Armidale Animal Breeding Summer Course 2006

Optimal Designs of Breeding Programs

Lecture Notes

prepared by

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1. Prediction of Multiple Trait Selection

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1.1 Introduction

To optimise the design of breeding programs a full understanding of selection index theory to predict the outcome of performance recording, genetic evaluation and subsequent selection is required. The selection index theory has first been described for livestock breeders by L.N. Hazel (1943) a scientist from Iowa State University. Not much has changed, the formula for selection indices Hazel developed some 60 years ago are still valid, although C.R. Henderson (1973) has shown that his mixed model equations (BLUP) are in fact Hazel's selection index, but make the calculation of selection indices computationally much easier.

1.2 Selection Index

The problem Hazel addressed is how to combine in an optimal way information on different individuals (relatives) **y** into a single number (index) **I** on which selection can be based. Hazel chose a linear approach.

$$\mathbf{I=b' (y-\bar{y})} \tag{1}$$

Where b' is a column vector of weightings which need to be calculated and y a row vector of observations. Note in this very general form the vector **y** can include single observations on one trait from different animals, or single observations for different traits on one or more animals, as well as group means, eg mean of all progeny.

The solution for **b'** come from the following equation which is also referred to as normal equation.

$$\mathbf{Pb = Gv,}$$

$$\mathbf{b = P^{-1}Gv}$$

Where **P** is a matrix of size n (n = number of different observations) of Covariances between the observations **y**, **G** is a genetic covariance (scalar, vector or matrix) between **y** and **I** of size n*m, where m is the number of traits considered in the index and **v** is m*1 vector of economic weights.

In its simplest form a single information on the candidate for selection $\mathbf{b = h^2v}$, and if **v** =1 the index is the EBV in the units the trait was recorded.

In the past animals breeders developed rather lengthy tables from which to extract the different values of b for various number of relatives for different species, e.g. in pigs where the data from full sibs (litter mates) and half sibs had to be combined with data

from progeny. When calculating the variance matrix **P** one had to consider if the candidate own performance was included in the litter mean or not as this affected the covariances. Such calculations are today there to test students ability to understand how to calculate variances and covariances of different types of observations.

Henderson's development of the mixed model equations (MME) particularly with the animal model and subsequent proof that they are identical to the index equations have made index calculations relatively easy. Once the MME are solved and the EBVs for all animals and all traits are available, they only need to be multiplied for each animals with the vector of economic weight **v** to get the index. The only difference between the two approaches is: In the mixed model equations ȳ is replaced by ß̂ the Best Linear Unbiased Estimate (BLUE) of **ß** the fixed management group effect from the mixed model equations.

1.3 Variance of Index and accuracy

The Index **I = b' (y-ȳ)** is a linear combination of y, therefore the variance of this linear combination is

$$\textbf{Var (I) = b' var(y) b = b'Pb}$$

From this the accuracy of the selection index r^2 can be calculated as

$$\textbf{r}^2 = \textbf{Var(I) / Var (T)}$$

Where **T** is the true breeding value which has a variance

$$\textbf{Var (T) = v'G}_\textbf{m}\textbf{v}$$

with $\textbf{G}_\textbf{m}$ being the genetic covariance matrix of the m traits in the breeding objective.

1.4 Prediction of response to selection

Selection response per generation or in other words the genetic superiority of selected animals versus unselected is described by the well known equation from Rendel and Robertson (1950)

$$\textbf{?G = i * r * s}_\textbf{T}$$

Where i= standardized selection differential, r = correlation between true (T) and estimated index (I) and s_T = standard deviation of true breeding values $(Var(T))^{1/2}$.

So the prediction of selection response for an Index is derived in the same manner as for a single trait. Often we are not only interested in the selection response for the aggregate breeding value, the index but in the expected changes in individual traits. This is calculated from the regression of an individual trait on the index

$$\mathbf{reg}_{(t;I)} = \mathbf{b'G_t} / \mathbf{Var(I)}$$

Where $\mathbf{reg_{(t;I)}}$ is the estimated regression coefficient of trait t on I, and $\mathbf{G_t}$ is a the column vector of matrix $\mathbf{G}$ related to trait t. The regression coefficient $\text{reg}_{(t;I)}$ gives us the units of increase in trait t for one unit increase in the index value.

To get a feel for where we are going in our selection we commonly use a standardized selection differential $\mathbf{i}$ of 1 which is equivalent to selecting about the best 38% of animals.

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2. Definition of the Breeding Objective

Adopted from D. Fewson

2.1 Comments on the development and definition of breeding objectives

The starting point of a systematic selection program is a reliable definition of the breeding objective. A false definition of breeding objectives has negative consequences for animal production and, in extreme cases, there will be no benefit from breeding at all.

During the 19th century the breeding goal consisted mainly of a detailed description of the desired form and performance characteristics. After introducing performance testing, certain targets of performance were included in setting the breeding goals, e.g. a cow with 5000 kg milk. A general description of a breeding objective and the definition of targets does not answer important questions, including how to classify animals that do much better than the defined performance goal, how to weigh the deviations in different performance traits and how to combine these deviations to make a general assessment?

The introduction of the selection index (Hazel, 1943) has stimulated discussions about definition of the breeding objective. For this the performance traits to be improved have to be defined and the weights relevant to these traits have to be calculated. The methods of defining the breeding objective have been discussed only during the last two decades. Some basic papers should be mentioned: Brascamp et al., 1985; Dickerson, 1970; Harris et al., 1984; James, 1982, 1983, 1986; Smith, 1983. These papers discuss extensively how the returns (R) and the costs (C) have to be considered in setting the breeding goal, and whether they are best considered as profit (R-C) or as a quotient (R/C or C/R).

2.2 Economic or biological approach

For a breeding organisation the value of improving a trait depends eventually on the effects of this improvement on the income and costs from sales of breeding products. The chances of selling breeding products depend on the position of the organisation in a competitive market. The amount of breeding products, which can be sold, may be more dependent on inferior traits than on superior traits compared with competitors. Therefore, for a breeding organisation the economic importance of a trait tends to decrease with its superiority against competitors and vice versa. In the long term, however, the breeding objective should ensure that the profitability on the commercial level is improved as far as possible as this is actually the level where the breeding products are purchased.

An economic approach to defining the breeding objective starts with the returns and the costs of animal production and uses these parameters to define the economic importance of single traits. The marginal outputs and the marginal inputs associated with change in each trait have to be determined and then economically valued. Different production conditions and varying price/cost relationships have an impact on returns and costs. This leads to an inconsistency of the economic importance of the performance traits, which is disadvantageous for the breeding program. Furthermore, future production conditions

have to be considered when defining breeding goals. This increases the uncertainty of any definition of breeding objectives. This is especially true in countries with a strong or even dominating influence of the government on the economy.

Fowler et al. (1976) suggest for pigs a biological approach for defining a breeding goal based on the composite trait lean tissue feed conversion. Such an attempt has the advantage of being independent of changes in the production requirements as well as of changes in prices and costs. A suggestion of Bakels (1987) to use total lifetime milk production as a breeding goal, is also a biological approach of defining a breeding objective. This is independent of production conditions and of prices and costs, and indirect traits such as longevity, fertility and calving ease are then automatically included in the breeding objective.

The biological approaches combine the advantages of having a long term stability with the disadvantage of often not considering other important aspects such as meat quality, labour costs and housing requirements. Open questions also arise when several traits have to be improved simultaneously. Examples are milk and meat in dual purpose cattle and meat, wool and in some cases also milk in sheep.

Thus economic models for defining breeding goals seem to be worthwhile, and one should carefully consider the biological consequences of selecting for them. In this context, the impacts on traits such as longevity and fertility have to be taken into account. Such traits should be directly included in the breeding objective.

Some mention should be made of derailments which have occurred due to a one-sided definition of breeding objectives. As an example I would like to point out the Pietrain pig breed in Germany. This breed was selected for extremely high lean meat content. This resulted in a substantial reduction of the metabolic stability. At one stage 20 percent of young boars are not able to mate and fertilise, however the problem has now been addressed. Breeding herds of the Belgian Blue, another example of an extreme meat breed, have a high proportion of homozygote double muscled animals. Caesarean for calving is normal practise in many herds. From the viewpoint of animal welfare these developments have to be considered as derailments though perhaps not all breeders would agree. Due to our ethical responsibility there are consequently some restrictions on extreme selection. I can't offer a recipe, but with a multi-trait definition of the breeding objective considering also indirect traits, the danger of wrong developments is certainly decreased. Another option is to set restrictions in order to prevent the decline of traits such as fertility and longevity when there are antagonistic relationships.

Restrictions might also become necessary when a reliable assessment of future prices and costs is not possible. In comparison to a straight economic definition of breeding goals, any restriction implicates losses in genetic gain. With large deviations from the real economical conditions, these restrictions might cause a substantial decrease in breeding efficiency.

2.3   Calculation level

Generally, a selection response achieved at the breeding level should lead to some improvement of animal production. As with any technical advance, it is transmitted to the level of consumers and there it causes either a decrease in costs or an improvement of

quality. It is to decide, at which level of the pyramid the benefits of breeding measures can be used for calculating the economic value of traits in the breeding objective.

Many factors determine the demand for and the price of breeding products (semen, embryo, live animal). At the time of buying a breeding product, the client is generally not in the position to assess the benefit from a genetic improvement. Therefore there is some doubt that success in selling breeding products is a basis to draw conclusions for the economic weights of traits (eg Phenotype, showring versus Genotype). This is so, even though the breeder is obviously interested in maximising his income from sales.

The effects of genetic improvement on the sale of final animal products, however, and on the efficiency to produce them, seem to be more important and can be analysed in detail. As the commercial producers are purchasers of breeding products, a breeding objective directed towards increasing the efficiency of commercial production should ultimately also have favorable effects on the sale of breeding products.

Any genetic improvement results eventually in a reduction of consumer prices for products of a given quality or in an increase in product quality. But the relationships of these criteria with the traits to be improved are not high enough to take these as a basis to calculate economic weights.

Therefore it seems reasonable to define breeding objectives for the efficiency of commercial production. But one should also take care of improvement of product quality, which presently might be ignored but which is expected to have an effect on future prices.

2.4   Time aspects

Any present selection affects commercial production after a time lag. This is mainly true for selection of males and females for planned matings intended to get males for the next generation. Only offspring of the second generation contribute to an improvement of the efficiency on the commercial level. When one expects to benefit from genetic progress at least for two generations, the breeding objective should refer to prices, costs and environmental conditions in 2-4 generations. This may not cause problems in species with a short generation interval. In cattle, however, having a generation interval of about 5 years, the conditions of production after 10-20 years are hard to predict. This is mainly true for countries with a restricted free market. Any breeding objective may then involve some speculation. Here it seems worth mentioning that the geneticist or breeder trying to define breeding objectives needs cooperation with competent specialists in economics and marketing.

The time horizon on the commercial level is much shorter. The commercial producer buys breeding products with which he can immediately get a high profit under the present production/marketing conditions. Thus there is obviously some conflict between the long term objectives needed at the breeding level and the short term requirements of the commercial level.

The quota regulation for the European milk market was first determined for milk yield only. The price per kg milk, however, was also dependent on fat content. Thus the commercial producers and also breeders demanded a higher weighting on fat content in

the breeding objective. Then the regulations were extended to fat yield also, and in some countries the producers asked for more weighting on protein yield. Due to the expanded recording of protein content the regulations are expected to be extended to protein yield as well. The breeding objective should be defined free from these short term changes of conditions.

Another example in Germany the price for pig carcasses was mainly determined by the lean meat percentage. Quality criteria have almost no effect. An extreme selection for increased meat percentage had a detrimental effect on meat quality. More weighting for meat quality, however, would reduce the gain in meat percentage and this was rejected by most producers in the pig industry. To compete in the market, breeders were forced to supply breeding animals with extremely high meat percentage. Some breeding organisations simultaneously developed special lines with good meat quality but reduced meat percentage. The market for these breeding products was initially very small. However for some years now there has been an increasing demand for pig meat with improved quality. A special market for "lean meat programs" is developing. This is another example showing that long term breeding objectives are advantageous.

2.5   Traits for the breeding objective

All criteria with a major impact on the **efficiency of commercial production** should be reflected in the traits chosen for the breeding objective. This statement is open to different interpretations as the term "major impact" is ambiguous. It should first be noted that in addition to the primary performance traits such as growth rate, feed conversion and feed intake, lean meat percentage and fleece weight, there are also secondary (or indirect) traits such as longevity, fertility and calving ease which should be considered as traits having a major impact on efficiency. Furthermore, criteria of product quality are also related to economic efficiency. This holds, for example, for traits like fibre diameter, meat quality and milk protein content. This can also be true for traits like milkability or disease resistance.

The major impact of a trait on the efficiency of commercial production should be able to be validated. It is obvious that with increasing knowledge new criteria may be found to be involved in future breeding objectives. The term major implies also that a limitation should be set to the number of traits involved in the breeding objective. A number of 10 to 15 traits may usually be enough to describe the whole performance of a population or of a breeding product.

Let me again emphasise the point that only economic aspects are valid for the choice of traits in the breeding objective. The genetic parameters are considered later when the breeding values are estimated. It does not matter whether the traits chosen can be measured or whether auxiliary traits will be utilised to predict them. Even if no predictive traits are available the traits will be important for selection whenever there are genetic correlations to other traits. This can also prevent the occurrence of unwanted detrimental effects due to genetic antagonisms.

2.6   Discounting

As costs and returns can occur at different times for different traits there is a reason for discounting. The gene flow method presented in this course, can be used to discount

components of return. The number of discounted expressions indicates the time and the frequency of trait expression. However, the improvement of accuracy through this rather sophisticated approach is limited when calculation is related to reasonable units of production. Such a unit may be for example a cow with all her offspring. In pigs the calculations may refer to a slaughter animal or to a whole litter. Then discounting can be neglected as it does not change the relative values of the traits significantly, and relative rather than absolute values are required for defining the breeding objective.

In a crossbreeding system with specialised sire and dam lines the realisation of production and reproduction traits differs very much between populations. Again, the gene flow method provides suitable estimates of the number of discounted expressions for each line as it considers properly the gene flow in purebred as well as in crossbred groups for both production and reproduction traits. For species with a low reproductive performance the advantage of the gene flow method should be exploited. In pigs and poultry the following rough weighting may be sufficient:

Sire line: Production performance only
Dam line: All of reproduction and half for production traits

2.7   Different environments

In different production environments the economic value of traits should be calculated accordingly. In extremely unfavourable environments animals with completely different performances are required. Conventional traits such as growth rate, meat proportion and twinning rate lose their dominating role. Other traits such as resistance against cold, drought and poor feed quality become more important. Animal production under these conditions may be best done with adapted breeds. Adapted hill breeds available for harsh conditions in many countries show us how adaptable our livestock can become through selection. Under these conditions natural selection is of major importance and this should be supported by relevant breeding objectives.

Better use of unfavourable environments can be made by regional cooperation. The "stratification" system developed in the British sheep industry is a good example. As in case of specialised sire and dam lines, different breeding objectives have to be defined for the breeds according to their role in the stratification. The beef industry in northern Australia is developing its own form of specialization separating reproduction properties from production (back grounding, finishing, feedlots) properties.

2.8   General definition of the breeding objective

After having dealt with a number of single aspects of defining a breeding objective, a general definition should now follow:

Develop vital animals which will ensure that profit is as high as possible under future commercial conditions of production

Such a general definition of the breeding objective contains all the important aspects to be considered when defining the breeding objective for a particular breed:

1.   An economic definition of the breeding objective

2. The vitality of the animals is taken into account
3. Production on the commercial level is considered
4. Future conditions are considered.

This general definition has now to be translated into a concrete breeding objective for the population considered. It is performed in two steps:

- Choice of the traits in the breeding objective
- Weighting of the traits with economic coefficients or values.

A linear function is appropriate to express a quantitative definition of the breeding objective. This is the function for the total (aggregate) breeding value:

$$A_T = \mathbf{v'a}$$

A_T Total breeding value
$\mathbf{v}$ Vector of economic weights
$\mathbf{a}$ Vector of breeding values for the traits in the breeding objective

Here no discounting is assumed. When discounting is to be involved the number of discounted expressions has to be considered for each trait:

$$v_i{}^* = v_i\, N_i$$

$v_i{}^*$ adjusted coefficient for the economic value for trait i
v_i coefficient derived from a production function
N_i Number of discounted expressions for trait i

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3. Gene Flow

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3.1   Introduction

To evaluate different designs for breeding programs or to judge the value of a single selection decision for a breeding or production unit one has to know when and how often returns can be realised from this decision.   McClintock and Cunningham (1974) introduced the "discounted expression" as a mean to calculate these returns.

The classical theory of response to selection (Dickerson and Hazel 1944, Rendel and Robertson 1950) allows us to calculate the rate of response at an equilibrium stage. However, with overlapping generations as we nearly always have in livestock improvement programs, the genetic improvement from any round of selection is not passed through the population immediately. In fact the response can be very erratic in early years (Hill 1971, Hinks 1971).

Hill (1974) developed a framework in matrix notation which allows, with relatively easy calculations, the following of "genes" through a population and the deterministic calculation of expected genetic gain.

In his paper Hill writes: "Whilst the methods do not enable us to compute results which cannot be obtained in other ways, such a those of Hinks (1971, 1972), they considerably simplify the analysis, provide a general solution and enable standard computer routines for matrix operations to be used. The basic structure and some of the matrix results have recently been obtained independently by J.M. Elsen (personal communication)."

In this chapter I want to illustrate Hill's method of calculation of discounted expressions. For the example calculations I used a program (GFLOW) developed by Brascamp (1978).

3. 2   The P-Matrix of gene transmission

The first requirement in Hill's method is the development of the so-called P-matrix which describes the transmission of genes and ageing in all tiers of a breeding and production population.

In a breeding program we generally distinguish a number of pathways of gene transmission, e.g. sire to sire and sire to cow. In dairy cattle breeding programs the former is normally a subset of the latter. But in most beef breeding herds no difference is made between these two groups. I assume however, this is the case in my beef example and describe my simple population with the following P-Matrix.
Bulls are used in the herd when they are in their second and third year to produce replacement female and slaughter stock. In their fourth, now progeny tested they are used once to breed replacements bulls, which are born when the bulls are 4 years old.
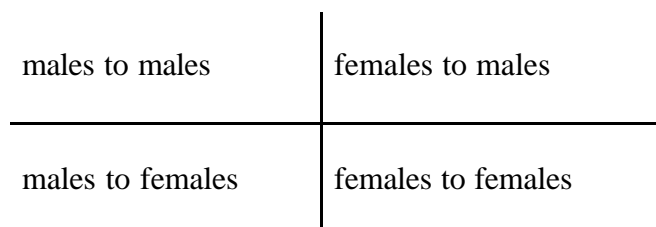Females have their first calves when two years and stay in the herd until they are 10 years of age to produce replacement females and slaughter stock. After being recorded

with two calves their calves number four and five are used to breed replacement bulls. Cows are culled and die at a steady rate during their lifetime.

Table 1. **P**-Matrix for example beef population

	Donors Age Classes Males				Females									
Receptors	1	2	3	4	1	2	3	4	5	6	7	8	9	10
1	0	0	0	0.5	0	0	0	0	0.3	0.2	0	0	0	0
2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	1	0	0	0	0	0	0	0	0	0	0	0
1	0	0.15	0.25	0.1	0	0.12	0.10	0.08	0.06	0.04	0.04	0.03	0.02	0.01
2	0	0	0	0	1	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	1	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	1	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	1	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	1	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	1	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	1	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	1	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	1	0

This P matrix has four distinct blocks which are describing the gene contribution of the four pathways.

males to males	females to males
males to females	females to females

The first row in each block represents the proportion of genes coming from the different age classes. In our example 50% of the genes of young bulls come from bulls which are 4 years old when their progeny are born. For females the proportion of genes from their sires are 15%, 25% and 10% for 2,3 and 4 year old bulls, respectively.

Bulls or females for this matter of age class 2 receive 100% of their genes from animals (Donors) of age class 1, therefore the 1. This "diagonal" part of the P-Matrix with ones is defining the ageing of the animals. Note that all rows add to 1.

Let us now follow the genes of a group of animals. We assume for our first example that a breeder decides to purchase proven bulls or semen in year 0 which he uses to breed replacement bulls. The selection differential for these bulls is known. Calves are born in year 1 and will be 1 year old in year 2.

Then let **m** be a vector of gene frequencies in the age classes in all tiers and sex groups originating from the initial animals (four year old bulls in our example), and $\mathbf{m}_{(1)}$ the vector of gene frequencies in the age sex classes from which the genes come.

Thus $\mathbf{m'}_{(1)} = (0\ \ 0\ \ 0\ \ 1\ \ 0\ \ 0\ \ 0\ \ 0\ \ 0\ \ 0\ \ 0\ \ 0\ \ 0\ \ 0)$

and $\mathbf{m}_{(2)} = \mathbf{P}\mathbf{m}_{(1)}$

$$\mathbf{m}_{(t)} = \mathbf{P}\mathbf{m}_{(t-1)} = \mathbf{P}^t \mathbf{m}_{(1)} \qquad\qquad [1]$$

Table 2 presents the proportion of genes in each age group in different years which flow through the population from this one input of genes.

Table 2. Vector **m'** in year 2 to 10, 15, 20, 25, 30 and 50 for the example population

Year	Sire age class				Cow age class									
	1	2	3	4	1	2	3	4	5	6	7	8	9	10
2	.5	.0	.0	.0	.1	.0	.0	.0	.0	.0	.0	.0	.0	.0
3	.0	.5	.0	.0	.0	.1	.0	.0	.0	.0	.0	.0	.0	.0
4	.0	.0	.5	.0	.087	.0	.1	.0	.0	.0	.0	.0	.0	.0
5	.0	.0	.0	.5	.135	.087	.0	.1	.0	.0	.0	.0	.0	.0
6	.25	.0	.0	.0	.068	.135	.087	.0	.1	.0	.0	.0	.0	.0
7	.03	.25	.0	.0	.031	.068	.135	.087	.0	.1	.0	.0	.0	.0
8	.02	.03	.25	.0	.07	.031	.068	.135	.087	.0	.1	.0	.0	.0
9	.026	.02	.03	.25	.098	.07	.031	.068	.135	.087	.0	.1	.0	.0
10	.183	.026	.02	.03	.067	.098	.07	.031	.068	.135	.087	.0	.1	.0
15	.071	.135	.040	.033	.057	.073	.092	.073	.048	.067	.098	.070	.031	.068
20	.054	.076	.11	.052	.070	.062	.073	.084	.070	.057	.073	.092	.073	.048
25	.063	.060	.076	.094	.077	.070	.066	.073	.080	.070	.062	.073	.084	.070
30	.079	.066	.065	.076	.073	.075	.071	.068	.073	.077	.070	.066	.073	.080
50	.072	.071	.071	.073	.072	.072	.072	.072	.072	.072	.071	.071	.072	.072

As can be seen from these numbers it takes quite some time to have a reasonably equal proportion of genes in all age classes. As these imported bulls also contribute 20% of the male genes when producing females the first females with genes of these sires will be born in year 1 and will be one year old in year 2. Notice that age class 0 (birth) of animals is not included in the **m** vectors nor in the **P** matrix. After the initial input it will take another 2 years before more of the genes flow into the female herd. The equilibrium which in our situation is only reached after about 50 years is 0.072.

This equilibrium can also be calculated using the elements of a vector **v** which contains the reproductive value of each group of animals. The reproductive value is the expected contribution this group of animals is making in the future or (1 - contribution from the past), e.g. sire to sire including sire to dam year 4 pathways: 1 - (.15+.25)) = 0.6 .

This reproductive value has to be divided by twice the generation interval L.

$$\lim_{t \to \infty} \mathbf{P}^t \mathbf{m}_1 = \mathbf{v}/2L$$

$$L = (L_{mm} + L_{mf} + L_{fm} + L_{ff})/4$$

With L = ((4+2.9+5.4+4.4)/4) = 4.175 units (years) for our model population

$$\lim_{t \to \infty} \mathbf{P}^t \mathbf{m}_{(1)} = \mathbf{1} * 0.6/(2*4.175) = \mathbf{1} * 0.0719$$

In our introductory example we have followed the genes of one specific group of animals which produced offspring of both sexes and a simplified situation where the animals of interest were available at that time. This is not the normal case for a breeding program and we therefore now investigate the calculations for individual pathways where we have to include the growing and testing time of these animals. Our aim is to calculate the genetic superiority G which flows into the population from the different pathways separately.

3.3   Analyses of the gene flow of separate Pathways

For this we introduce some additional vectors and matrices.

Q   matrix defining the ageing only, this also being the P-matrix with reproduction lines set to zero.

$\mathbf{R}_j$ matrix defining gene transmission from the pathway j

n   vector of gene frequency in the age classes in year 1 first generation.

Note that eg. in a four pathway model

$$\mathbf{P} = \mathbf{Q} + \mathbf{R}_{SS} + \mathbf{R}_{SD} + \mathbf{R}_{DS} + \mathbf{R}_{DD}$$

where subscript e.g. SD denotes the path sire to dam
Then we calculate

$$\mathbf{n}_t = \mathbf{Q}\mathbf{n}_{t-1} \qquad [2]$$
and

$$\mathbf{m}_t = \mathbf{R}\mathbf{n}_{t-1} + \mathbf{P}\mathbf{m}_{t-1} \qquad [3]$$

where $\mathbf{m}_{(1)}$ is a vector of zeros.

The first term in [3] describes the distribution of the genes of the selected animals to direct (1. generation) progeny. Once these selected animals are dead or culled $\mathbf{n}_t$ becomes zero and they do not contribute anymore. The second part of [3] then describes the distribution from the direct progeny to later generations.

Example: Pathway sire to sire where we start in year one with one year old bulls which will be performance tested and then progeny tested before a final selection will be made to breed the next generation of young bulls from them, i.e. Two stage selection.

In year 1 vector $\mathbf{n}_{(1)}' = (1\ 0\ 0\ 0\ \ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0)$

From [2] we can calculate vector $n_{(2)}$ to $n_{(t)}$

$n_{(2)}$	$n_{(3)}$	$n_{(4)}$	$n_{(5)}$	..	$n_{(t)}$
0	0	0	0	..	0
1	0	0	0	..	0
0	1	0	0	..	0
0	0	1	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
0	0	0	0	..	0
0	0	0	0	..	0

As can be seen from these vectors, $\mathbf{n}_{(t)}$ becomes a vector of zeros in year five (sires are four years old when their last progeny are born) thus the first term in equation [3] becomes zero and [3] becomes equal to [1].

The vectors $\mathbf{m}_{(t)}'$ for years 2 to 10, 15 20 25 30 and 50 are presented in table 3:

Table 3. Vector $\mathbf{m}'$ in year 2 to 10 15 20 25 30 and 50 for the example population. Pathway Sire to Sire

Year	Sire age class 1-4				Cow age class 1-10									
	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	..0
2	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
3	.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
5	.5	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
6	.0	.5	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
7	.0	.0	.5	.0	.075	.0	.0	.0	.0	.0	.0	.0	.0	.0
8	.0	.0	.0	.5	.125	.075	.0	.0	.0	.0	.0	.0	.0	.0
9	.25	.0	.0	.0	.059	.125	.075	.0	.0	.0	.0	.0	.0	.0
10	.0	.25	.0	.0	.0	.059	.125	.075	.0	.0	.0	.0	.0	.0
15	.019	.043	.177	.023	.063	.033	.050	.086	.063	.023	.059	.125	.075	.0
20	.043	.029	.053	.127	.072	.060	.045	.060	.081	.063	.033	.050	.086	.063
25	.084	.048	.040	.061	.061	.068	.059	.050	.060	.072	.060	.045	.060	.081
30	.063	.074	.052	.047	.056	.061	.065	.059	.054	.061	.068	.059	.050	.060
50	.061	.061	.059	.059	.060	.060	.060	.060	.059	.060	.061	.059	.059	.060

As we have here only considered one pathway and its reproductive value at 4 years of age is 0.5, we have

$$\lim_{t \to \infty} \mathbf{P}^t\mathbf{m}_{(1)} = \mathbf{1} * 0.5/(2 * 4.175) = \mathbf{1} * 0.0599$$

Table 3 demonstrates that the bulls themselves are not included in the m vectors (ageing of the original animals does not contribute) and that, due to the fact that they have to be progeny tested first, only in year 5 do we have the first genes in the next generation. A second pathway is of course Sire to Dams which are selected from tested young bulls and from which the Sires of Sires will be selected later. Their contribution for our example can be calculated by using R_{SD} in [3] and is presented in Table 4.

To calculate the genetic superiority of animals born in later generations $r_{(t)}$ that can be attributed to the selection differential achieved in the one round of selection, we can replace the vector $\mathbf{m}$ with a vector $\mathbf{s}$ that contains the superiority of the selected animals ? G = selection differential.

$$\mathbf{s} = \mathbf{m}_{(0)}\Delta G$$

$$\mathbf{r}_{(t)} = \mathbf{P}^t\mathbf{s} \qquad\qquad [4]$$

or

$$\mathbf{r}_{(t)} = \mathbf{m}_t\Delta G$$

Table 4. Vector **m**' in year 2 to 10 15 20 25 30 and 50 for the example population.
Pathway Sire to Dam

Year	Sire age class				Cow age class									
	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	..0
2	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
3	.0	.0	.0	.0	.150	.0	.0	.0	.0	.0	.0	.0	.0	.0
4	.0	.0	.0	.0	.250	.150	.0	.0	.0	.0	.0	.0	.0	.0
5	.0	.0	.0	.0	.118	.250	.150	.0	.0	.0	.0	.0	.0	.0
6	.0	.0	.0	.0	.045	.118	.250	.150	.0	.0	.0	.0	.0	.0
7	.0	.0	.0	.0	.051	.045	.118	.250	.150	.0	.0	.0	.0	.0
8	.45	.0	.0	.0	.046	.051	.045	.118	.250	.150	.0	.0	.0	.0
9	.105	.45	.0	.0	.041	.046	.051	.045	.118	.250	.150	.0	.0	.0
10	.085	.105	.45	.0	.044	.041	.046	.051	.045	.118	.250	.150	.0	.0
15	.040	.064	.077	.047	.058	.056	.069	.077	.063	.044	.041	.046	.051	.045
20	.054	.051	.068	.074	.064	.058	.054	.059	.063	.058	.056	.069	.077	.063
25	.065	.055	.054	.065	.061	.062	.059	.058	.062	.064	.058	.054	.059	.063
30	.062	.063	.057	.056	.059	.061	.061	.059	.058	.061	.062	0.59	.058	.062
50	.060	.060	.059	.060	.060	.060	.060	.060	.060	.060	.060	.060	.060	.060

4. Calculation of discounted expressions

Hans Graser

Up to now we have only considered the gene distribution originating from specified groups of animals. However, to compare different breeding schemes we have to calculate returns made in the future in present day values i.e. discounted values, and have to account for the fact that different traits are expressed at different times and with different frequencies. For example, improved growth rate or yearling weight is expressed and returns can be generated once in the life of a descendant when it is about one year old. Improved female fertility or milk yield is sex limited but will be realised repeatedly at or after each parturition during a female's life.

To accommodate this a vector $\mathbf{w'}$ is required showing the realisation of genetic improvement. This realisation vector is assumed constant over time.

Another new variable is the discount factor

$$c = 1/(1 + d)$$

with d being discount rate per time unit.

So far we have only talked about years and meant time units. A time unit in this context is defined as the time between calvings, lambings, farrowings etc. For cattle it is quite convenient to use one year and for pigs half a year. However, if one wants to be very precise in the calculations then the discount factor can be easily adjusted, to accommodate e.g. the average calving interval of ~380 days in dairy populations.

The discounted expression (returns) in year t is then:

$$X_{(t)} = c^t \, \mathbf{w'r}_{(t)}$$

and the total discounted expressions for the first T years are:

$$y_{(T)} = \sum_{t=0}^{T} x_{(t)}$$

Example: For our model population we assume improvements to yearling weight which are realised by the sale of heavier yearling store cattle. For simplicity increased weight of culled cows and bulls is offset by higher maintenance cost and therefore of no value.

Assuming 90% calving we have 0.40 males per cow to sell (0.05 are required to replace old bulls) and 0.21 heifer yearlings (0.24 are needed to replace cows), thus the total realisation is 0.61 resulting in a realisation vector.

$$\mathbf{w'} = [0\ 0\ 0\ 0\ 0.61\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0]$$

Table 4 represents the total discounted expressions $y_{(T)}$ after different time periods for 1kg superiority for yearling weight of the selected pathways sire to sire and sire to dam and 3 different discount rates 0, 0.05 and 0.10 respectively.

Table 5. Total discounted returns $y_{(T)}$ for pathway sire to sire and sire to dam calculated using different discount rates for one unit of improvement

| | Pathway | | | | | |
| | Sire to sire | | | Sire to dam | | |
Discount rate	0	0.05	0.10	0	0.05	0.10
Year 2	0	0	0	0	0	0
3	0	0	0	0.092	0.074	0.064
4	0	0	0	0.244	0.205	0.173
5	0	0	0	0.316	0.261	0.218
6	0	0	0	0.343	0.281	0.233
7	0.046	0.033	0.023	0.375	0.304	0.244
8	0.122	0.084	0.059	0.403	0.323	0.262
9	0.158	0.107	0.074	0.428	0.339	0.273
10	0.172	0.116	0.080	0.455	0.355	0.283
15	0.352	0.212	0.133	0.652	0.460	0.341
20	0.546	0.293	0.164	0.834	0.536	0.374
30	0.906	0.398	0.201	1.199	0.643	0.408
50	1.638	0.504	0.219	1.930	0.748	0.426

As can be seen from this table the first returns from pathway sire to sire don't occur until year 7 compared to year 3 for sire to dam. Further, if a realistic discount rate =0.05 is applied, the majority of total maximum discounted returns are accumulated after about 30 years for low discount rate and after about 20 years if the discount rate is at the higher end.

The lower values for pathway sire to sire will of course be compensated by an increase in ?G, otherwise it would make no sense to breed young bulls from 4 year old sires.

Note while the vector **m** of gene proportion is independent of the trait considered, discounted expression will be different for different traits, a) because they can be affected by different discount factors, and b) because certain traits can occur more than once in an animals life, e.g. milk yield.

For further discussion on this method read Hill, 1974.

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5. ZPLAN - a PC Program to Optimise Breeding Programs

H.-U. Graser and G. Nitter

5.1   Introduction

ZPLAN is designed to optimise selection strategies in livestock breeding. Various breeding programs and their parameters are defined by the user and the program calculates a number of criteria such as genetic gain for the breeding objective, genetic gain for single traits and return of investment minus costs (profit).

Using the gene-flow method and selection index procedures, the program enables to "simulate" different breeding plans in any livestock species. It can be applied for plans with several subpopulations, for populations used in a crossbreeding scheme and it considers several tiers in the scheme such as nucleus, multiplier and production levels.

The program has two main steps. First a basic situation of a breeding program is defined and evaluated. In a second step, alternative strategies are defined by varying certain parameters of the basic situation and results for the criteria mentioned above are presented in tables.

For the basic situation parameters are read from the parameter file and stored as vector A(). A subroutine called NBILD allows to specify relationships among parameters in vector A() and to define new A-parameters. This subroutine is to be written by the user. After calculation of the basic run and varying the parameters in vector A(), variation runs can be calculated for which the subroutine NBILD plays a major role.

A first version of the program was written by Karras (1984) and further developed by Niebel. It was based on the thesis of Niebel (1974) and on the gene-flow method described by Hill (1974), Elsen and Mocquot (1974) and Brascamp (1978). The present version contains marginal changes of Niebel's extension such as the inclusion of maternal effects and modifications in the format of outputs. A preliminary detailed description of the parameter file considering the last changes will be handed out separately.

The ZPLAN program is written in FORTRAN. It is tested with a FORTRAN 77 compiler. The user is expected to have basic FORTRAN programming knowledge to be able to develop the user-defined subroutine NBILD and also another subroutine called NUMBER. All real variables in the program are single precision variables.

The program is based on a pure deterministic approach. Compared to stochastic simulation models so far available its advantage is a multi-trait modelling including return and costs over a given time horizon and the program is fast. Only one round of selection is considered. Thus insufficiencies of the approach may be the lack of accounting for reduced genetic variance due to selection and inbreeding. Although selection intensities are derived for finite population sizes, a bias may occur due to correlated index information in a family structure (Meuwissen, 1991). Furthermore, a deterministic program such as ZPLAN cannot consider the variance of responses such as

in a stochastic simulation. A problem may also be the restriction to a closed population where returns from external sales of breeding products in a competitive market are not taken into account (Dekkers and Shook, 1990).

5.2   General information

A clear understanding of the arrangements of the elements in vector (A) is required for handling the program. These are presented in Table 1. The table shows also where more details about their use are given. This is either the description of the record number (in the separate handout) or the chapter number.

Table 1.   Summary of parameters stored in vector A( )

Position in A( )	Parameters	Record number [chapter]
1-20	Proportion of dams in the various tiers	7, 8
21-1000	Free; defined by the user	7, 8
	e.g. technical and biological coefficients	
1001-1100	Grouping of traits in tables H and F	6
1101-1200	Grouping of selection groups in table G	19
1201-1230	Position of elements in table E	15
1231-1275	Not used	-
1276-1290	Various input and operator parameters	2
1291-1295	Operators for constructing formulas	32, 33
1296-1299	Not used	-
1300	Proportion of the active breeding population	[3.3]
1301-1400	Parameters specific for population 1	10, 11
1401-1500	dto, for population 2	10, 11
...		...
2501-2600	dto, for population 13	10, 11
2601-2700	Numerator values to calculate selection proportions	30
2701-2800	Denominator values to calculate selection proportions	[3.2]
2801-3000	Cost components	12, 13
3001-3200	Cost discounting times	14
3201-3500	Not used	-

When the program was adjusted to use it on a PC, some more limits of dimensions had to be imposed compared to the original program. Table 2 shows the limits for the various constants under which the program has so far been tested. The user can try to change these dimensions and adapt them to his particular demands.

Table 2.   Limits of dimensions in ZPLAN

Description and symbol of the constant		Dimension
Traits	NMD	30
Information sources of the selection index	MID	11
Traits from all information sources of the selection index	NII	45
Traits with repeated measurements of one information source	NMW	5
Populations	NPLD	4
Selection groups	NSGD	30
Sex-age classes in a selection group	NSAC	15
Maximum value of the product NMD NPLD NSGD	NNAW	6000
Columns in the generation matrix (the limits of NSAC and NSGD cannot be totally exploited)	IDIP	55
Reproduction rows in the generation matrix	NRZD	10
Rows in the generation matrix realizing genetic gain	NRLSD	9
Cost groups	NCCO	15
Number of (A) elements to calculate cost groups	NCA	20
Position of (A) elements to calculate cost groups	IPCA	15
Investment period in time units	NJD	25

5.3   Description of the ZPLAN program

The program contains the main segment and a number of subroutines. Its structure is presented in Figure 1. The function of the main segment and of the subroutines are described below.

5.3.1   Main segment ZUPLAN

The main segment reads and stores the parameters of the parameter file (except INDEX parameters), lists them and calls subroutines. Furthermore, it controls variation runs and prepares results of these variations from a temporary file to summarize tables and their output.

The sequence of reading the parameters in the main segment is as follows:

- Input and output control parameters
- Parameters for traits
- Biological and technical coefficients
- Parameters specific for subpopulations
- Parameters for breeding costs
- Parameters for generating the transmission matrix
- Parameters for discounting
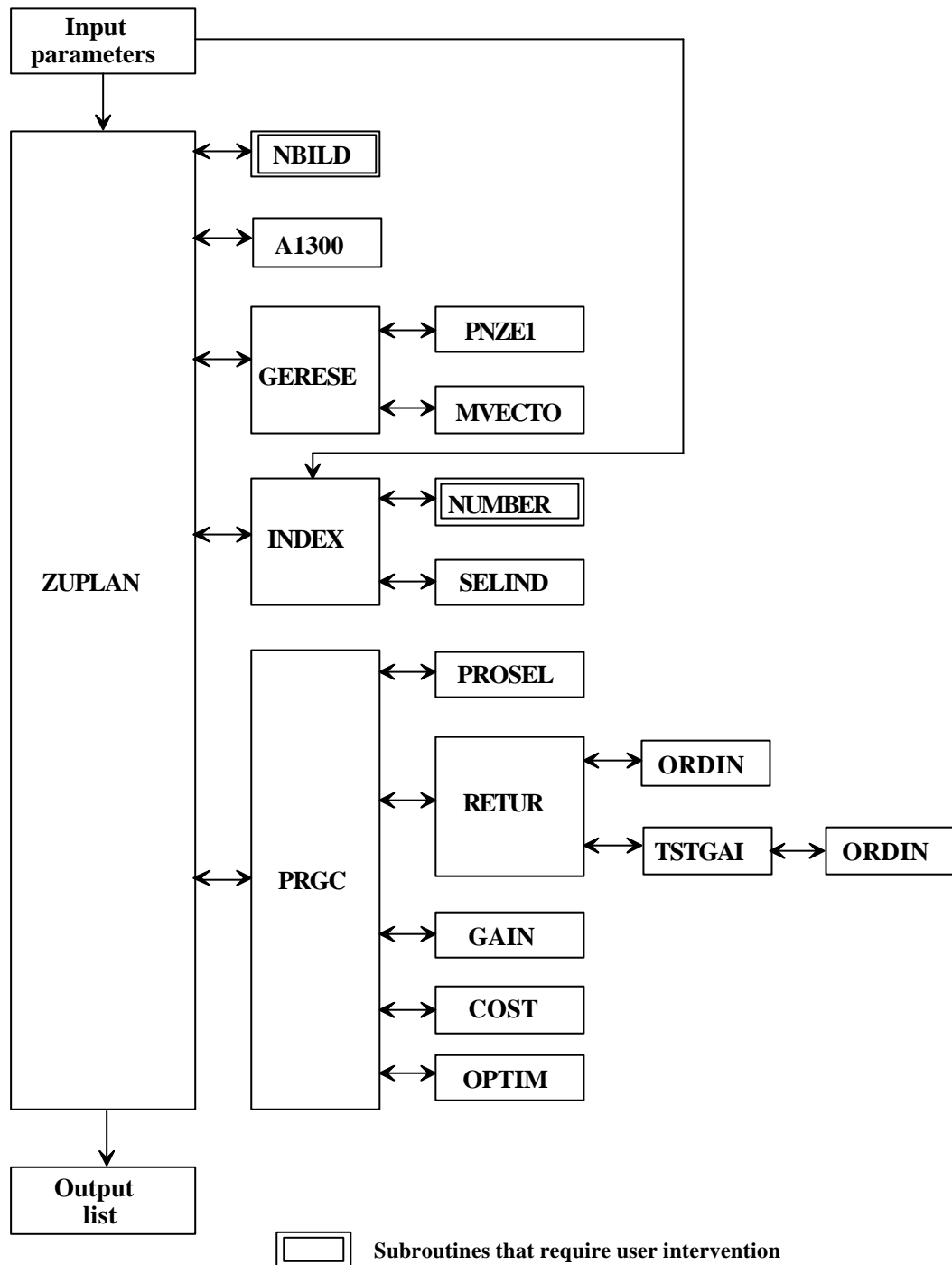- Parameters for variation and optimization

Figure 1.   Structure of the ZPLAN program

5.3.2   Subroutine NBILD

This subroutine has to be developed by the user. One of the purposes of it is to define the selected and proven animals in each selection group to get the proportion of replacements and thus the selection intensities. These can also be calculated directly using the parameters defined in the (A)-vector. But NBILD gives more flexibility (see IOPT (10) in record numbers 1 and number 30).

When NBILD is applied to calculate the selected proportion of replacements, a certain part of the (A)-vector has to be used. Values A(2601) to A(2700) are the numbers of selected animals in a particular selection group. These are related to the corresponding numbers of tested animals A(2701) to A(2800). The values A(2601) and A(2701) correspond to the first selection group, A(2602) to A(2702) to the second selection group and so on.

The subroutine NBILD allows also to define the relationship among parameters in the (A)-vector. It is especially important when certain biological and technical coefficients or other parameters are to be varied. Changing the values of one parameter may influence a number of others in a certain breeding plan. For example, after performance testing in a testing station the number of young bulls available for test matings depends on their survival rates, their semen quality and on the size of the station. This in turn has an influence on the gene proportion of young bulls in the population.

5.3.3   Subroutine A1300

Subroutine A1300 calculates the value of element A(1300) in the (A)-vector. This is the proportion of the "active population" or animals in the breeding unit causing breeding costs and for which the cumulated genetic response is calculated. It also checks for an incorrect input of the proportion of realization rows. In this case it stops and displays an error message.

5.3.4   Subroutine GERESE

GERESE is based on a subroutine of Karras (1984). It calculates the components of the gene flow procedure such as

- the transmission matrix
- the realization vectors (h)
- the reproduction matrices
- the number of standardized and discounted expressions of the traits.

In the first step the distribution of sex-age classes is calculated for various selection groups. It is assumed that culling rates are constant in the whole production period (Weber, 1976). Then the P, Q (aging matrix) and R matrices as well as h-vectors are derived and the subroutine MVECTO is called to develop the m-vectors. From these the number of standardized and discounted expressions are calculated. Finally, from the elements in the P-matrix the generation intervals are calculated for each selection group.

Subroutine PNZE1

This subroutine is called by GERESE to find the position of certain non-zero elements in any row of the P-matrix. It allows to increase the speed of the program.

Subroutine MVECTO

MVECTO is called by GERESE to calculate the m-vectors according to the approach

described by Brascamp (1978).

5.3.5   Subroutine INDEX

Subroutine INDEX is an extension of the selection index program of Künzi (1976). It is used to get selection index equations. The program implies that the information sources are the same for all animals in a selection group. The parameters required are read directly from the parameter file (record numbers 22 to 29). An extension is that the economic values originally given in the parameter file are weighted by the number of discounted expressions found in GERESE. Thus they are different for each group, but their relative values change very little.

The main results of this subroutine are the genetic superiorities (gain per generation) of the selected animals in the genetic groups. Furthermore, the accuracy of estimated breeding values, their standard deviations and information about the two indexes in a two-stage selection are calculated.

Subroutine NUMBER

For information sources with more than one relative (half-sibs, full-sibs, offspring etc.) the number of members can be given directly through the parameter file or it is calculated in the subroutine NUMBER. Apart from NBILD this is another subroutine to be developed by the user.

Subroutine SELIND

This subroutine was developed by Cunningham and Mahon (1977) and is used to solve the index equations.

5.3.6   Subroutine PRGC

Subroutine PRGC gives an output of the basic run and controls further subroutines for calculating results of various breeding options (selection proportions, return, gain and costs).

Subroutine PROSEL

PROSEL calculates the proportion of selected animals for each selection group. The information required comes from NBILD or directly from A()-parameters; see IOPT(10).

Subroutine RETUR

RETUR is used to calculate the return from each selection group, for each single trait as well as for the total breeding value. This subroutine calculates also the selection intensities in case of situations where the selection group considered is the remainder of a preselected group, i.e. the best animals of this group have already been selected for another group. A formula of Cochran (1951) is used for this purpose:

$$i_2 = \frac{(b_1 + b_2)i_{1+2} - b_1 i_1}{b_2}$$

where b_1 and b_2 are the proportion of selected replacements for group 1 and 2 and i_1, i_2 and i_{1+2} are the corresponding selection intensities.

Furthermore, according to Niebel (1974) the following two subroutines are called in RETUR:

ORDIN   It calculates selection intensities for the selection groups. An approximate method for small samples is used according to Burrows (1972):

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

where i and i_∞ are the selection intensities for the finite and the infinite sample and N and n are the number of proven and selected animals respectively.

TSGAI   TSGAI calculates the genetic gain per generation of the selection groups after a two-step selection. This approximate method is described in Niebel and Fewson (1976).

Subroutine GAIN

It calculates the monetary genetic gain of the aggregate breeding value and the genetic gain per trait using the formula of Rendel and Robertson (1950).

Subroutine COST

This subroutine calculates the discounted breeding costs according to Niebel (1974). It distinguishes between fixed and variable costs.

Subroutine OPTIM

OPTIM is used to compare the results from all variation analyses. For short outputs an option is available to select the best ones for printing. The optimization criterion is defined in IVERSI(1).

5.4   Listing of results

Various combinations of IVERSI options in record number 1 are available to get a flexible combination of outputs. In a first run the values for IVERSI(1) to IVERSI(20) may be 1 0 9 0 8 1 1 2 0 1 1 1 0 1 1 1 0 0 1 0. In this combination only gene flow information from GERESE is printed. For special purposes a useful combination of options is obtained by arranging values for IVERSI(1), IVERSI(2) and IVERSI(6) as follows:

IVERSI(1)	Value of IVERSI(2)	IVERSI(6)	Kind of information
1	2	0	Index information from subroutine INDEX
1	0	1	Gene flow information from GERESE
1	1	1	Reduced GERESE information
1	0	0	Full GERESE and INDEX information
1	1	0	Reduced GERESE and INDEX information
2	0	2	Information of basic and variation runs[1]
2	Any	0	INDEX information with basic and variation runs

[1] Set IVERSI(4) = 1 when no basic information is desired

5.4.1   Input parameters

The program is controlled by a list of parameters in record numbers 1 and 2 (mainly input and output operators), 7 and 8 (biological and technical coefficients), 9 - 11 (specific parameters of subpopulations) and 12 -14 (cost parameters). As an option, the parameters of record numbers 7 to 14 can be printed after the first call of NBILD to control how they differ from the original parameters.

5.4.2   Results of the basic run

For the basic run a table is printed with the following results for each selection group:

SEL.ANIM   Number of selected animals

PROV.ANIM   Number of proven animals

SEL.PROP   Proportion of replacement selected

GEN.INTVAL   Generation interval

GENP*100   Offsprings' gene proportion from the parent group as defined in PMSTE(.5); record number 17 (in percent)

SEL.INT(i)   Selection intensity (i).   Value 0. in case of two-step selection

SD.BR.OBJ   Standard deviation of the total breeding value

RIAT   Correlation between selection index and estimated breeding value

GENE PROP   Long-term gene proportion of the group in the total population

GG BR.OBJ   Monetary genetic gain per generation for the total breeding value

GG ###   Genetic gain per generation for each trait ### in the breeding objective

SDE ##   Number of standardized and discounted expressions for the first maternal and the first growth/carcass trait

RETURN TOT   Total return for the group

RET ###   Return for trait ### in the breeding objective

Furthermore, overall results are printed for all subpopulations and for the total population. These are

- the genetic gain of all traits in the breeding objective
- the overall generation interval
- the overall monetary genetic gain
- the overall return per unit
- the return per unit for each trait in the breeding objective
- the overall costs and cost components per unit
- the profit per unit (overall return minus overall costs)

5.4.3   *Results of variation runs*

Tables A to H are listed according to options in IVERSI(11) to IVERSI(18) in record number 1. An introductory table contains the names for the parameters varied, their position in the (A)-vector and the variation levels for each factor (up to 9). Codes for these levels are printed in the following tables to indicate the variation steps. Thus, for example, when three factors are varied, the code combination 532111111 under "factor level" in tables A to H means

- the fifth level for parameter 1
- the third level for parameters 2
- the second level for parameters 3.

The contents of the tables A to H are:

A   Total genetic gain, profit, return, costs and return for all traits in the breeding objective

B   For each population: Total genetic gain, generation interval and genetic gain optional for all traits or for those in the breeding objective

C   For each selection group various results are listed similar to those of the basic run as shown in chapter 4.2

D   Summarized variable cost groups per unit according to ISPKO in record number 32

E   Any A-parameters of interest as defined in record number 15

F   Percentage return for summarized trait groups as defined in record number 6

G   Percentage return for summarized selection groups as defined in record number 19

H   Percentage monetary (total) genetic gain for the same trait groups as percentage return in table F

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