returns (NR) can be calculated with the methods described in chapter 3.

So for PETERSEN et al. 1974 (see formula 3.3)

$$NR = N \cdot \Delta G \cdot V / r - C \quad (4.1)$$

$$NR = R - C$$

where C stands for discounted costs.

LINDHE (1968) adopted a different method to compare returns and costs. He computed marginal rates of interest. Take 2 alternative schemes in Fig. 3.1 with costs C_1 and C_2 ($C_2 > C_1$). For both schemes he calculated yearly returns as

$$R_y = N \cdot \Delta G \cdot V \quad (4.2)$$

so ignoring $\sum_{n=1}^{\infty} \frac{1}{(1+r)^n}$ (see 3.4)

Then marginal rate of interest (m) was computed as

$$m = (R_{y_2} - R_{y_1}) / (C_2 - C_1) \quad (4.3)$$

and questioned if m is high enough to justify the additional costs $C_2 - C_1$.

Now, because $R = R_y / r$

$$\begin{aligned} R_2 - C_2 &= NR_2 \\ R_1 - C_1 &= NR_1 \\ \hline R_2 - R_1 &= C_2 - C_1 + \Delta NR \\ (R_{y_2} - R_{y_1}) / r &= C_2 - C_1 + \Delta NR \end{aligned}$$

and
$$m = r + \frac{\Delta NR}{C_2 - C_1} r$$

With the method of net returns scheme 1 and 2 are both optimal if $\Delta NR = 0$. In that case $m = r$. If $\Delta NR > 0$, $m > r$ and if $\Delta NR < 0$, $m < r$. So the criterion maximum net returns gives the same optimum scheme as LINDHE's marginal rate of interest provided that $m = r$. In the application of LINDHE extra investment was considered to be worthwhile if $m > .10$. So his method gives the same results as PETERSEN et al., using $r = .10$ with net returns.

4.1.2. Internal interest rate

The internal interest rate is the rate of interest for which discounted costs equal discounted returns.

A scheme with highest internal interest rate is considered to be optimal.

Returns are affected more by increasing r than costs because returns occur in later years. So, if $R - C$ is positive with $r = .10$, increasing r stepwise leads ultimately to the internal interest rate with $R = C$. It can be seen from Fig. 3.1 that R/C is larger at low cost levels than with high C . Consequently high internal interest rates will be found at low cost levels. This can be illustrated as follows. Denote undiscounted returns and costs as R_0 and C_0 and discounted (interest rate r) as R_r and C_r . Assume further $C_r = C_0 \left(\frac{1}{1+r}\right)^3$ and $R_r = R_0 \left(\frac{1}{1+r}\right)^{11}$

Scheme 1:

$C_0 = 4$
 $R_0 = 160$
 $R_{10}-C_{10} = 53$
 $R_0/C_0 = 40$
 $R_{10}/C_{10} = 18.7$
 $r(R_r=C_r) = 58.5 \%$

Scheme 2:

$C_0 = 11$
 $R_0 = 220$
 $R_{10}-C_{10} = 69$
 $R_0/C_0 = 20$
 $R_{10}/C_{10} = 9.3$
 $r(R_r=C_r) = 46.5 \%$

In the example above we see two schemes with low and high costs respectively. Following the net return criterion scheme 2 should be preferred, following the internal interest rate scheme 1.

Another criterion sometimes seen is R/C , which also leads to schemes with low costs.

4.1.3. Pay off period

With net returns both interest rate and the time period over which returns are to be evaluated have to be chosen beforehand. With internal interest rate only the time period has to be chosen, the (internal) interest rate is criterion.

With the pay off period only the interest rate has to be chosen, the time period is criterion. The pay off period is the time period over which returns have to be evaluated such that returns equal costs. A scheme with the shortest pay off period will be considered to be optimal.

As with internal interest rate this criterion leads to optimal schemes with low cost levels. HARING (1972) uses the pay off period in combination with net returns. The pay off period is adopted as a additional criterion, together with net returns.

4.2. Interest rate, inflation and risk

4.2.1. *Types of interest rate*

From table 3.3 it follows that choice of interest rate has large effect on discounted expressions and consequently on calculated financial returns from breeding schemes. Returns from one round of selection are affected much more by choice of interest rate than costs. Therefore the optimum scheme found may depend rather much on interest rate chosen.

SMITH (1978) gives a thorough discussion on the subject of interest rate and his arguments will be summarized here. He distinguishes three types of discount rates (interest rates).

- 1^o Opportunity cost rate, the cost of borrowing in the financial market.
- 2^o Social time preference rate, often lower than opportunity cost rates. This rate could be applied for long-term investments in the national interest, considering that for not purely economical reasons investments in f.e. roads and national parks should be made even though these investments don't 'pay' as well as e.g. investments in a factory for automobiles.
- 3^o A synthetic rate. This rate equals the social time preference rate. The point however is that both investments with high returns (discounted normally by the opportunity cost rate) and long-term investments with low returns (discounted normally by the social time preference rate) are discounted by the social time preference rate.

The definitions of interest rates above show that a simple choice can not easily be made. Other complicating factors are inflation rate, risk and tax rate.

4.2.2. Inflation

Seeing a bank lending interest rate as loan for lending money, this interest rate will include inflation. (Then the loan keeps its value irrespective of inflation). For cost-benefit analyses inflation should be excluded (ref. SMITH, 1978). In case of national breeding schemes inflation might be excluded in so far as the price of improved products (e.g. price of milk) follows the inflation rate. (RENKEMA, cited by BRASCAMP 1975, page 25).

An inflation free interest rate can be calculated from

$$(1+i) = (1+q)(1+t),$$

(SMITH, 1978) where i is bank lending rate, q inflation free interest rate and t inflation rate.

So

$$q = (i-t)/(1+t)$$

4.2.3. Risk

If the realization of returns is subject to risk, an increase of the discount rate will deal with this. If for example the probability that expected returns are indeed realized is $1-k$, the risk rate may be said to be k . The required rate of return to justify investment (and so the discount rate to work with, r) will be

$$r = (1+q)(1+t)/(1-k) - 1 \quad (\text{SMITH, 1978})$$

(Note that with small k : $(1-k) \approx 1/(1+k)$).

Further increase of required rates of returns are necessary if tax has to be paid for the returns of investment. For the evaluation of breeding schemes as discussed in chapter 3, it may be worthwhile to evaluate if risk on realization of expected returns increases further in future. This would lead to make the discount rate time dependent.

4.3. National breeding schemes vs commercial breeders

In all studies on economic optimization of breeding schemes financial returns are taken to result directly from genetic improvement of live-stock. This seems to me an approach of investment in the national interest, resulting in cheaper produced milk, pig meat and so on. If all animals in a nation improve with the same rate, it may very well be that individual farmers don't have much real advantage from it. In fact margins between in- and output may decrease. So from a national viewpoint the discount rate chosen may be low (2-3 % say) but from farmers' viewpoint it probably should be higher, e.g. to adjust for price changes lowering margins.

A very important assumption in all these calculations is that animal population size remains constant. If on the contrary the total (milk) production should stay constant, the population size - and the discounted expressions in subsequent years - should decrease by something like ΔG %. This still is, however, a national approach.

Suppose for example that two competing breeding programmes (A.I.studs) are in operation and that sales of semen is dependent on quality of bulls. Then the approach discussed above doesn't make much sense. Cost effectiveness does not follow any longer from costs versus discounted genetic improvement but probably on costs and expected sales. These sales of semen in turn may depend in the breeding scheme and the genetic improvement. This seems a more logical approach in general for commercial breeders (or breeding companies). The discount rate chosen for cost benefit analyses for breeding companies will be higher than for national breeding plans. The reason being that investment outside breeding might pay better.

It may not be immediately clear that expected sales are depending on genetic merit of breeding stock and consequently on genetic improvement, especially if relative merit of stocks is not known. The following example may illustrate that this relation probably exists. Suppose a commercial pig breeding firm associated with a feed producing company, where feedstuffs for the pigs are delivered by this feed producing company. If sales of pigs were independent of the genetic merit of the stock an obvious policy would be to select for higher feed conversion (and keep the pigs lean to avoid problems in selling slaughter pigs).

It seems to me that such a policy is against common sense and seems to prove the case.

Of course it will be very difficult to link sales to genetic improvement and in addition to higher discount rates for reasons indicated earlier also risk is probably rather high. In Table 4.1 a comparison of perspectives for investment appraisal in animal improvement is given.

Table 4.1 (from SMITH (1978))

Comparison of perspectives for investment appraisal in animal improvement

Perspective	Improvement in the national interest	Commercial breeding firm or breeder
Investment	Improvement of national breeding stocks	Improvement of own breeding stock
Time scale of investment and return	Long	Short
Returns to the investor	Large	Small
Reasons	(1) Value of improvement in all national commercial production (2) Permanent value of improvement over time (3) Value of successive improvements accumulates (4) Low risk of no returns	(1) Returns from extra breeding stock sold (2) Temporary value from competitive advantage (3) Successive improvements needed to maintain competitive position (4) High risk of no returns
Investment justified	Large	Small

4.4. Conclusion

The previous paragraphs indicate that no universal solution for economic evaluation of breeding schemes exists. Methods adopted (4.1.), discount rate chosen (4.2.), length of evaluation period, risk are subject of discussion and will vary by the situation involved.

One technical remark should be added here. In Chapter 3 (and in 4.1.) it was assumed that costs and returns associated with one round of selection were to be compared. For national breeding schemes this seems a reasonable approach. Especially if the evaluation period (T) is long it will give similar (or identical if $T = \infty$) results as the alternative: evaluate cumulative costs and returns associated with subsequent rounds of selection from now to T years ahead. For a commercial breeding firm this alternative approach may be more appropriate. In addition to this the pay off period may be not important for national programs, for commercial firms it probably is.

5. APPLICATION OF DISCOUNTED EXPRESSIONS

The term (standard) discounted expressions was introduced by McCLINTOCK and CUNNINGHAM (1974), as mentioned in chapter 3.6. and an application to computation of returns from breeding schemes has been illustrated in chapter 3.7. - 3.9.

McCLINTOCK and CUNNINGHAM developed this method to account for different expressions (both in number of occasions as in time) of various traits in an aggregate genotype. Economic weights should be adjusted for this difference.

In chapter 3.9. discounted expressions were used in relation to the method of HILL (1974). It seems worthwhile, therefore, to start this chapter with a comparison of both methods (5.1.).

After that, the application to definition of the aggregate genotype will be summarized (5.2.).

5.1. Comparison of the geneflow methods based on McCLINTOCK and CUNNINGHAM (1974) and HILL (1976)

The method of McCLINTOCK and CUNNINGHAM may be summarized as follows:

1. Compute the expected number of individuals in each generation and year, expressing the genotype transferred in initial mating.
2. Multiply each expression with the additive genetic relationship between the individual of initial mating and the individuals in which the expression is measured (generation).
3. Multiply each expression with the discount factor for the year in which the expression takes place.

The following simple example may illustrate the rules above.

Suppose we have a population of dairy cows. The first lactation takes place in the second year of age, the second in the third year, the third in the fourth year. Of all animals having a first lactation, 60 % has a second and 40 % has a third. So in any one year 50 % of the cows are in first lactation, 30 % in second and 20 % in third. Now we wish to compute the number of discounted expressions of one successful insemination. This insemination takes place in year 1. The number of first lactation heifers

in year 4 resulting from this insemination will be 0.5, because the replacement rate is 50 % (the example is infeasible).

In Table 5.1 further numbers are given.

In year 5 we will get 0.3 second lactation cows and in year 6 0.2. All of these are second generation animals (considering the bull to be first generation). Assuming that the relative contribution of females to replacements is independent of age, in year 6 we will get $0.5 \cdot 0.5 = 0.25$ third generation first lactation animals. In Table 5.1 the picture is completed up to year 10. It should be mentioned that genes are transmitted from second to later generations by females only.

Up till now, we applied rule 1, and now we apply rule 2.

In year 4 we have .5 animals expressing $\frac{1}{2}$ of bull's genotype. This gives .25 discounted expressions (with discount rate 0.).

In year 8, for example, we have .29 third generation animals, expressing $.29 \cdot \frac{1}{2} = .0725$ of bull's genotype and .125 fourth generation animals, each expressing $1/8$ of bull's genotype. (Adding to $.0725 + .01563 = .08813$).

In total, over 10 years the number of discounted expressions (with discount rate 0) equals .83329.

If the discount rate is not zero, the discounted expressions in year k have to be multiplied by $1/(1+r)^k$.

Application of HILL's method to the example results in Table 5.2.

Of the total matrix P after year 3 we only need the lower right quarter, being

$$P_{22} = \begin{pmatrix} 0. & .25 & .15 & .10 \\ 1. & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix}$$

P_{11} , P_{12} and P_{21} are 0.

See for definition matrix P section 8.4. and appendix.

Table 5.1 The method of McCLINTOCK and CUNNINGHAM (1974) applied to an example (see text). Interest rate is 0. Numbers of animals from one insemination in different years and generations.

year	generation 2	generation 3	generation 4	generation 5	discounted expressions
4	.5				.25
5	.3				.15
6	.2	.25	=.25		.1625
7		.15+.15	=.30		.075
8		.10+.09+.10=.29	.125	=.125	.08813
9		.06+.06=.12	.075+.15	=.225	.05813
10		.04=.04	.050+.09+.145=.285	.0625	<u>.04953</u>
					.83329

Table 5.2 The method of HILL (1974) applied to an example (see text). Interest rate is 0. Proportion of genes from a bull expressed in males and females in different years and age classes.

year	age classes						discounted expressions
	males		females				
	1	2	1	2	3	4	
1	1.	0.	0.	0.	0.	0.	
2	0.	1.	0.	0.	0.	0.	
3	0.	0.	.5	0.	0.	0.	
4			0.	.5	0.	0.	.25
5			.125	0.	.5	0.	.15
6			.075	.125	0.	.5	.1625
7			.08125	.075	.125	0	.075
8			.0375	.08125	.075	.125	.08813
9			.04406	.0375	.08125	.075	.05813
10			.02907	.04406	.0375	.08125	<u>.04953</u>
							.83329

In chapter 3.9. we already discussed an example. So the figures in Table 5.2 will not be illustrated with respect to the fraction of bull's genotype expressed in different lactation and years.

In year 4 females in age class 2 (first lactation heifers) contain in average 50 % of bull's genotype. First lactation animals represent 50 % of all cows in year 4, so the number of discounted expressions is .25.

In year 8 this is $.8125 \cdot .5 + .075 \cdot .3 + .125 \cdot .2 = .08813$, as before.

Both methods give identical results in this example. This will generally be so, provided that assumptions made in both applications are identical. The difference in methods is a matter of sequence of computations;

McCLINTOCK & CUNNINGHAM: numbers, dilution of genes, discounting

HILL : dilution of genes, numbers, discounting.

In general it seems to me that HILL's method is easier to handle, because it is easier to adapt complicating assumptions. Two examples are discussed below.

1. DANELL et al. (1976) have extended McCLINTOCK and CUNNINGHAM's method to two pathways: sires to offspring and dams to offspring. Subdivision of offspring to males and females (in terms of generation interval) complicates their extension further. With HILL's method it is easy to deal with various pathways of gene transmission.
2. In the original papers of HILL and McCLINTOCK and CUNNINGHAM, the contribution of age classes (or lactation) is proportioned to their occurrence. In practice this is normally not so. With HILL's method it is easy to deal with this by defining the contribution of age classes to offspring (in matrix P) and the relative occurrence differently (see BRASCAMP, 1975 , Appendix 1 and 2). With McCLINTOCK and CUNNINGHAM's method it is more difficult to adjust the model for a difference between relative contribution of age classes to replacement and relative occurrence of offspring. DANELL et al. define three probabilities between mating and replacement:
 1. F_i (and P_j), probabilities that matings with males (females) of different age classes will be successful when the females (males) are 100 % fertile.
 2. L_j , number of progeny surviving to maturity per successful mating in different female age classes.
 3. Q_j , the probability of a surviving descendant being used as

replacement within the population.

To deal with the problem discussed above Q_j should be depending on j , the female age class. The corresponding element in the P-matrix would be $\frac{1}{2}P_j L_j Q_j / \sum P_j L_j Q_j$.

An additional parameter in DANELL et al. is

4. V_j , the probability that a breeding female entering the first age class still will be present in age class j .

So the relative occurrence of age class j is $V_j / \sum V_j$.

5.2. The definition of the aggregate genotype

In this chapter the effect of discounted expressions on the economic weights in an aggregate genotype will be discussed.

Traditionally, the economic weight of a trait is defined as the change in financial (better may be costs) associated with one unit change of the trait. As demonstrated by McCLINTOCK and CUNNINGHAM (1974) the economic weight should not only depend on the marginal returns (or costs) but also on discounted expressions.

The first example of the correction of economic weights for number of expressions probably is SMITH (1964) in the definition of aggregate genotypes for specialized sire and dam lines. He works with two traits, X_D (reproductive performance, e.g. litter size) and X_S (productive traits, e.g. growth rate during the fattening period). The relative economic weight (a) of G_D to G_S is defined as the value of one unit change in X_D relative to the value of n units change in X_S , n being the number of offspring per dam. Considering the reproductive performance of a dam as a trait of that dam, the aggregate genotype for a sire line should be G_g (because no expression of sire's X_D takes place in crossed offspring). Further the aggregate genotype of the damline should be $aG_D + \frac{1}{2}G_S$, because dams show 1 expression X_D in crossed offspring and $\frac{1}{2}n$ expressions X_S in crossed offspring (the n expressions are accounted for in a). These definitions of aggregate genotypes are equal to those of DANELL et al. (1974) for commercial herds with discount rate zero. Commercial herds are defined as obtaining all replacements from outside the own herds. The discounted expressions for B-traits (equivalent to X_D) and A-traits

(equivalent to X_g) are (DANELL et al.) $.74$ and $.74 \cdot \frac{1}{2} \cdot n$, where $.74$ is the average non-return rate of female age classes and n is littersize.

CUNNINGHAM and McCLINTOCK (1974) applied their 'discounted gene flow method' to a situation of dual purpose cattle with beefcrossing (a fraction k of dual purpose cows crossed with beef bulls). The relative magnitude of discounted expressions for dairy and beef traits (E_d and E_b) depend on

1. Cow replacement rate: If cow replacement rate decreases E_d decreases because of lower discount factors. The number of expressions per generation will be equal, within a certain number of years lower. E_b will increase because of a higher number of expressions.
2. Beef crossing: For dairy traits the number of discounted expressions per insemination (dual purpose and beef) will remain constant with increasing k .

Per dual purpose insemination, however, E_d will increase because the number of replacements per dual purpose insemination has to increase to keep the population size constant.

If $E_d = 1$ with $k = 0$, $E_d = 1/(1-k)$ gives the dependency of k (CUNNINGHAM and McCLINTOCK, 1974, Table 3).

For beef traits the number of discounted expressions per insemination (i.e. dual purpose expressions from both dual purpose and beef insemination) will decrease with increasing k because potential 'dual purpose beef' expressions are replaced by 'beef'. Per dual purpose insemination E_b is affected only slightly.

BRASCAMP (1974) found in his study that relative discounted expressions

for dairy and beef traits not only depended on the factors mentioned above, but to a small degree also were different per pathway. The reason being that he assumed unequal probabilities for dairy offspring of young and proven bulls to enter the dairy herd as replacement.

DANELL, RÖNNINGEN, STRÖM, ANDERSSON and SUNGREN (1976) extended McCLINTOCK and CUNNINGHAM's method to two pathways (genes are transmitted by females and males, in McCLINTOCK and CUNNINGHAM's original paper by females only (as in the example in chapter 3.1.)) and worked out the model for a hierarchy with nucleus, sub-nucleus and commercial herds. Their extension was exemplified by a pig breeding situation.

For slaughter and fattening traits they find small differences in discounted expressions. This is a matter of numbers: fattening expressions are counted in both slaughter animals and replacement animals. The ratio between discounted expressions for fattening traits and reproductive traits were discussed before and equalled half the littersize for females in commercial herds (discount rate zero).

For nucleus herds this ratio is larger. Simplified this may be seen as follows (D = reproduction, S = fattening, discount rate = 0 and $n = 7$).

generation	females		males	
	D	S	D	S
1	.74	-	-	-
2	.37	2.59	.37	2.59
3	.37	2.59	.37	2.59
4	.37	2.59	.37	2.59
5	<u>.37</u>	<u>2.59</u>	<u>.37</u>	<u>2.59</u>
	2.22	10.36	1.48	10.36

Females in the first generation express .74 D (as in commercial). Each female is replaced by one new one, expressing half the additive genetic merit (so generation 2 gives .37). Generation 3 remains .37 because genes are transmitted to the third generation offspring by both females and males, doubling the $\frac{1}{2} \cdot .37$.

With the same argument S is expressed in the second generation as 2.59 (as in the commercial) and stays at that level in later generations. For males the situation is equal to females except there is no generation 1 expression for D.

The actual figures calculated by DANELL et al. are 14.29, 2.38, 14.71 and 1.70 (instead of 10.36, 2.22, 10.36 and 1.48), but the very simple approach illustrates - I think - the reason of the difference between commercial and nucleus.

Another application of discounted expressions may be to attach a financial value to the genetic superiority of a breeding animal. Suppose for example that the economic value of growth rate in pigs per gram equals Skr .05 (DANELL et al.). For a nucleus boar with a genetic superiority of 100 grams the financial value of 1 insemination would be $100 \cdot 0.05 \cdot 9.38 = 46.9$ Skr, 9.38 being the discounted expressions with interest rate 10 %, compared with an average boar (more realistic would be to give such a financial value for a set of traits together). From a population viewpoint it is reasonable to take into consideration genetranmission via all different paths. To take a dairy cattle example again, females don't transmit genes to the next generations of females through females alone, but also through males. From the viewpoint of an individual farmer however, perhaps only transmission from females to females (after the initial insemination) should be included in the calculation.

One point should be mentioned discussing the financial value of an insemination in contrast to returns of a breeding scheme (i.e. discounted expressions in both cases). It concerns the probability that one single insemination results in a first generation expression.

Consider again a dairy cow example with replacement rate $1/C$. For returns from a breeding scheme - i.e. discounted expression per cow - the number of first generation first lactation heifers is $1/C$. In case of the financial value of one single insemination consider a farmer with a stable herd size of n cows. Suppose nK inseminations per year are performed, including repeated inseminations. Annually n/C cows will be replaced, so the number of first generation first lactation heifers per insemination is $1/KC$.

For later generations no further differences occur. If the replacement rate is independent on the age of the dam of the replacement heifer, in both cases the probability that a female age class gives a female replacement is $1/C$, irrespective non return rate (expressed in K).

It should be pointed out that in this approach to the financial value of one single insemination sales of offspring from the insemination are not

taken into account. Only expressions in the own herd are considered. MCGILLIARD (1978) computed net returns per single insemination where in principle discounted expressions are adopted - with a somewhat different algebra. As indicated above, only genes transmitted from females to females are included.

(For discussion one point in the paper of MCGILLIARD might be raised (see paper). He seems to assume a replacement rate of $2 \cdot .155 = .31$, according to matrix Y in the paper and there are totally $\frac{1}{2} \cdot 1.356$ expressions of sire's predicted difference in first generation offspring within 10 years.

The factor $\frac{1}{2}$ stands for conception rate. Question: what's the implicit meaning of 1.356, being larger than 1?).

6. SELECTION DIFFERENTIAL AND MATRIX OF GENETRANSMISSION P

In chapter 3 discounted financial return (R) from a breeding scheme is calculated as

$$R = \sum_i E_i I_i \quad (6.1)$$

where I_i are genetic superiorities (genetic selection differentials) for different pathways of gene transmission and E_i are weighing factors: discounted expressions (per cow). It follows from (6.1) that discounted expressions are assumed to be independent on genetic superiorities. This assumption has computational advantages. In a situation of dual purpose cattle for example, a breeding scheme can be described by 5 parameters: proportion of inseminations with young bulls, progeny group size, number of doses semen available per proven bull, population size and proportion selected after performance testing (parameters needed in addition to this are assumed to be biologically determined).

Discounted expressions depend on only one of the 5 parameters, the proportion of inseminations with young bulls. If e.g. 6 alternatives are to be studied for this parameter, only 6 sets of discounted expressions are to be computed, instead of e.g. 10.000 sets, if this number of combinations of parameters are to be studied in total and if discounted expressions depend on I, and so on all parameters.

In this chapter the assumption of independence of discounted expressions and genetic superiorities will be discussed using the papers of BICHARD et al. (1973) and HOPKINS and JAMES (1977). They assume a situation where the selection criterion is known before reproductive age (as in sheep, pigs, beef cattle, but not in dairy cows). Their approach would lead to a P-matrix (describing ageing of breeding animals and transmission of genes to the next generation) which is not constant.

In section 6.2. we will discuss the systems called progeny selection and parent selection as studied by HOPKINS and JAMES. Finally in section 6.3. the validity of geneflow methods in prediction of returns will be discussed more generally.

6.1. Selection differential and genetransmission

Consider a situation in which potential breeding animals are tested before reproductive age. The question is which animals are to be selected to replace parents which (randomly with respect to the selection criterion) left the population. Suppose, that the tested animals are offspring of two age groups of dams and a single age group of sires (this is the example of BICHARD et al., 1973). Then there are two genetic subsets of offspring which differ $G/2$ in average genetic merit because the dams age groups differ G with a genetic gain of G .

Finally suppose there are equal numbers of dams in both age groups giving equal numbers of offspring (N females per subclass). We need $2n$ replacement females. For simplicity we leave male selection out of the argument.

Now we can distinguish three ways to select replacement females (BICHARD et al., 1973).

- a. selection with equal proportions within dam age classes
- b. phenotypic selection
- c. selection with adjustment for genetic difference between both subsets of offspring.

In case a the female to female part of the P matrix will be $\begin{pmatrix} 1/2 & 1/2 \\ 1/2 & 1/2 \end{pmatrix}$, for both age classes of contribute equally to replacement females. In case b this is not so. There will be a tendency to select more offspring from the youngest dams, being $1/2 G$ better in average. In case c we will see that this tendency is even stronger.

Now we will consider the genetic superiority of female replacements.

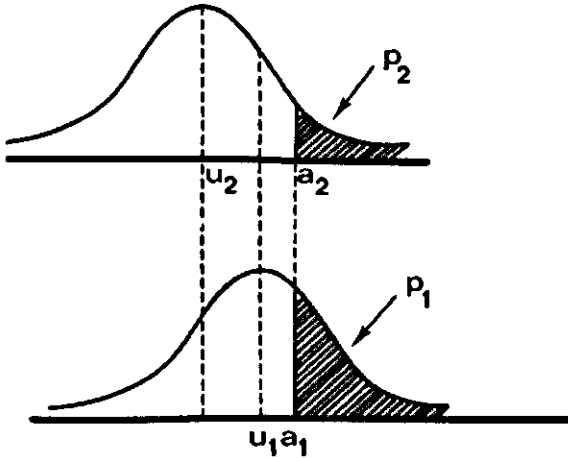
In case a we select n/N females from both subsets giving a selection intensity i . If the average genetic merit of all offspring in the first age class is μ_1 , $\mu_2 = \mu_1 - 1/2 G$, resulting in an average of $(\mu_1 + \mu_2)/2$ or $\mu_1 - 1/4 G$. The average genetic merit of individuals selected in the first subset is $\mu_1 + ih^2\sigma_p$ and in the second $\mu_2 + ih^2\sigma_p$, averaging to $\mu_1 - 1/4 G + ih^2\sigma_p$. So the average genetic differential in case a is $ih^2\sigma_p$.
Or $I_a = ih^2\sigma_p$ (6.1)

In case b the situation is different. In Fig. 6.1 the distributions of

the two subsets of offspring are given.

The difference between μ_1 and μ_2 is $\frac{1}{2}G$ and truncation selection in both distributions will be such that a_2 and a_1 are at the same level.

Fig. 1. Phenotypic distribution of two sets of offspring



If we put the phenotypic standard deviation on 1 and $x_2 = a_2 - \mu_2$ and $x_1 = a_1 - \mu_1$ (x_1 and x_2 are truncation points in both standard normal distributions).

We get

$$x_2 = x_1 + \frac{1}{2}G \quad (G \text{ in phenotypic standard deviation units})$$

(because

$$\begin{aligned} a_2 &= a_1 \\ a_2 - \mu_2 &= a_1 - \mu_2 \\ a_2 - \mu_2 &= (a_1 - \mu_1) + \frac{1}{2}G \end{aligned}$$

So we can find p_1 and p_2 knowing that if we select n_i individuals from both subgroups,

$$\begin{aligned} n_1 + n_2 &= 2n \\ n_1/N + n_2/N &= 2n/N \\ \frac{p_1 + p_2}{2} &= n/N = p \end{aligned}$$

where p is the fraction selected in both agegroups in case a.

The average within dam age class genetic selection differential now is

$$I_{bl} = (p_1 i_1 + p_2 i_2) h^2 \sigma_p / (p_1 + p_2) \quad (6.2)$$

The average genetic selection differential relative to all potential replacements is

$$I_{b2} = \frac{p_1(\mu_1 + i_1 h^2 \sigma_p) + p_2(\mu_2 + i_2 h^2 \sigma_p)}{p_1 + p_2} - \frac{1}{2}(\mu_1 + \mu_2)$$

$$I_{b2} = \frac{(p_1 i_1 + p_2 i_2)}{p_1 + p_2} h^2 \sigma_p + \frac{1}{2}G\left(\frac{1}{2} - \frac{p_2}{p_1 + p_2}\right) = I_{b1} + \frac{1}{2}G\left(\frac{1}{2} - \frac{p_2}{p_1 + p_2}\right) \quad (6.3)$$

In case c the situation is similar to case b, but now we adjust breeding values in both groups for the genetic difference between groups. In case b we implicitly corrected phenotypic values in both groups.

So now,

$$h^2 x_2 = h^2 x_1 + \frac{1}{2}G$$

or

$$x_2 = x_1 + \frac{1}{2}G/h^2$$

Because $h^2 < 1$, we see that in case c x_2 and x_1 will be further apart than in case b.

I_{c1} is calculated according to (6.2) and I_{c2} according to (6.3) with values for p_i and i_i different from case b.

In Table 6.1 the situation is illustrated numerically with

$(p_1 + p_2)/2 = p = .10$, $h^2 = .25$, $\sigma_p = 1$ and $G = .05$

($p = .10$ assumes that at least 5 females are born per mating).

Table 6.1 Numerical example of 3 types of selection among progeny

	p_1	x_1	i_1	p_2	x_2	i_2	I	L ♀
case a	.1000	1.2817	1.7546	-	-	-	$I_a = .43865$	1.5
case b	.1022	1.2693	1.7443	.0978	1.2943	1.7652	$I_{b1} = .43863$	1.489
							$I_{b2} = .43891$	1.5
case c	.1088	1.2333	1.7146	.0912	1.3333	1.7976	$I_{c1} = .43811$	1.456
							$I_{c2} = .43921$	1.5

In Table 6.1 we see that going from case a to c increasingly more replacements are selected from the young age group of dams. In Table 6.1

also the generation interval for females is given, assuming that first offspring is born at 1 year of age and second at 2 years of age of the dams.

For the situation $L\bar{q} = 1.5$ it can be seen that I increases. That is, the average genetic selection differential of selected offspring relative to all offspring increases.

On the other hand, it can be seen that I decreases from a to c when I is defined as the weighted within dam age group genetic selection differential.

It has been shown by JAMES (1977) that the stable annual genetic gain may be computed by either of two ways¹⁾:

1. Defining genetic selection differentials relative to all candidates for selection and defining generation intervals as the average parental age at birth of all offspring.
2. Defining genetic selection differentials as the weighted within parental age class selection differentials and defining generation intervals as the average age of parents at birth of selected offspring.

1) In the notation of JAMES (for simplicity he also assumes selection in females only)

S = selection differential relative to all candidates of selection

\bar{T}_Q = weighted within parental age class selection differential

\bar{A} = average age of parents (sires and dams) at birth of all offspring

\bar{A}_R = average age of parents at birth of selected offspring

G = stable annual genetic gain

He shows that
$$\frac{1}{2}S = \frac{1}{2}\bar{T}_Q + (\bar{A} - \bar{A}_R)G$$

Now
$$G = \frac{\frac{1}{2}S}{\bar{A}} = \frac{\frac{1}{2}\bar{T}_Q + (\bar{A} - \bar{A}_R)G}{\bar{A}_R + (\bar{A} - \bar{A}_R)}$$

So
$$\bar{A}_R G + \bar{A}G - \bar{A}_R G = \frac{1}{2}\bar{T}_Q + \bar{A}G - \bar{A}_R G$$

and
$$\bar{A}_R G = \frac{1}{2}\bar{T}_Q$$

So
$$G = \frac{\frac{1}{2}\bar{T}_Q}{\bar{A}_R}$$

So for I_{b1} the appropriate generation interval is $(1 \cdot .1022 + 2 \cdot .0978) / (.1022 + .0978) = 1.489$.

From I_a , I_{b2} and I_{c2} together with the appropriate generation intervals (1.5) we can see that G increases from a to c . Because Table 6.1 was calculated assuming $G = .05$, it is obvious that only for case c this is an equilibrium value. If a selection scheme is adopted using c , G will stay at $.05$. But a change to system b will cause a slight drop of G and as a consequence of this a change in p_1 and p_2 until a new, lower, equilibrium value is reached.

For application of the discounted gene flow techniques we need in the P -matrix the contribution of different age classes to replacements. So effectively generation intervals are adopted according to definition 2 above. Consequently genetic selection differentials used should be computed as weighted within parental age class selection differentials. Secondly, the actual contribution of age classes will depend on method of selection and on genetic differences between age groups. If the P -matrix is applied for the effect of one round of selection without affecting the existing stable annual genetic improvement (because a program runs already for a long time) the P -matrix will be constant. If, however, the one round of selection studied affects the genetic gain, the P -matrix will not be stable.

For the evaluation of different breeding schemes it seems to me not necessary to work (if at all possible) with a non-stable P -matrix. For the evaluation of selection experiments, however, it may be worthwhile because the interpretation of results may be more critical. HOPKINS and JAMES (1978, manuscript not yet published) deal with the latter situation.

It may be noted that BRASCAMP (1975) defined the contributions of parental age groups to offspring (in matrix P) solely to reach predecided generation intervals. (See section 3.9.). Selection differentials were computed ignoring age classes, being selection within one normal distribution with all age classes. In fact, this assumes equal proportions selected from various age classes and is in conflict with the definition of P . In view of the previous discussion the procedure followed is obviously not correct (but it may be the only practicable procedure).

6.2. Progeny selection and parent selection

HOPKINS and JAMES (1977) studied two systems of selection, progeny selection and parent selection, with examples in sheep and beef cattle. In both species the selection criterion is available before first mating. I will not go into the algebra of the systems described in the paper. Only the differences will be explained and some results will be given. In addition to a sheep example (from HOPKINS and JAMES) a pig example will be given and the dairy cattle situation will be touched.

Progeny selection involves selection of replacements among tested offspring to replace parents who left the population for reasons uncorrelated with the breeding objective. So selection takes place only once: before first mating. In doing so, some potential replacement animals will not serve replacement even though they may be genetically better than parents in the population. Higher genetic improvement can be achieved by culling some parents such that all remaining age groups (i.e. parents of different ages together with replacements) have the same average genetic merit. This system is called parent selection. It should be pointed out that this system does not involve multi stage selection problems as discussed in Chapter 2 as long as selection takes place solely on the criterion measured before first mating. It is decided before replacement which animals replace to keep one year (or litter), which smaller fraction 2 years, and so on.

HOPKINS and JAMES distinguish the following systems:

1. progeny selection
 - i allowing for genetic effects of parental age
 - ii phenotypic selection
 - iii selection of equal proportions from each parental age group
(These are the systems discussed in section 6.1.).
2. parent selection
 - i allowance for genetic effect of own age - based on one record
 - ii phenotypic selection
 - iii correct allowance for genetic effect of own age - based on mean of records accumulated over the individual's lifetime.

(It might be possible to adapt 2i with correct allowance for genetic effects of parental and own age, but that will be very complicated.

HOPKINS and JAMES modify the heritability within parental age subclasses for progeny selection to the within own age heritability. The latter will be somewhat larger in general because of more genetic variation among parents).

If there are N_f female age classes and N_m male age classes there will be $N_f + N_m - 1$ parental age subclasses with average genetic merit differing $\frac{1}{2}G$ from one to another. (For example $N_f = 2$, $N_m = 2$, parental age classes with different genetic merit are 11; 12 and 21; 22).

In Table 6.2 results are given for 1i and 2i, referring to sheep.

Table 6.2 Results for progeny selection and parent selection in case of sheep (HOPKINS and JAMES, 1977)

parental/own age class	progeny selection(1i)		parent selection (2i)	
	males	females	males	females
1	.0629	.818	.0441	.838
2	.0385	.748	.0126	.674
3	.0224	.667	.0028	.467
4	.0124	.577	.0005	.269
5	.0066	.483	.0001	.126
6	.0033	.390	.0000	.046
7	.0016	.302		
8	.0007	.225		
9	.0003	.160		
10	.0001	.000		
11	.0001	.000		
G/h^2	.4751	.4751	.5350	.5350

Assumption:

$F = .80$ (fertility rate: number of progeny per mated female surviving to birth of first offspring)

$M = 35$ (number of females mated per male)

$h^2 = .25$

$V = .85$ (survival rate from one age to the next by 'natural' causes)

$N_f = 6$

$N_m = 6$

$A = 1$ (age at 1 year before birth of first offspring)

The example in Table 6.2 shows that parental selection (i.e. additional culling among parents) improves G rather much. In order that the example is not misleading it should be mentioned that HOPKINS and JAMES show that the difference between progeny and parent selection decreases if less age groups are considered and further that for the sheep example G for parent selection reaches a nearly constant maximum if $N_f (=N_m) = 6$ and for progeny selection G reaches a maximum if $N_f (=N_m)$ is 4 to 5 and decreases with more subclasses. In that situation the systems differ not much.

For pigs a similar tendency holds and the example in Table 6.3 refers to a situation with $N_f = 4$ and $N_m = 2$.

Table 6.3 Results for progeny selection and parent selection in case of pigs

parental/own age class	progeny selection (1i)		parent selection (2i)	
	males	females	males	females
1	.0319	.2668	.0190	.2799
2	.0114	.1478	.0015	.0688
3	.0035	.0709		.0085
4	.0009	.0292		.0005
5	.0002	.0103		
G/h ²	.8475	.8475	.9020	.9020

Assumption:

F = 6 M = 16 h² = .30 V = .70 N_f = 4 N_m = 2 A = 1

G/h² is per half year.

Table 6.3 would lead to the following 'practical' situation in case of parent selection:

100 matings/half year result in 300 potential female replacements

Of those 84 will be mated for the first litter (.2799·300)

15 will be mated also for the second litter (.0688·300·.70)

1 will be mated also for the third litter (.0085·300·.70²)

And for boars: 5.7 (.0190·300) will be used half a year and .315 (.0015·300·.70) will be used also the second half year. (This should add to 6.25).

These computations indicate that a situation common to breeding companies, where sows are kept only a short time in the nucleus and boars are used very limited, is close to the 'ideal' situation.

Also in 'national' programs boars are often used not very long while replacement of nucleus boars often is from young dams.

In dairy cattle SYRSTAD (1972) showed that more intensive culling has very limited effects on genetic improvement, partly because there is not much room for it. Secondly, especially in dairy cows, more intensive culling may improve genetic gain but a drawback of this is that the average milk yield of the herd will decrease because of large age effects on this trait. It has been shown by KORVER (1977) that effects of culling strategies on financial returns are far more important from the short term point of view (direct effects on average herd yield) than from a long term point of view (genetic improvement).

To some extent the same is valid in pigs. An additional point in pigs is that in order to select for fertility it will probably be worthwhile to keep females longer. In general this will be true if traits selected for cannot be measured early in life.

6.3. Some general remarks on the P-matrix

In 6.1. we saw that application of a constant P-matrix may be erratic because parental age groups may contribute variably to replacements. Another problem should be mentioned. The P-matrix defines average gene transmission from parents to offspring. For genes from individual parents this will not be so. It is likely that genes from better parents - better in terms of genetic merit - will represent a larger part of all genes in the population when time goes on. To attach financial value to one insemination as in 5.2., the size of this effect will depend on the genetic merit of this insemination compared with competitors. Because generally no information will be available on the merit relative to competitors and because this will vary from farmer to farmer the 'best' solution seems just to assume average gene transmission.

In the computation of financial returns of a breeding scheme average genetic superiorities of parents are multiplied by discounted expression. Again discounted expressions are computed using the P-matrix. It is

likely that genes from the parents with highest genetic superiority among all parents selected will get a larger influence in the population. So using average genetic superiority and constant P probably underestimates realized gains. I'm not sure if one should account for this effect - provided that it is possible - because it may interfere with the computation of genetic superiorities in later rounds of selection.

Of course, the problems mentioned are not unique for the P-matrix. They will exist whatever method to evaluate gains is adopted. Simply always is assumed that the problems don't exist.

7. REPORTS OF GROUP WORK

Aspects of various breeding schemes in dairy cattle, pigs, sheep and laying hens have been studied in group work. Use was made of the computer program GFLOW, described in chapter 8. The reports of the 6 groups are summarized in this chapter. The original texts have been edited somewhat in order to fit them in a common framework. At the end of this chapter the input cards for GFLOW are listed for each group in order to make recomputation of results possible.

The subjects studied were:

1. Selection of dairy bulls on progeny or half-sister records.
2. Selection of dairy bulls on progeny records and on records of milk yield of bull's mates influenced by fetal effects.
3. Subdivision of a dairy A.I.-population in nucleus and commercial cows.
4. An evaluation of the pig breeding scheme in Sweden.
5. Economic comparison of two different breeding schemes for sheep meat production.
6. Evaluation of a breeding scheme producing C(BA) commercial laying hens.

7.1. Selection of dairy bulls on progeny or half-sister records

Kjeld Kragelund, Maria Tuiskula, Elisabeth Persson

A comparison of breeding schemes based on half-sister and progeny selection of bulls has been carried out on the basis of the paper of OWEN (1975). The assumptions about the generation intervals are those of BRASCAMP (1975), as presented in Table 7.1. The percentage of inseminations with young bulls in the progeny testing scheme (A) is assumed to be 20 %, as in the case of OWEN.

The genetic gain obtained in scheme A is compared with the gain obtainable in different alternative half-sister testing schemes (B1-B5) (Table 7.2.). In schemes B1 and B2 80 % of the cows are mated with the 20 best bulls, and 20 % are mated with the remaining 30 bulls. In schemes B3-B5 all selected bulls are used equally to the whole cow population. It appears from Table 7.2. that the stable genetic gain from the scheme of half-sister testing is 75-85 % of the gain in the progeny testing scheme.

Changes in the breeding structure of scheme B result in varying genetic gain, but in every case scheme A was superior to B.

The progeny testing scheme (A) was compared with the half-sister schemes B1 and B4 by means of discounted expressions according to BRASCAMP (1975). The discounted return is calculated assuming a genetic standard deviation (σ_A) of 400 kg milk and a net income of 0.5 Mark per kg milk. The results in Table 7.3. show that during a period of 20 years schemes of half-sister testing are superior to the scheme with progeny testing, whatever interest rate is used. When longer time periods are considered the returns of the progeny testing scheme increases relative to the other schemes.

The advantage of the half-sister schemes are increasing with increasing interest rate.

It should be noted that a comparison between different schemes ought to be between the respective schemes at optimum. This is not necessarily the case in our comparison.

REFERENCES: see chapter 9.

7.2. Selection of dairy bulls on progeny records and on records of milk yield of bull's mates influenced by fetal effect

Britta Danell, Matleena Haapa, Sampo Sirkkomaa

In recent years some studies have been done on the effect of the fetus in the dams on milk yield during the lactation following the birth of the calf (SKJERVOLD et al., 1975 and ADKINSON et al., 1977). Both investigations show effects, although small, of the sire of fetus and also significant genetic correlation between the fetal and direct milk trait expressed in sire's progeny. It can therefore be questioned if the fetal effect can be used to predict genetic merit for milk yield and thus decreasing generation intervals. VAN VLECK (1978a) developed genetic models for the fetal effects and in another study (1978b) he calculated expected responses where direct genetic and fetal effects were combined in a selection index. The study here concerns only the first aspect.

The genetic model implies that a fetus contains $\frac{1}{2}F_S + \frac{1}{4}F_{MGS} + \frac{1}{4}F_{MGD}$, fetal effects transmitted by the sire of fetus, maternal grandsire and granddam. The maternal grandsire part, however, is completely confounded

Table 7.1. Selection intensities, accuracies and generation intervals for the progeny testing scheme (A) and the half-sister testing scheme (B1).

Scheme	Path	Number tested	Number chosen	Percentage selected	i	r _{IA}	i.r. _{IA}	L
A	SS	30	2	6.7	1.83	0.96	1.76	6.75
	SD	30	6	20.0	1.08*	0.96	1.04	5.95**
	DS	25 000	50	0.2	3.17	0.60	1.90	6.00
	DD	--	--	--	--	--	--	4.50
						$\Sigma=4.70$		<u>23.20</u>
B 1	SS	500	50	10.0	1.76	0.48	0.84	4.75
	SD	500	50	10.0	2.12***	0.48	1.02	2.75
	DS	25 000	2 500	10.0	1.76	0.60	1.06	6.00
	DD	--	--	--	--	--	--	4.50
						$\Sigma=2.92$		<u>18.00</u>

* $0.8 \cdot 1.4 + 0.2 \cdot 0 = 1.08$

** $0.8 \cdot 6.75 + 0.2 \cdot 2.75 = 5.95$

*** $0.8 \cdot 2.15 + 0.2 \cdot 1.99 = 2.12$

Table 7.2. Genetic gain for different breeding schemes.

Alternative	Size of half-sib group	Number of candidate bulls	Number of bulls selected	Number of elite cows	ΔG	$\frac{\Delta G \text{ half-sister}}{\Delta G \text{ progeny}}$
A	160	30	6	150	$0.20\sigma_A$	---
B1*	160	500	50	2500	$0.16\sigma_A$	0.80
B2*	300	500	50	2500	$0.16\sigma_A$	0.80
B3	160	500	50	2500	$0.15\sigma_A$	0.75
B4	160	500	25	2500	$0.17\sigma_A$	0.85
B5	160	1000	25	5000	$0.17\sigma_A$	0.85

*20 best bulls are mated to 4000 cows and the remaining 30 bulls to 667 cows.

Table 7.3. Comparison of discounted returns per cow for breeding schemes based on half-sister testing (B1 and B4) and on progeny testing scheme (A).

Evaluation over:	20 years	40 years
Interest rate (r)	.00	.10
	.05	0.00
	0.05	0.05
Interest rate (r)	.10	0.10
Progeny test (A)	320	150
	76	978
Half-sister test (B1)	382	206
	120	954
Half-sister test (B1)	1.19	1.38
<u>Progeny test (A)</u>	<u>1.58</u>	<u>1.98</u>
Half-sister test (B4)	399	211
	120	987
Half-sister test (B4)	1.25	1.41
<u>Progeny test (A)</u>	<u>1.58</u>	<u>1.01</u>
	304	116
	336	154
	1.11	1.34
	345	157
	1.13	1.35

with grandsire's direct effect, because the maternal grandsire of the fetus is the sire of the dam, and thus included in sire's progeny test based on the yield of his daughters.

In the present study two alternatives were studied.

Alt. I. In a basic breeding program the discounted expressions for direct milk and fetal effects were calculated using GFLOW.

Alt. II. The same assumptions but 20 % of the sires to breed sons were selected after progeny testing for fetal effects.

The fetal effect here is assumed only to influence the lactation following birth of calves and it is also assumed that culling takes place at the end of that lactation.

A part of the P-matrix has been given below. It concerns only transmission of genes for sire to son, daughter and fetus. Because it is assumed that the fetus affects one lactation only, one additional single row (and column) in the P-matrix is needed. Because dam to fetus effect is confounded with direct effect the corresponding elements in matrix P are zero.

	sires to:						
	age class of sire						
	1	2	3	4	5	6	7
son	0	0	0	0	0	.125	.375
daughter		.021	.061	0	0	.104	.313
fetus	.025	.075	0	0	.1	.3	0

For Alt. II the sire to son row is 0 0 0 .1 0 .1 .3

The elements in the row sire to fetus are placed one age class (year) earlier than the corresponding elements in the row sire to daughter to obtain the expression in dam's following lactation contemporary with the calf being 1 year old (age class 1).

Discounted expressions for path SS, SD and DS were calculated. In Alt. II where 20 % of SS were selected on their genetic merit for fetal effect the path SS were split into two by using two different R-matrices SS_p for expressions due to selection on total effects and SS_p due to selection after progeny testing for milk. R-matrix for SS_p contains only 0.1 for age class 4 and R-matrix SS_p contains 0.1 and 0.3 for age classes 6 and 7. 20 Years were considered and interest rate was .10. The dairy expressions

were time adjusted with +0.48.

RESULTS .

The number of discounted expressions per cow for the different paths in both alternatives are given below in Table 7.4.

Table 7.4. Number at discounted expressions.

Path	Alt. I		Alt. II	
	Dairy	Fetal	Dairy	Fetal
SS _F	0	0	0.016	0.026
SS _P	0.048	0.0918	0.039	0.075
PB	0.175	0.229	0.175	0.229
DS	0.054	0.104	0.056	0.106

Assuming a selection differential (in units of genetic standard deviations for direct effect σ_g) of 1.2 for SS (SS_F, SS_P), 0.6 for SD and 0.8 for DS together with repeatabilities of 0.9 for progeny testing and 0.7 for cow selection the gross returns were calculated. The correlation between the two traits (r) was varied and in addition to that the genetic standard deviation (σ_F) for fetal effects relative to σ_g . The results are presented in Table 7.5.

Table 7.5. Gross returns from the two breeding schemes I and II in σ_g units.

r	σ_F/σ_g			
	1,0	0,5	0,1	0,0
1,0	I 0,4576	I 0,3171	I 0,2047	I 0,1766*
	II 0,4774	II 0,3313	II 0,2145	II 0,1680
0,5	I 0,3171	I 0,2468	I 0,1906	I 0,1766*
	II 0,3367	II 0,2567	II 0,1926	II 0,1680
0,1	I 0,2047	I 0,1906	I 0,1794*	I 0,1766*
	II 0,2242	II 0,1969	II 0,1716	II 0,1680
0,0	I 0,1766	I 0,1766	I 0,1766*	I 0,1766*
	II 0,1961	II 0,1820	II 0,1708	II 0,1680

*Alt. II gives less returns than Alt. I if $r < 0.1$ and $\sigma_F/\sigma_g < 0,1$

The schemes give equal gross returns when:

$$r = 0,1 \quad \text{and} \quad \sigma_F/\sigma_g > 0,2605$$

$$\text{or } \sigma_F/\sigma_g = 0,1 \quad \text{and} \quad r > 0,3718$$

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Am.Dairy Sci.Assoc.73rd Annual Meeting.

7.3. *Subdivision of a dairy A.I.-population in nucleus and commercial* Inger Edfors-Lilja, Lars Elofson, Tapani Hellman

The problem of this study may be considered in two ways.

1. Is it worthwhile to split a dairy A.I.-population in a nucleus and a commercial.
2. To describe a model which is possibly more representative (with a nucleus) for many A.I.-schemes because the parents of bulldams are more often bullsires and bulldams then described by a model without a nucleus. It should be recognized that a nucleus does not refer to specific herds but refers to cows with a particular pedigree.

The population in this study consists of 300 000 cows which in the first alternative are divided in nucleus and commercial cows. In the second alternative no division is done. The replacement rate in both alternatives is 0.30. Alternative 1: The nucleus consists of 60 000 cows (1/5 of 300 000). The five best proven bulls are used in nucleus. The next best

12 proven bulls are used on commercial cows. The 17 proven bulls are selected from 100 young bulls. The young bulls are recruited only after first lactation nucleus cows. The female replacements in the nucleus are recruited after first, second and, partly, third lactation nucleus cows. All the young bulls are tested on commercial cows. The commercial cows are recruited after a part of third lactation nucleus cows, 4th, 5th, 6th and 7th lactation nucleus cows and commercial cows of first to seventh lactation. For details see the input cards at the end of this chapter.

Alternative 2: No division is done in nucleus and commercial cows. Young bulls are recruited from first lactation cows as in alternative 1.

17 Proven bulls are selected from the 100 tested young bulls. The proportion of genes from different age classes are shown in the P-matrix.

The selection intensities for the different paths in the two alternatives are as follows:

Path		Alternative	
		1	2
Sire to son	SS	5/100 = 5 %	5/100 = 5 %
Proven bull to nucleus ♀	PB _N	5/100 = 5 %	17/100 = 17 %
Proven bull to commercial ♀	PB _C	12/100 = 12 %	
Dam to son	DS	2000/18000 = 11 %	2000/45000 = 4.4 %

The selection differentials are shown in Table 7.6. The discounted expressions for the paths are shown in Table 7.7. In Table 7.7. are also given the returns per cow computed as $R = \sum_i E_i I_i$, where E_i are the discounted expressions for the paths and I_i = selection differentials.

With the parameters used in this example alternative 1 is the most suitable. I.e. establishment of a nucleus of cows seems profitable. In this example a nucleus is established consisting of the best 20 % of the whole population and these are mated with elite sires (when no nucleus: sires to breed sons). After that the nucleus is closed. Replacements are from matings of nucleus dams and elite sires. Open nucleus systems are generally more effective as shown by JAMES (1977). The problem of open nucleus systems with overlapping generations has been discussed by HOPKINS (1978). In practice an open nucleus system would result in use of semen of elite-

bulls (bull sires) for the upper part of cows (with respect to cow index) only, without looking at pedigree as in our case.

REFERENCE

Hopkins, I.R., 1978. Some optimum age structures and selection methods in open nucleus breeding schemes with overlapping generations. Anim.Prod.26:267-276.

Table 7.6. Selection differentials for alternatives 1 and 2.

Path	r_{IH}	σ_H^2	Alternative 1			Alternative 2		
			P%	i	I	P%	i	I
SS	.96*	8	5	2.063	15.844	5	2.063	15.844
PB _N	.96	8	5	2.063	15.844	17	1.490	7.779
PB _C	.96	8	--	1.251**	9.608	--	--	--
DS	.50	8	11	1.709	6.836	4.4	2.117	8.468

* 170 daughters

$$**i_{.12} = (.17i_{.17} - .05i_{.05}) / .12$$

Table 7.7. Discounted expressions per cow and returns for the two alternatives.

interest-rate	alter-native	discounted expressions				returns σ_H^2
		SS	PB _N	PB _C	DC	
.0	1	.740	.751	.416	1.095	35.11
	2	.777	.973		1.143	29.56
.10	1	.129	.145	.133	.268	7.45
	2	.135	.247		.281	6.44

7.4. An evaluation of the pig breeding scheme in Sweden

Andreas Christensen, Nils Lundeheim, Gunilla Ral

Gene flow and discounted expressions were computed for the Swedish pig breeding scheme and the Dutch (herdbook) breeding scheme¹⁾. The main difference between both schemes is the definition of nucleus, sub-nucleus and commercial. In Sweden special nucleus herds are established which are the only herds producing boars for breeding. In the Netherlands no nucleus herds exist. In the Dutch situation a pig is considered to be a nucleus pig if the father is a A.I.-boar and the mother a sow of which one litter is station tested. Boars are produced by this combination only and is considered nucleus if it is an A.I.-boar and sub-nucleus if it is a natural serving boar. Potential nucleus females have nucleus parents and enter nucleus after successful station test of one litter. In Table 7.8. the gene flow of both situations is summarized.

Table 7.8. Gene flow in pig breeding schemes in Sweden and the Netherlands (P-matrix, summarized).

	Sweden					the Netherlands ²⁾					
	No♂	N♀	C♀	S		Ao♂	T♀	Ho♂	H♀	C♀	S
Nucleus ♂	50	50	0	0	A.I. ♂	50	50	0	0	0	0
Nucleus ♀	50	50	0	0	Top ♀	50	50	0	0	0	0
Commercial ♀	50	8	42	0	Herdbook ♂	50	50	0	0	0	0
Slaughterpigs	50	0*	50	0	Herdbook ♀	18	16	32	34	0	0
					Commercial ♀	17	0	33	27	23	0
					Slaughterpigs	5	0*	45	12	38	0

*Approx.

For details of the P-matrix see the inputcards for GFLOW, at the end of this chapter.

It has been assumed for Swedish circumstances that boars used in nucleus herds have a higher breeding value than boars used in commercial herds. The same holds for females. Therefore, the following paths have been distinguished (and R-matrices are defined accordingly).

¹⁾ The Dutch system has been included as it served as example in the course.

²⁾ Data from NIEUWENHUIS & RUTGERS (1978, not yet published).

$N\sigma$ to N-replacement

$N\sigma$ to commercial ♀ (includes direct slaughter offspring)

$N\eta$ to N-replacement

$N\eta$ to commercial ♀ (includes direct slaughter offspring)

$C\eta$ to commercial ♀ (" " " ")

Further it has been assumed that annually 15 000 matings are performed in nucleus herds. In whole Sweden 500 000 matings. About 3 500 000 pigs are slaughtered annually.

Per year 12 000 boars are on-farm tested and 300 boar replacements are needed in nucleus. The corresponding figure for commercial herds is 4000 boars. In nucleus herds 25 000 gilts are on-farm tested annually and 4000 replacements are needed. In whole Sweden 100 000 gilts are tested, while 100 000 replacements are needed.

In Table 7.9. discounted expressions per slaughterpig are given, with an evaluation period of 20 years (40 half years) and an interest rate of 10 %.

Table 7.9. Discounted expressions per slaughterpig.

	Sweden		the Netherlands
$N\sigma$ - N	1.783	A.I. σ - offspring	2.564
$N\eta$ - N	1.805	$T\eta$ - offspring	2.423
$N\sigma$ - C	0.685	$H\sigma$ - offspring	0.557
$N\eta$ - C	0.045		
$C\eta$ - C	0.647		

Comparison of both systems based on Table 7.9. is difficult where the assumptions for e.g. generation intervals are unequal. The low values for $N\sigma$ - C, $N\eta$ - C, $C\eta$ - C and $H\sigma$ - offspring are caused by the fact that their contribution to slaughterpigs (from one round of selection) is zero after some years because their genes are continuously replaced by new Nucleus to Nucleus genes in later years.

Table 7.10. gives selection differentials for the paths in Table 7.9. in Swedish conditions.

Table 7.10. Selection differentials in index units ($\sigma = 2.37$).

$N\sigma^{\#} - N$	5.57
$N\phi - N$	1.52
$N\sigma^{\#} - C$	2.61
$N\phi - C$	0.40
$C - C$	0.30

For the Dutch conditions these values are not known but may theoretically be expected to be higher for A.I. $\sigma^{\#}$.

From Tables 7.9. and 7.10. it follows that the returns per slaughterpigs from one round of selection ($\sum_i I_i E_i$) is 18.72 discounted index units. The return from one year of selection for whole Sweden would amount to the financial value of 3 500 000*18.72 index units.

CONCLUSION

1. On-farm-test in commercial herds gives relatively low financial returns ($.3 \cdot .647/18.72 = 1.04\%$ of total returns)
2. Sales of females from nucleus to commercial herds contributes hardly to total returns ($.045 \cdot .40/18.72 = 1 \text{ }^{\circ}/\text{oo}$)
3. The path $N\sigma^{\#}$ - commercial increases in value with increasing A.I.-usage.

7.5. *Economic comparison of two different breeding schemes for sheep meat production*

Zofia Kurowska, Ulla Katajamäki, Hilikka Kenttämies, Siv Österberg

ASSUMPTIONS

The Finnsheep population consists of 50 000 ewes. The recorded flocks which consist of 8 000 ewes form the nucleus population, the other 42 000 ewes form the subnucleus. The average litter size is 2.5 lambs. The lambs are slaughtered at half a year of age. The ewes are kept for 5 years and the rams for 2 years. Every year 200 ram lambs from the nucleus population are performance tested. One hundred rams are selected

forbreeding. All the ewes in the nucleus are either mated or inseminated with tested rams. In one scheme 5 % of the subnucleus ewes are mated to tested rams in the other we use A.I. and 30 % of the subnucleus ewes are inseminated with semen from tested rams. The schemes are evaluated for a period of 20 years.

CALCULATIONS

The financial returns for the two breeding schemes were calculated. In both cases we counted with no interest rate or with a rate of 10 %.

The net return for one kg meat is 3 Fmk. Annually 100 000 lambs in the whole population are slaughtered.

The financial returns in case A (5 % mating with tested rams in the subnucleus) and case B (30 % insemination in subnucleus) are:

$$\begin{aligned} R_{0\%} &= 525\,690 \text{ mk/year} & A \\ R_{10\%} &= 206\,115 \text{ mk/year} \end{aligned}$$

$$\begin{aligned} R_{0\%} &= 742\,815 \text{ mk/year} & B & \text{see for details} \\ R_{10\%} &= 286\,935 \text{ mk/year} & & \text{Tables 7.11. and 7.12.} \end{aligned}$$

CONCLUSIONS

Supposed that the artificial insemination with frozen semen on sheep works and that the costs for it are the same as for using natural mating and transporting the rams to the farms, the A.I. would offer a big advantage in terms of financial return.

It will take a very long time to reach a steady state in case A, because the number of tested rams used in the subnucleus population is so low.

In Table 7.11. the gene flow (P-matrix) has been summarized for both alternatives.

Table 7.11. Summary of gene flow.

	Case A: 5 % of rams in commercial from nucleus					Case B: 30 % of rams in commercial from nucleus				
	No [♂]	N _♀	SN [♂]	SN _♀	S	No [♂]	N _♀	SN [♂]	SN _♀	S
Nucleus [♂]	50	50	0	0	0	50	50	0	0	0
Nucleus _♀	50	50	0	0	0	50	50	0	0	0
Sub-nucleus [♂]	2.5	0	47.5	50	0	15	0	35	50	0
Sub-nucleus _♀	2.5	0	47.5	50	0	15	0	35	50	0
Slaughter	10	8	40	42	0	21	8	29	42	0

In Table 7.12. Selection differentials and discounted expressions (evaluated over 20 years) are summarized.

Table 7.12. Genetic selection differentials and discounted expressions per slaughterlam (evaluation period is 20 years).

path	sel.diff.(kg)	discounted expressions			
		case A	case B	0	.10
No [♂] - offspring	.8	.757	.290	1.849	.695
N _♀ - sons	.5	.286	.089	.691	.212
N _♀ - offspring	.2	.308	.125	.517	.176
SN [♂] - offspring	.3	2.244	.939	1.191	.553
SN _♀ - sons	.15	.902	.299	.513	.181
SN _♀ - other offspring	.1	1.336	.590	1.137	.542

*interest rate

7.6. Evaluation of a breeding scheme producing C(BA) commercial laying hens Sven-Olov Rosberg, Hans-Bernhard Bentsen, Einar J. Einarsson

A breeding system was studied where three strains A, B and C (each consisting of 450 _♀ and 50 [♂]) were used to produce 4000 BA_♀ to be mated with 400 C[♂] resulting in 320 000 C(BA) commercial laying hens. In each strain eggs were collected at about one year of age to produce the next

generation. To produce hybrids collection of eggs in the three strains continues resulting in an average age of parents of 1.25 years at birth of offspring. In BA and C(BA) eggs are collected one year from a half year of age, resulting in an generation interval of 1 year.

For details of gene transmission see the input cards at the end of this chapter. A summary is given in Table 7.13.

Table 7.13. Summary of gene flow.

	A♂	A♀	B♂	B♀	C♂	C♀	BA♀
A♂	50	50					
A♀	50	50					
B♂			50	50			
B♀			50	50			
C♂					50	50	
C♀					50	50	
BA♀		50	50				
C(BA)♀					50		50

In Table 7.14. discounted expressions per commercial laying hen are given for 6 paths of which 4 are different. (Evaluation period 10 years.)

Table 7.14. Discounted expressions per commercial laying hen.

path*	interest 4 %	10 %
Sire to offspring A		
Dam to offspring B	0.672	0.467
Dam to offspring A		
Sire to offspring B	0.896	0.653
Sire to offspring C	2.035	1.536
Dam to offspring C	1.568	1.115
Total	<u>5.171</u>	<u>3.771</u>

*For definition of paths see R-matrices in input cards

It can be seen that we may put more costs in line C than in the other lines because these efforts lead to higher returns than for other paths.

In Table 7.14. the discounted expressions for the different paths are added because the genetic selection differential is equal for all paths (4.5 egg).

The net-value for 1 additional egg per laying hen per year is .10 Nkr.

Assuming that of 320 000 commercial hens 10 % is lost during the raising period and during the laying period 288 000 hens benefit of the increased genetic merit.

The assumptions result in a total return of the breeding scheme per round of selection evaluated over 10 years of $5.171 \cdot 4.5 \cdot 288\ 000 \cdot .1 = \text{Nkr } 844\ 344$ with interest rate 4 % and Nkr 607 824 with interest rate 10 %.

INPUT DATA USED IN GROUP WORK

7.1. Input data

HALFSIB

1 40 3 3 .0 .05 .10

18 5

1 4 .125

1 5 .375

1 8 .11

1 9 .09

1 10 .07

1 11 .055

1 12 .04

1 13 .035

1 14 .025

1 15 .02

1 16 .02

1 17 .02

1 18 .015

6 2 .125

6 3 .375

6 7 .125

6 8 .110

6 9 .075

6 10 .05

6 11 .04

6 12 .03

6 13 .025

6 14 .015

6 15 .01

6 16 .01

6 17 .005

6 18 .005

0 0 .0

.0 .0 .0 .0 .0 .0 .25 .157 .13 .089 .063 .045 .036 .027 .018 .018 .009 .009

SIBS TO SON

1

1 4 .125

1 5 .375

0 0 .0

1 .488

MILKPRODUCTION

1 2

SIBS TO DAUGHTER

1

6 2 .125

6 3 .375

0 0 .0

1 .488

MILKPRODUCTION

1 2

DAM TO SIRE

6

1 8 .110

1 9 .09

1 10 .07

1 11 .055

1 12 .04

1 13 .035

1 14 .025

1 15 .02

1 16 .02

1 17 .02

1 18 .015

0 0 .0

1 .488

MILKPRODUCTION

1 2

0

PROVEN

1 40 3 3 .0 .05 .10
20 7

1 6 .125
1 7 .375
1 10 .110
1 11 .09
1 12 .07
1 13 .055
1 14 .04
1 15 .035
1 16 .025
1 17 .02
1 18 .02
1 19 .02
1 20 .015
8 2 .025
8 3 .075
8 6 .1
8 7 .3
8 9 .125
8 10 .11
8 11 .075
8 12 .05
8 13 .04
8 14 .03
8 15 .025
8 16 .015
8 17 .01
8 18 .01
8 19 .005
8 20 .005
0 0 .0

.0 .0 .0 .0 .0 .0 .0 .0 .25 .157 .130 .089 .063 .045 .036 .027 .018 .018 .009
.009

SIRES TO SON

1
1 6 .125
1 7 .375
0 0 .0
1 .488
MILKPRODUCTION
1 2

SIRES TO DAUGHTER

1
8 6 .1
8 7 .3
0 0 .0
1 .488
MILKPRODUCTION
1 2

DAN TO SON

8
1 10 .11
1 11 .09
1 12 .07
1 13 .055
1 14 .04
1 15 .035
1 16 .025
1 17 .02
1 18 .02
1 19 .02
1 20 .015
0 0 .0
1 .488
MILKPRODUCTION
1 2
0

7.2. Input data

DIRECT SIRE EFFECT

2 40 3 1 .10

20 7

1 0

1 6 .125

1 7 .375

1 10 .11

1 11 .09

1 12 .07

1 13 .055

1 14 .04

1 15 .035

1 16 .025

1 17 .02

1 18 .02

1 19 .02

1 20 .015

8 6 .10439559

8 7 .31318677

8 2 .020604408

8 3 .061813225

8 9 .125

8 10 .11

8 11 .075

8 12 .05

8 13 .04

8 14 .03

8 15 .025

8 16 .015

8 17 .01

8 18 .01

8 19 .005

8 20 .005

21 1 .025

21 2 .075

21 5 .1

21 6 .3

0 0 .0

.0 .0 .0 .0 .0 .0 .0 .0 .2496 .157 .1297 .0092 .0629 .0449 .0359 .0269 .018

.018 .009 .009 1.

SIRES TO SON

1

1 6 .125

1 7 .375

0 0 .0

2 .4879 .0

DAIRY

1 2

DIRECT SIRE EFFECT

1 3

SIRES TO DAUGHTERS

1

8 6 .10439559

8 7 .31318677

21 5 .1

21 6 .3

0 0 .0

2 .4879 .0

DAIRY

1 2

DIRECT SIRE EFFECT

1 3

DAMS TO SON

0

1 13 .5

0 0 .0

2 .4879 .0

DAIRY

1 2

DIRECT SIRE EFFECT

1 3

0

DIREKT SIRE EFFEKT ALT.2

2 40 4 1 .10

20 7

1 0

1 4 .10

1 6 .10

1 7 .30

1 10 .11

1 11 .09

1 12 .07

1 13 .055

1 14 .04

1 15 .035

1 16 .025

1 17 .02

1 18 .02

1 19 .02

1 20 .015

8 6 .10439559

8 7 .31318677

8 2 .020604408

8 3 .061013225

8 9 .125

8 10 .11

8 11 .075

8 12 .05

8 13 .04

8 14 .03

8 15 .025

8 16 .015

8 17 .01

8 18 .01

8 19 .005

8 20 .005

21 1 .025

21 2 .075

21 5 .1

21 6 .3

0 0 .0

.0 .0 .0 .0 .0 .0 .0 .0 .2496 .157 .1297 .0892 .0629 .0449 .0359 .0269 .018

.018 .009 .009 1.

SIRE TO SON FETAL EFFEKT

1

1 4 .10

0 0 .0

2 .4879 .0

DAIRY

1 2

SIRE OF FETUS FETAL EFFEKT

1 3

SIRE TO SONS PRG TEST

1

1 6 .10

1 7 .30

0 0 .0

2 .4879 .0

DAIRY

1 2

SIRE OF FETUS FETAL EFFEKT

1 3

SIRE TO DAUGHTERS

1

8 6 .10439559

8 7 .31318677

21 5 .1

21 6 .3

0 0 .0

2 .4879 .0

DAIRY

1 2

SIRE OF FETUS FETAL EFFEKT

1 3

DAUS TO SON

8

1 13 .5

0 0 .0

2 .4879 .0

DAIRY

1 2

SIRE OF FETUS FETAL EFFEKT

1 3

0

7.3. Input data

WITH NUCLEUS

3 25 4 3 .0 .1 .2

13 6

7 0

1 0

1 6 .5

1 8 .5

7 6 .5

7 8 .225

7 9 .165

7 10 .11

14 2 .2

14 6 .3

14 10 .006

14 11 .026

14 12 .019

14 13 .011

14 15 .131

14 16 .096

14 17 .08

14 18 .061

14 19 .044

14 20 .026

21 2 .2

21 6 .3

21 15 .15

21 16 .11

21 17 .09

21 18 .07

21 19 .05

21 20 .03

0 0 .0

.0 .0 .0 .0 .0 .0 .0 .06 .044 .036 .028 .02 .012 .0 .24

.176 .144 .112 .08 .048 .6

SIRE TO SONS

1

1 6 .5

0 0 .0

2 .488 -1.

DAIRY

2 2 3

BEEF

1 4

SIRE TO N-DAMS

1

7 6 .5

0 0 .0

2 .488 -1.

DAIRY

2 2 3

BEEF

1 4

SIRE TO C-DAMS

1

14 6 .3

0 0 .0

2 .488 -1.

DAIRY

2 2 3

BEEF

1 4

DAMS TO SONS *2.

1

1 6 .5

7 6 .5

14 2 .2

14 6 .3

21 2 .20

21 6 .30

0 0 .0

2 .488 -1.

DAIRY

2 2 3

BEEF

1 4

1

NO NUCLEUS

2 25 3 3 .0 .10 .20

13 6

1 0

1 6 .5

1 8 .5

7 2 .16

7 6 .34

7 8 .15

7 9 .11

7 10 .09

7 11 .07

7 12 .05

7 13 .03

14 2 .16

14 6 .34

14 8 .15

14 9 .11

14 10 .09

14 11 .07

14 12 .05

14 13 .03

0 0 .0

continued next page

.0 .0 .0 .0 .0 .0 .3 .22 .18 .14 .1 .06 .06

SIRES TO SONS

1

1 6 .5

0 0 .0

2 .488 -1.

DAIRY

1 2

BEEF

1 3

SIRES TO DAUGHTERS

1

7 6 .34

0 0 .0

2 .488 -1.

DAIRY

1 2

BEEF

1 3

DAMS TO SONS *2.

1

1 6 .5

7 2 .16

7 6 .34

0 0 .0

2 .488 -1.

DAIRY

1 2

BEEF

1 3

0

7.4. Input data

SVINPROBLEM SVERIGE

3 40 5 5 .0 .025 .05 .075 .10

10 5

5 0

1 0

1 2 .15

1 3 .15

1 4 .15

1 5 .05

1 7 .2

1 8 .150

1 9 .1

1 10 .05

6 2 .15

6 3 .15

6 4 .15

6 5 .05

6 7 .2

6 8 .15

6 9 .1

6 10 .05

11 2 .15

11 3 .15

11 4 .15

11 5 .05

11 7 .03

11 8 .02

11 9 .02

11 10 .01

11 12 .17

11 13 .13

11 14 .08

11 15 .04

16 2 .15

16 3 .15

16 4 .15

16 5 .05

16 12 .2

16 13 .15

16 14 .1

16 15 .05

0 0 .0

.0 .0 .0 .0 .0 .016 .012 .008 .004 .000 .304 .288 .192 .096 1.

TOPSIRE-TOP

1

1 2 .15

1 3 .15

1 4 .15

1 5 .05

6 2 .15

6 3 .15

6 4 .15

6 5 .05

0 0 .0

2 .0 .0

SLAUGHTER

1 4

LITTERSIZE

2 2 3

TOPSIRE-COM

1

11 2 .15

11 3 .15

11 4 .15

11 5 .05

16 2 .15

16 3 .15

16 4 .15

16 5 .05

0 0 .0

2 .0 .0

SLAUGHTER

1 4

LITTERSIZE

2 2 3

TOPDAM-TOP

6

1 7 .20

1 8 .15

1 9 .1

1 10 .05

6 7 .20

6 8 .15

6 9 .1

6 10 .05

0 0 .0

2 .0 .0

SLAUGHTER

1 4

LITTERSIZE

2 2 3

TOPDAM-COM

6

11 7 .03

11 8 .02

11 9 .02

11 10 .01

0 0 .0

2 .0 .0

SLAUGHTER

1 4

LITTERSIZE

2 2 3

COMMERCIALDAM

11

11 12 .17

11 13 .13

11 14 .08

11 15 .04

16 12 .20

16 13 .15

16 14 .1

16 15 .05

0 0 .0

2 .0 .0

SLAUGHTER

1 4

LITTERSIZE

2 2 3

0

NUCLEUS DAM SDN

4
 1 5 .05
 1 6 .15
 1 7 .15
 1 8 .10
 1 9 .05
 0 0 .0
 1 -.5

MEAT PRODUCTION

1 5

NUCLEUS DAM OFFS

4
 4 5 .15
 4 6 .15
 4 7 .10
 4 8 .05
 4 9 .05
 19 5 .024
 19 6 .024
 19 7 .014
 19 8 .008
 19 9 .008
 0 0 .0
 1 -.5

MEAT PRODUCTION

1 5

SUBNUCLEUS SIRE OFFS

10
 10 11 .14
 10 12 .21
 13 11 .14
 13 12 .21
 13 11 .14
 13 12 .21
 19 11 .116
 19 12 .174
 0 0 .0
 1 -.5

MEAT PRODUCTION

1 5

SUBNUCLEUS DS

13
 10 14 .05
 10 15 .15
 10 16 .15
 10 17 .10
 10 18 .05
 0 0 .0
 1 -.5

MEAT PRODUCTION

1 5

SUBNUCLEUS DAM OFFS

13
 13 14 .15
 13 15 .15
 13 16 .10
 13 17 .05
 13 18 .05
 19 14 .126
 19 15 .126
 19 16 .084
 19 17 .042
 19 18 .042
 0 0 .0

1 -.5

MEAT PRODUCTION

1 5

0

8. TECHNICAL NOTES

The objective of this chapter is to give some FORTRAN functions and sub-routines which might be useful in computer programmes.

8.1. Intensity of selection

Selection intensity equals $\frac{1}{p\sqrt{2\pi}} \int_x^{\infty} te^{-\frac{1}{2}t^2} dt = \frac{z}{p}$, where

p is proportion selected from a standard normal distribution, x is the truncation point and z is the absciss at that point ($z = \frac{1}{\sqrt{2\pi}} e^{-\frac{1}{2}x^2}$)

In computer programmes tables and interpolations may be used in finding i given p .

An approximation may be the formula of SMITH (1969),

$$i = .8 + .41 \ln\left(\frac{1}{p} - 1\right).$$

Far better approximations can be got by using a formula given by ABRAMOWITZ AND SEGUN (1968), to find x given p . For other purposes the formula for p given x may be useful.

As noted in chapter 2, the selection intensity z/p is biased upward if selection is from small numbers. NIEBEL and FEWSON (1976) compared three methods to adjust for this and found the adjustment by BURROWS (1972) to be useful. According to BURROWS:

$$i = i_{\infty} - \frac{(N-n)}{2n(N+1)} i_{\infty},$$

where i is the adjusted intensity of selection, $i_{\infty} = z/p$, N the number of individuals selected from and n the number of individuals selected.

Programs

1. FUNCTION XNOR (PROB), finds x, given p

```

      FUNCTION XNOR(PROB)
C X-VALUE WITH INTEGRAL X TO INFINITY IN N(0,1) IS PROB
C NEEDED FUNCTION XNORMD(PROB)
      IF(PROB.LT..5)GO TO 1
      AP=1.-PROB
      XNOR=-XNORMD(AP)
      GO TO 2
1     XNOR=XNORMD(PROB)
2     RETURN
      END
      FUNCTION XNORMD(PROB)
C X-VALUE WITH INTEGRAL X TO INFINITY IN N(0,1) IS PROB (PROB.LE..5)
C ABRAHAWITZ AND SEGUN (1968) 26.2.23
      T=SQRT(ALOG(1./(PROB*PROB)))
      XNORMD=T-(2.515517+T*(.802853+T*.010328))/(1.+T*
1     (1.432788+T*(.189269+T*.001308)))
      RETURN
      END

```

2. SUBROUTINE SINT (PROB,N,SI), finds i, given p and N

2.1.

```

      SUBROUTINE SINT(PROB,N,SI)
C SELECTION INTENSITY WITH PROPORTION SELECTED IS PROB
C SELECTION FROM N INDIVIDUALS
C IF N=0, CORRECTION FOR SMALL NUMBERS IS NEGLECTED
C CORRECTION WITH BURROWS (1972) BIOMETRICS 28, 1091
C NEEDED FUNCTION XNOR(PROB)
      IF(N.EQ.0)GO TO 1
      XN=N
      SN=PROB*XN
      CDR=(XN-SN)/(2.*SN*(XN+1))
      GO TO 2
1     CDR=0.
2     X=XNOR(PROB)
      Z=.39894228*EXP(-.5*X*X)
      SI=Z/PROB
      SI=SI-CDR/SI
      RETURN
      END

```

2.2.

```

FUNCTION SINTVI(P,N)
C
C SELECTION INTENSITY AS A FUNCTION OF P
C
C P=PROPORTION SELECTED
C N=POPULATION SIZE. IF N=0, CORRECTION FOR SMALL NUMBERS
C IS BYPASSED. CAUTION: DON'T USE N > 16382 ON 16 BIT COMPUTERS
C
C UNCORRECTED SELECTION INTENSITY IS CALCULATED TO AN ACCURACY
C FOR BETTER THAN .025% FOR VALUES OF P>.001 USING POLYNOMIAL
C APPROXIMATION. THE FOLLOWING 3RD DEGREE POLYNOME COULD BE USED
C INSTEAD OF THE 5TH DEGREE POLYNOME, IF AN ACCURACY OF BETTER
C THAN .45% FOR VALUES OF P>.005 IS SUFFICIENT
C
C SINTVI=((( (-.00337777*T+.0129558)*T+.420200)*T+.797885)*C
C
C THE 1ST DEGREE APPROXIMATION SINTVI=(.41*T+.8)*C HAS AN ACCURACY
C OF ABOUT 3% FOR VALUES OF P>.005

C 3RD AND 5TH DEGREE POLYNOMIAL COEFFICIENTS ESTIMATED BY
C V. VILVA, INSTITUTE OF ANIMAL BREEDING, AGRICULTURAL RESEARCH
C CENTRE, VANTAA, FINLAND
C
      R=1./P-1.
      T=ALOG(R)
      IF(P.LE..5)GO TO 1
      T=-T
      C=R
      GO TO 2
1     C=1.
2     SINTVI=(((( (-.0000991394*T+.00218171)*T-.0175066)*T+
* .0455729)*T+.399041)*T+.79788456)*C
C
C CORRECTION FOR SMALL NUMBERS (BURROWS (1972) BIOMETRICS 20,1091)
      IF(N.NE.0)SINTVI=SINTVI-R/(FLOAT(N+N+2)*SINTVI)
C
      RETURN
      END

```

3. FUNCTION PNOR (X), finds p, given x

```

FUNCTION PNOR(X)
C INTEGRAL X TO INFINITY IN N(0,1)
C NEEDED FUNCTION PNORMD(X)
  IF(X.LT.0.)GO TO 1
  PNOR=1.-PNORMD(X)
  GO TO 2
1  XX=-X
  PNOR=PNORMD(XX)
2  RETURN
  END
FUNCTION PNORMD(X)
C INTEGRAL MINUS INFINITY TO X IN N(0,1), (X.GE.0.)
C ABRAHAWITZ AND SEGUN (1968) 26.2.23
  T=1./(1.+2316419*X)
  Z=.39894228*EXP(-.5*X*X)
  PNORMD=1.-Z*(T*(.31938153-T*(.356563782-T*(1.781477937-T*
1  (1.821255978-T*1.330274429))))))
  RETURN
  END

```

8.2. Random digits from $N(0,1)$

For Monte Carlo simulation we need independent drawings from a standard normal distribution.

The following subroutine gives random digits, two at a time.

```

SUBROUTINE RDCHI2(U1,U2)
C DRAWINGS (U1 AND U2) FROM A BIVARIATE NORMAL DISTRIBUTION
C U1 AND U2 ARE UNCORRELATED
C METHOD BOX AND MULLER, AMS 29 (1958) 610
C VAN MONTFORT, OCTOBER 1972
  R=SQRT(-2.*ALOG(RAN(.31415)))
  U2=RAN(.31415)*6.2831853
  U1=R*COS(U2)
  U2=R*SIN(U2)
  RETURN
  END
FUNCTION RAN(A)
  IF(MERK.EQ.123456)GO TO 10
  MERK=123456
  C=536870912.
  X=A*C
10  X=43.*X
  K=X/C
  X=X-K*C+1.
  RAN=X/C
  RETURN
  END

```

This subroutine produces reproducible sets of normal deviates.

8.3. Choleski procedure

A subroutine to calculate matrix D (see chapter 2.3.) from a correlation matrix R is given below. Matrix R (dimension N) is supposed to be stored as an array with $N*(N+1)/2$ elements. If $N = 4$ as follows: 11, 12, 13, 14, 22, 23, 24, 33, 34, 44.

```

SUBROUTINE CHOL(N,R,D)
C PRODUCES A TRIANGULAR UNDER MATRIX (D) FROM A CORRELATION
C MATRIX R. R EQUALS D MULTIPLIED BY D-PRIME.
C R IS STORED AS A UPPER ARRAY. DIMENSION MATRICES N*N.
  DIMENSION R(400),D(20,20),RV(20,20)
  DO1I=1,N
  DO1J=I,N
  L=(I-1)*N-(I-1)*I/2+J
1  RV(J,I)=R(L)
  DO2I=1,N
  DO2J=1,N
2  D(I,J)=0.
  D(1,1)=1.
  DO3J=2,N
  L=J-1
  DO4I=1,L
  L1=I-1
  SOM=0.
  IF(L1.EQ.0)GO TO 4
  DO5K=1,L1
5  SOM=SOM+D(J,K)*D(I,K)
4  D(J,I)=(RV(J,I)-SOM)/D(I,I)
  SOM=0.
  DO7K=1,L
7  SOM=SOM+D(J,K)*D(J,K)
3  D(J,J)=SQRT(1.-SOM)
  RETURN
  END

```

8.4. GFLOW

The program provides computation of gene flow and discounted expressions for any population structure and associated breeding scheme. Further it provides the possibility to compute time lags between different tiers (e.g. nucleus, sub-nucleus, commercial) and between sexes.

The program is written according to the theory described by HILL (1974) and BRASCAMP (1975). In matrix notation the theory applied is as follows:

P matrix defining gene transmission and ageing

Q matrix defining ageing

R matrix defining gene transmission through one or more selected paths only

m vector with gene frequencies in defined age classes in all tier by sex subclasses originating from the initial age class

n as m, but describing the situation in the first generation

h incidence vector describing the relative frequency of expression of a certain trait by all age classes in various tiers and both sexes

E cumulative discounted expressions

r interest rate

The computational procedure is as follows:

Define an initial n vector (normally all elements are zero, except one element. This element will equal 1, representing that individuals in that age class in a certain tier and sex contain 100 % of its own genes. This is the group of individuals of which the flow of genes through the population is to be evaluated.

Now for any one year t

$$n_t = Qn_{t-1}$$

$$m_t = Rn_{t-1} + Pm_{t-1}$$

$$E_t = E_{t-1} + hm_t \cdot \left(\frac{1}{1+r}\right)^t$$

The program computes hm_t using only those parts of the vectors which refer to the expression of specific traits. See input description.

The initial m-vector is zero. So transmission of genes from the initial age group (in vector n) to the first generation is described by R: only transmission through selected paths (from n to m). After that transmission is through P.

Example

Suppose a population described by P

		donors										
		No♂			N♀			C♀			slaughter	
age class		1	2	3	1	2	3	1	2	3	1	
receptors	No♂	1	0	.5	0	0	.5	0	0	0	0	0
		2	1	0	0	0	0	0	0	0	0	0
		3	0	1	0	0	0	0	0	0	0	0
	N♀	1	0	.25	.25	0	.25	.25	0	0	0	0
		2	0	0	0	1	0	0	0	0	0	0
		3	0	0	0	0	1	0	0	0	0	0
	C♀	1	0	.25	.25	0	0	0	0	.25	.25	0
		2	0	0	0	0	0	0	1	0	0	0
		3	0	0	0	0	0	0	0	1	0	0
slaughter		0	.25	.25	0	.05	.05	0	.20	.20	0	
incidence vector (h)		0	0	0	0	.10	.10	0	.40	.40	7	

Matrix P describes a situation where breeding animals live 3 age classes, in pigs e.g. producing 2 litters = 1½ year.

Nucleus ♂ are recruited from 1 year old nucleus boars only and from 1st litters only. The .5 in case of No♂ to No♂ describes that the boars are 1 year old at birth of male replacements. The first age class refers to animals of ½ year old. So explicitly the .5 mentioned reads: males in age class 1 in 'year' t receive .5 of their genes from males which are in age class 2 in 'year' t-1. A 'year' refers to 26 weeks in case of pigs. Nucleus female replacement is recruited from boars of both age classes (No♂ are used 1 year) and from both litters of dam equally. Commercial female replacement is performed from commercial dams and nucleus boars. Slaughterpigs receive 50 % of their genes from nucleus boars, 10 % from nucleus sows and 40 % from commercial sows (the ratio nucleus to commercial is 1:4, effect of boar replacement is ignored).

The 1's represent ageing. E.g. the 1 from No♂ age class 1 to No♂ age class 2 reads: males in age class 2 in 'year' t receive 100 % of their genes

from males which are in age class 1 in 'year' $t-1$ (because they get one 'year' older).

The incidence vector (h) describes the relative expression of e.g. the trait litter size (relative to the whole sow population) and one litter results in 7 slaughter pigs.

If we wish to compute the gene flow through the population for the path N_0^{σ} to N_0^{σ} only we define matrix R containing all zeroes except the elements giving gene transmission from N_0^{σ} to N_0^{σ} .

Further the initial vector n is 1 in the first element and 0 elsewhere. The program computes gene flow and discounted expressions from birth of the nucleus boars, even though the 1 in vector n is in age class 1 ($\frac{1}{2}$ year of age).

(For evaluation of path N_4^{σ} to N_0^{σ} for example, the fourth element in vector n should be put to 1.)

The definition of vector h causes discounted expressions to be computed per litter, also for slaughter value. If the last element in vector h is put on 1 (instead of 7) the discounted expression for slaughter value is computed per slaughter pig (results are 7 times as small).

If discounted expressions are computed per litter the discounted expression per successful insemination in nucleus would be 5 times as large in this case because $1/5$ of all litters is born in nucleus.

Notes to input description on page 8.9.
For further remarks see page 8.10.

*free FORMAT normally means: separate input values by a blanc or a comma. Punch values I (integer) without decimal point and F (floating point, real) with decimal point. If more continuation cards are needed (e.g. for card type 5) the application may be computer dependent.

**A year is the equidistant time period between two subsequent age classes. Interest rates given in card type 1 refer to those years. The same for card type 9.

Input description for program GFLOW for computation of gene flow and discounted expressions (some explanation after last card)

card type	number of cards	symbol	format	meaning
1	1	JOB	col 1-20	job name
2	1	NH	free* I	number of tiers
		NY	free I	number of years** to be evaluated
		NP	free I	number of paths to be evaluated
		NR	free I	number of alternative interest rates
		RE	free F	NR alternative interest rates
3	NH	NT	free I	number of age classes within this tier
		NM	free I	number of male age classes within this tier. If only one sex is to be distinguished put NM = 0
4	number of non-zero elements in P-matrix	I	free I	row identification in P-matrix
		J	free I	column identification in P-matrix
		P	free F	value of this element in P-matrix. The ones for ageing should be excluded. The program provides them automatically. <u>End with 0 0 .0</u>
5	1	H	free F	incidence vector, with number of elements equals <u>total</u> number of age classes
<u>NP sets of cards type 6-11 (so a separate set for each path)</u>				
6	1	INAME	col 1-20	name of this path
7	1	NM1	free I	place of 1 in initial n-vector
8	number of non-zero elements in R-matrix	I	free I	row identification in R-matrix
		J	free I	column identification in R-matrix
		R	free F	value of this element in R-matrix <u>end with 0 0 .0</u>
9	1	ND	free I	number of separate sets of discounted expressions
		COR	free F	ND additional time adjustments (years)
<u>ND sets of cards type 10 and 11</u>				
10	1	JNAME	col 1-20	name of this set of discounted expressions
11	1	NSUB	free I	number of tier by sex subclasses included in this set
		LS	free I	NSUB identifications of subclasses, identified by subclass rank order
12	1	NEND	free I	value: 0 STOP 1 CONTINUE with card type 1 4 CONTINUE with card type 4

Remarks to input

1. The elements in the P-matrix give implicate generation intervals defined as the average age of parents at birth of replacements.
2. There is no need to have consistency in the elements of the incidence vector. In the example the last element may be either 7 or 1, resulting in discounted expressions per litter or per slaughtering respectively. See remark 4..
3. To evaluate a path there are sometimes several choices to card type 7 and 8. See for example chapter 7.1 to 7.3, 3 different solutions for path dam to son.
4. Card types 9-11 for the example in this chapter may read:

(9) 2 0. 0. The 2 refers to 2 sets of discounted expressions to be computed: litter size and slaughter value. The additional time adjustment is 0. in both cases. Since litters are born when females are in age class 2 or 3, there is not time adjustment. The same is true for slaughter pigs, because pigs are slaughtered at $\frac{1}{2}$ year of age: age class 1. When pigs are slaughtered at $\frac{1}{2}$ year of age, the second zero should be -.5, which is $\frac{1}{2}$ year (an age class is half a year).

(10) LITTER SIZE

(11) 2 2 3 There are 4 tier by sex subclasses: 1 = $N\sigma$, 2 = $N\phi$, 3 = $C\phi$ and 4 = slaughter pigs. To evaluate litter size, only gene frequencies in females and the female part of the incidence vector should be included in m_t^f . Therefore (11) should be 2 (number of subclasses), 2 ($N\phi$) 3 ($C\phi$). For slaughter value only slaughter pigs are of interest. So (11) should be 1 (subclass), 4 (slaughter pigs).

(10) SLAUGHTER VALUE

(11) 1 4

5. The sum of elements in rows of P should be lower or equal 1. Given a closed population the sums should equal 1. This is not longer true if gene imports are done from outside the population. Sums should equal 1, if the 'foreign' source of genes is included as additional in tier in P.

Computation of cumulative genetic gain and time lag with CFLOW

1. Cumulative genetic gain may be defined as the sum of discounted expressions in a particular age class, caused by continuous application of the same breeding program, with the interest rate put to zero. This is true because the (cumulative) discounted expressions in a certain age class in a given year may be interpreted in two ways:
 - a. The sum of discounted expressions in that age class up to that year resulting from one round of selection.
 - b. The sum of discounted expressions in that age class in that particular year resulting from repeated rounds of selection, performed several years before.

If we for example want to know the cumulative genetic gain from several repeated rounds of selection expressed in age class 1 of a certain tier by sex subclass this can be computed by:

- putting the corresponding element in the incidence vector to 1. and the other elements corresponding to that tier by sex subclass to 0.
- defining cards type 10 and 11 properly.

2. The time lag between expression of genetic gain in two selected age classes (generally the same age in two different tiers) may be defined as the difference in cumulative genetic gain in these two age classes divided by the stable annual genetic gain. (Just think of that.) This may be computed in two ways:
 - a. Apply the trick given in 1 for both age classes.
 - b. Put the corresponding element in the first age class to 1. and in the second age class to -1. (In the incidence vector.)

Stable annual genetic gain follows from the output as the equilibrium gene frequency in all age classes provided that enough years are evaluated. In some cases, depending on the definition of matrix P, stable annual genetic gain may never be reached. In that case one figure for the time lag is senseless too.

It should be added that the division by stable annual genetic gain causes the time lag to be expressed in years (i.e. the equidistant time period between two subsequent age classes). Without this division it is expressed in units of genetic superiority.

The method described here applies for computation of the time lag in

expression of genetic superiority of one pathway (or more pathways with identical selection differential). If it has to be computed for the effect of all pathways together, the program does not provide a direct answer. Cumulative genetic gains may be computed for all pathways separately, however. Multiplication of cumulative genetic gains for several pathways with respective genetic selection differentials gives the total cumulative genetic gain, as created by selection via these different paths. The difference between total cumulative genetic gain divided by the total stable annual genetic gain again gives the appropriate time lag. See for theory about time lag BICHARD (1971) and HILL (1974).

C PROGRAM GFLOW
 C
 C THIS PROGRAM PRODUCES GENEFLOW AND DISCOUNTED EXPRESSIONS
 C BY THE METHOD OF HILL (ANIM PROD 18(1974)117-139)
 C IT IS SUPPOSED TO WORK FOR ANY TYPE OF POPULATION STRUCTURE.
 C POPULATION STRUCTURE IS DEFINED BY SUBDIVISION OF THE
 C POPULATION IN 'TIERS', NUCLEUS, SUB-NUCLEUS ETC
 C AS ALL STANDARD PROGRAMS IT MAY CONTAIN ERRORS SO ALWAYS
 C CHECK OUTPUT CAREFULLY. PREPARED FOR SCANDINAVIAN POST-
 C GRADUATE COURSE IN HELSINKI. AUG 28-SEPT 8 1978, E.U. BRASCAMP,
 C RES INST FOR ANIMAL HUSBANDRY, BOX 501, ZEIST,
 C THE NETHERLANDS

C
 DIMENSION JOB(10),COR(5)
 DIMENSION NT(5),NM(5),NS(5,2),NE(5,2),O(40,40),P(40,40)
 DIMENSION R(40,40),RE(10),KS(10),KE(10),H(40),INAME(10)
 DIMENSION JNAME(10,10),XM(40),XMFIX(40),LS(5,10)
 DIMENSION IM(40),SDE(5,5)
 DIMENSION LSUB(5)
 40 READ(5,103)JOB
 WRITE(8,205)JOB
 205 FORMAT(1H1,'JOBNAME: ',10A2,/1H ,/1H)
 WRITE(9,205)JOB
 READ(5,*)NH,NJ,NP,NR,(RE(I),I=1,NR)
 DO11I=1,NH
 READ(5,*)NT(I),NM(I)
 IF(1.EQ.1)GO TO 2
 J=I-1
 NS(I,1)=NE(J,2)+1
 GO TO 3
 2 NS(I,1)=1
 3 NS(I,2)=NS(I,1)+NM(I)
 NE(I,1)=NS(I,2)-1
 NE(I,2)=NS(I,1)+NT(I)-1
 1 CONTINUE
 WRITE(8,300)NH
 WRITE(8,301)
 DO302I=1,NH
 302 WRITE(8,303)I,NT(I),NM(I)
 300 FORMAT(1H ,20X,'NO OF TIERS = ',I2)
 301 FORMAT(1H ,14X,'TIER AGECLASSES MALE AGECLASSES')
 303 FORMAT(1H ,15X,I2,7X,I2,12X,I2)
 J=0
 DO17I=1,NH
 J=J+1
 IF(NM(I).EQ.0)GO TO 18
 KS(J)=NS(I,1)
 KE(J)=NE(I,1)
 J=J+1
 18 KS(J)=NS(I,2)
 KE(J)=NE(I,2)
 17 CONTINUE

```

C PRODUCE Q-MATRIX
  NDIM=NE(NH,2)
  WRITE(8,304)NDIM
304  FORMAT(1H ,21X,'TOTAL NUMBER OF AGE CLASSES = ',I2/1H /1H )
  DO 60I=1,NDIM
  DO 60J=1,NDIM
60   D(I,J)=0.
      DO5I=2,NDIM
      J=I-1
      Q(I,J)=1.
      DO6K=1,NH
      DO6L=1, 2
      IF(I.EQ.NS(K,L))GO TO 7
6    CONTINUE
      GO TO 5
7    Q(I,J)=0.
5    CONTINUE
C DEFINE P-MATRIX.
C READ NON-ZERO ELEMENTS ONLY, IDENTIFIED BY ROW AND COLUMN NUMBER
C DO NOT READ THE 1'S FOR AGEING
C END WITH A ZERO CARD
50   CONTINUE
      DO 51 I=1,NDIM
      DO 51 J=1,NDIM
51   P(I,J)=0.
9    READ(5,*)I,J,PP
      IF(I-1)0,90,90
90   P(I,J)=PP
      GO TO 9
8    CONTINUE
      DO11I=1,NDIM
      DO11J=1,NDIM
11   P(I,J)=P(I,J)+Q(I,J)
      DO310I=1,NDIM
      PP=0.00000000
      DO311J=1,NDIM
311  PP=PP+P(I,J)
      IPP=PP*10**8-1
      IF(IPP.GT.10**8)GO TO 999
310  CONTINUE
C DEFINE INCIDENCE-VECTOR (NDIM ELEMENTS)
  READ(5,*)(H(I),I=1,NDIM)
  WRITE(8,206)
206  FORMAT(1H , 'P-MATRIX',/1H )
      DO27I=1,NDIM
27   WRITE(8,200)(P(I,J),J=1,NDIM)
200  FORMAT(1H ,21(F5.3,1X))
      WRITE(8,201)
201  FORMAT(1H0,/1H /1H )
      WRITE(8,207)
207  FORMAT(1H , 'INCIDENCE VECTOR')
      WRITE(8,200)(H(I),I=1,NDIM)
      WRITE(8,201)
      DO12JJ=1,NP
      READ(5,103)(IAME(I),I=1,10)
103  FORMAT(10A2)

```



```

C DEFINE INITIAL N-VECTOR AND R-MATRIX PER PATHWAY
C INPUT R-MATRIX AS P-MATRIX
  READ(5,*)NM1
  DO13I=1,NDIM
  XM(I)=0.
13  XMFIX(I)=0.
  XM(NM1)=1.
  XMFIX(NM1)=1.
  DO14I=1,NDIM
  DO14J=1,NDIM
14  R(I,J)=0.
10  READ(5,*)I,J,RR
  IF(I-1)15,91,91
91  R(I,J)=RR
  GO TO 10
15  CONTINUE
  WRITE(8,200)INAME
200  FORMAT(1H , 'R-MATRIX',4X,10A2,/1H )
  DO28I=1,NDIM
28  WRITE(8,200)(R(I,J),J=1,NDIM)
  WRITE(8,201)
C DEFINE FOR DISCOUNTED EXPR WHICH TIER AND SEX FREQ ARE TO BE INCLUDED
  READ(5,*)ND,(COR(I),I=1,ND)
  DO20I=1,NR
  DO20J=1,ND
20  SDE(I,J)=0.
  DO16I=1,ND
  READ(5,103)(JNAME(I,J),J=1,10)
  READ(5,*)NSUB,(LS(I,J),J=1,NSUB)
16  LSUB(I)=NSUB
  II=0
  WRITE(8,209)INAME
209  FORMAT(1H , 'GENE FREQUENCIES, ORIGINATING FROM',4X,10A2/1H )
  WRITE(9,210)INAME
210  FORMAT(1H , 'DISCOUNTED EXPRESSIONS, ORIGINATING FROM',4X,
* 10A2/1H )
  WRITE(9,305)ND
305  FORMAT(1H , 'THERE ARE ',I2,' SETS OF DISCOUNTED EXPRESSIONS',
* ' , IDENTIFIED AS : ')
  DO306I=1,ND
306  WRITE(9,307)I,(JNAME(I,J),J=1,10),COR(I)
307  FORMAT(1H , 2X,I2,2X,10A2, ' TIME ADJ.= ',F7.3)
  WRITE(9,308)NR,(RE(I),I=1,NR)
308  FORMAT(1H , 'WITHIN THESE THERE ARE ',I2,' INTEREST RATES : ',
* 10(F4.2,1X)/1H )
  WRITE(9,201)
  DO19KJ=2,NJ
  CALL PATHSE(P,0,R,XM,XMFIX,DH,NDIM,II)
  II=II+1

```

```

C WRITE FREQUENCIES
WRITE(8,204)KJ,(DM(I),I=1,NDIM)
204  FORMAT(1H ,I2,1X,25(F4.3,1X))
      DO21KD=1,ND
      DO21KR=1,NR
      REN=(1./(1.+RE(KR)))**KJ
      X=COR(KD)
      REN1=(1./(1.+RE(KR)))**X
      REN=REN*REN1
      NSUB=LSUB(KD)
      DO21KSUB=1,NSUB
      I=LS(KD,KSUB)
      K=KS(I)
      L=KE(I)
      DO21J=K,L
21    SDE(KR,KD)=SDE(KR,KD)+H(J)*DM(J)*REN
C WRITE STANDARD DISCOUNTED EXPRESSIONS
WRITE(9,214)KJ,((SDE(I,J),I=1,NR),J=1,ND)
214  FORMAT(1H ,I2,18(F7.3))
19   CONTINUE
      WRITE(8,201)
      WRITE(9,201)
12   CONTINUE
      WRITE(8,201)
      WRITE(9,201)
      READ(5,*)NEND
      IF(NEND-1)30,40,50
999  WRITE(8,313)I
      DO314I=1,NDIM
314  WRITE(8,200)(P(I,K),K=1,NDIM)
313  FORMAT(1H ,ROW ',I2,' IN MATRIX P GIVES A SUM LARGER THAN 1.',
*    ' THERE MAY BE MORE ERRORS!' /1H )
30   CONTINUE
      END
      SUBROUTINE PATHSE(P,Q,R,XM,XMFI,DM,NDIM,II)
      DIMENSION P(40,40),R(40,40),Q(40,40),XM(40),XMFI(40),DM(40),B(40)
      IF(II.GT.0) GOTO 1
      DO 2I=1,NDIM
      DM(I)=0.
      DO 2 J=1,NDIM
2    DM(I)=DM(I)+R(I,J)*XMFI(J)
      GOTO 100
1    CONTINUE
      DO3I=1,NDIM
      B(I)=0.
      DO3J=1,NDIM
3    B(I)=B(I)+Q(I,J)*XMFI(J)
      DO5I=1,NDIM
5    XMFI(I)=B(I)
      DO4I=1,NDIM
      DM(I)=0.
      DO4J=1,NDIM
4    DM(I)=DM(I)+R(I,J)*B(J)+P(I,J)*XM(J)
100  CONTINUE
      DO6I=1,NDIM
6    XM(I)=DM(I)
      RETURN
      END

```

9. LITERATURE

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10. APPENDIX. Reprint of BRASCAMP (1975) (partly)

2 Summaries of papers

2.1 Paper I: The economic value of genetic improvement in milk yield

The approach to calculate the economic value in milk yield is illustrated in Fig. 1. The closed circles in Fig. 1 represent batches of offspring from groups of parents for four generations. For each batch the number of (female) offspring entering the dairy herd can be calculated. By inclusion of the genetic relationship between selected parents and animals in a batch, the total genetic superiority of parents expressed by the units of this superiority are for instance, kg (of milk) or money units. To obtain the economic value of the total genetic superiority expressed in a batch of offspring, the monetary value is discounted to a reference year. The birth of young bulls (Parents YB in Fig. 1) is taken as reference year (Year 0). Summing the discounted value of genetic superiority for all batches results in the economic value of genetic improvement for all four generations.

Another approach (Lindhé, 1968; Lindström, 1971) to estimate the economic value

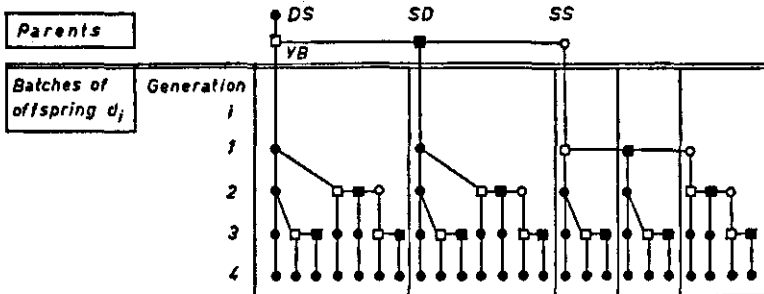


Fig. 1. The parents and the batches of offspring (d_i) when four generations of offspring are taken into consideration.

DS = dams to breed son; YB = young bulls of generation zero; SD = sire to breed daughter; SS = sire to breed son; ● = batch of offspring; □ = young bulls; ■ = proven bulls to breed daughter; ○ = sires to breed son.

of genetic improvement is based on the value of the annual genetic improvement (ΔG) estimated with the formula of Rendel & Robertson (1950). The economic value of genetic improvement is then estimated as a linear function of ΔG .

For comparison of both approaches a discount factor was introduced for the time lag between Year 0 and the expression of genetic improvement in females in the population. This discount factor was calculated as the ratio between the estimate of the economic value of genetic improvement over four generations and the estimate made with the linear function of ΔG .

Conclusions can be summarized as follows: the relative contribution of Path SS (sire to breed son) to the monetary returns is lower than to ΔG . For Paths SD (proven bulls) and DD (dam to breed daughter) the opposite is true. The relative contribution of Path DS (dam to breed sire) to both returns and ΔG is about equal.

The discount factor for the time lag is not a constant. Most important is the increase of the discount factor with increasing numbers of doses of sperm per bull. The discount factor based upon 10% interest rate ranges from 0.28 - 0.30 for 3000 doses per bull up to 0.35 - 0.40 for 80000 doses per bull.

Further the effect of the decrease of the population size has been studied, assuming a decrease during about 25 years with a constant rate q per year. The value of genetic improvement decreases roughly to $(1-q)^{16}$ times the value of genetic improvement when the population size is constant.

3 Comparison of generation approach and year approach

In Papers I and III discounted expressions per cow have been calculated for four generations. With these discounted expressions returns from breeding schemes have been calculated in Papers II and III. In this chapter discounted expressions per cow are calculated for a certain number of years, instead of for a number of generations. These calculations are done with the method described by Hill (1974). In Section 3.1 that part of Hill's approach needed to calculate discounted expressions per cow is explained. This approach is illustrated with an example. Further some extensions are described. The notation of Hill (1974) is followed.

In Section 3.2 the methodology of calculating discounted expressions based upon generations is compared with the approach based upon years for the example situation. Discounted expressions as given in Papers I and III (four-generations approach) are compared with discounted expressions based upon years. Assumptions used in these calculations are consistent with those in Papers I and III and are given in appendices. Implications for the conclusions of the papers will be discussed.

3.1 Year approach: methods

The crucial question in Hill's approach is: which part of the genes (genetic superiority) of a certain group of animals (selected parents) is expressed in animals in subsequent years. Let us consider this in a simple unrealistic example, in which bulls produce female offspring when they are 2 years of age (untested young bulls, YB) and when they are 4 years old (proven bulls, SD). Bulls (SS) produce male offspring (young bulls) when they are 4 years of age. Females (DS and DD) survive up to 3 years of age and produce an equal number of offspring at 2 and 3 years old.

The genetic makeup of sexes and age classes starting from bulls of Age 1 in Year 0 is given in Table 2 for this example. In Year 0 only bulls of Age 1 contain 100% of their own genes. In Year 1 these bulls are one year older, so Age class 2 contains 100% of the genes of bulls of Age class 1 in Year 0. In Year 1 the bulls reach reproductive age. So in Year 2 the females of Age class 1 contain 10% of the genes of the bulls considered, as young bulls perform 20% of the inseminations and transmit 50% of their genes to an offspring. In Year 2 bulls of Age class 3 and females of Age class 1 contain genes of bulls considered but they are not of reproductive age. So from Year 2 to Year 3 the animals only grow one year older and have no offspring.

In Year 4, bulls of Age class 1 contain 50% of the genes of bulls considered transmitted by the bull fathers of Year 3. Further they contain $\frac{1}{2} \times 0.5 \times 10\% = 2.5\%$ of genes from cows of Age class 2. The remaining $\frac{1}{2}$ they get from cows of Age class 3, but the latter contain no genes of bulls considered. Females of Age class 1 contain 40% of genes transmitted by proven bulls and 2.5% transmitted by cows of Age class 3 ($\frac{1}{2} \times 0.8 \times 1 + \frac{1}{2} \times 0.5 \times 0.10 = 0.425$).

This process of ageing and reproduction can be formalized as follows. Define a Matrix **P** as

$$P = \begin{bmatrix} 0 & 0 & 0 & 0.5 & 0 & 0.25 & 0.25 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0.1 & 0 & 0.4 & 0 & 0.25 & 0.25 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix}$$

The blocks in **P** correspond to paths of gene transmission

$$\begin{bmatrix} \text{sire to breed} & & \text{dam to breed} \\ \text{son (SS)} & & \text{son (DS)} \\ & & \\ \text{sire to breed} & & \text{dam to breed} \\ \text{daughter} & & \text{daughter} \\ \text{(YB and SD)} & & \text{(DD)} \end{bmatrix}$$

The Matrix **P** describes reproduction and ageing for the example in Table 2. The actual makeup of **P** is given in Appendix 1.

Ageing alone can be described by a Matrix **Q**:

$$Q = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix}$$

Table 2. Genetic makeup of sexes and age classes in an example situation.

Year	Age class								Explanation
	males				females				
	1	2	3	4	1	2	3	3	
0	1	0	0	0	0	0	0	0	
1	0	1	0	0	0	0	0	0	
2	0	0	1	0	0.10	0	0	0	
3	0	0	0	1	0	0.10	0	0	
4	0.525	0	0	0	0.425	0	0.10	0	$(0.10 = \frac{1}{2} \times 0.2 \times 1)$
5	0.025	0.525	0	0	0.025	0.425	0	0	$(0.525 = \frac{1}{2} \times 1 \times 1 + \frac{1}{2} \times 0.5 \times 0.10)$ $(0.425 = \frac{1}{2} \times 0.8 \times 1 + \frac{1}{2} \times 0.5 \times 0.10)$
6	0.10625	0.025	0.525	0	0.15875	0.025	0.425	0	$(0.025 = \frac{1}{2} \times 0.5 \times 0.10)$ $(0.10625 = \frac{1}{2} \times 0.5 \times 0.425)$
7	0.1125	0.10625	0.025	0.525	0.115	0.15875	0.025	0	$(0.15875 = \frac{1}{2} \times 0.2 \times 0.525 + \frac{1}{2} \times 0.5 \times 0.425)$ $(0.1125 = \frac{1}{2} \times 0.5 \times 0.025 + \frac{1}{2} \times 0.5 \times 0.425)$ $(0.115 = \frac{1}{2} \times 0.2 \times 0.025 + \frac{1}{2} \times 0.5 \times 0.025 + \frac{1}{2} \times 0.5 \times 0.425)$

A column vector $m(t)$ describes the genetic makeup of sexes and age classes in Year t , starting from the situation in Year 0, $m(0)$. So

$$\begin{aligned} m'(0) &= (1 \ 0 \ 0 \ 0 \mid 0 \ 0 \ 0) \text{ and} \\ m'(5) &= (0.025 \ 0.525 \ 0 \ 0 \mid 0.025 \ 0.425 \ 0) \end{aligned}$$

Now

$$m(t) = P m(t-1) = P^t m(0) \quad (\text{Hill, 1974}) \quad (1)$$

The genetic makeup of sexes and age classes by reproduction alone is given by

$$m(t) = (P^t - Q^t) m(0) \quad (\text{Hill, 1974}) \quad (2)$$

Milk traits Returning to the example, let us consider what the previous reasoning means in terms of genetic improvement of milk traits. Suppose that the genetic superiority of young bulls (by selection of bull dams, see Fig. 1), is 1 kg of milk. Then the first returns are attained in Year 3 when the average superiority of cows in Age class 2 is 0.10 kg of milk. Per cow in Year 3 this is 0.05 kg because only half of the lactating cows in a year are of Age 2.

The discounted expression per cow (δ_3) in Year 3 can be calculated as $0.05 \times \left(\frac{1}{1+r}\right)^3$.

Here r stands for the interest rate and discounting is done to the value in Year 0. (The actual monetary value of 1 kg = 1). This can be formalized as

$$\delta_t = m'(t) h \left(\frac{1}{1+r}\right)^t \quad (3)$$

In the example $h' = (0 \ 0 \ 0 \ 0 \mid 0 \ 0.5 \ 0.5)$, the proportion of lactating cows in different age classes. In reality, however, the proportion of lactating cows in different age classes will not be equal. Furthermore, the average level and standard deviation of production in different lactations will not be equal. These effects should be included in h . The vector of fractions of lactating cows in different age classes will be noted here as g . For the actual assumptions of g and h see Appendix 2. Now the (cumulative) discounted expression per cow up to Year t is obtained by adding all δ_i from Year $i = 0$ to $i = t$.

To be in line with Paper I and Paper III cumulative discounted expressions per cow will be calculated for each path separately. In the example, the female offspring of Path SS will first lactate in Year 7 (Table 2) containing a fraction $\frac{1}{2} \times 0.2 \times 0.5 = 0.05$ of the genetic superiority of SS. For Path SD the first lactation occurs in Year 5, cows of Age class 2 containing $\frac{1}{2} \times 0.8 \times 1 = 0.4$ of the SD genetic superiority. This splitting of selection response by paths can be formalized by

$$n(t) = Q^t n(0) \quad (4)$$

$$m_j(t) = R_j n(t-1) + P m_j(t-1) \quad (5)$$

$n(0) = m(0)$, and $m_j(t)$ represents the genetic makeup of sexes and age classes in Year t for Path j . The vector $m_j(0)$ contains zeroes only. So for an isolated Year t

$$\delta_{jt} = m_j'(t) h \left(\frac{1}{1+r}\right)^t \quad (6)$$

where δ_{jt} is the discounted expression per cow for Path j in an isolated Year t .

In the example the R_j matrices for Path YB and SD are

$$R_{YB} = \begin{bmatrix} 0 & 0 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.1 & 0 & 0.4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$R_{SD} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

R_{SS} contains only the SS reproduction part of matrix P .

For the Paths SS, SD and YB the $n(0)$ vector equals $n'(0) = (1 \ 0 \ 0 \ 0 \ | \ 0 \ 0 \ 0)$ in the example; or generally, $n(0)$ contains all zeroes except males in Age class 1.

Equation (4) gives only ageing of the initial bulls. Note that $Q^t n(0) = 0$ when $t \geq (\text{number of male age classes})$ (Hill, 1974). The part $R_1 n(t-1)$ of Eqn 5 gives the genetic makeup of the offspring of the first generation, only via the path considered. The part $P m_1(t-1)$ gives reproduction of this first generation offspring and of later generations. This structure of separating reproduction by paths is seen also in Fig. 1.

The discounted expressions per cow for Path DS equal half those of Path YB, as follows from the position of DS in Fig. 1.