

Economic evaluation of breeding programs

Julius van der Werf

The ability to model breeding programs becomes an important part of strategic decisions about investment. The first question could be: is it cost effective to invest in breeding programs? How much can we afford to invest in measurement? Is it cost-beneficial to measure certain traits that are expensive to measure (e.g. a computer scan of whole carcass, eating quality taste panels, or feed intake). With new technologies similar questions are being asked: what is the cost-benefit from implementing genomic selection?

Assume a certain breeding program where the predicted rate of annual genetic gain is dG , which is expressed in monetary value, e.g. \$2/head. This figure can be calculated using equations [2] or [3] in this topic. It assumes that the economic values are expressed on a 'per head' basis, which could be per breeding female, or per animal sold (for slaughter). As genetic improvement is incremental and cumulative, the increase in merit after t years will be $t.dG$. The benefit for the whole population will be $N.t.dG$, where N is the total number of animals in the population expressing the improvement. If the cost of running the program is equal to C , the the benefit in year t will be $N.t.dG - C$. To assess costs and benefits, it is appropriate to discount future benefits. Money earned in the future will be of less value due to discounting. The discount factor for year t is $(1/r)^t$, where r is the discount rate is equal to the nominal interest rate, corrected for inflation. So the benefit in year t in net present value (NPV) will be equal to

$$(N.t.dG - C).(1/r)^t.$$

The benefit over time of this breeding program is illustrated in Table 15.2 and Figure 15.11. In the example it is assumed that $dG = \$2/\text{head}$, $N=20$ million and costs are 0.5 million. This is based on the structure in Fig 15.4, assuming a measurement cost of \$10 per breeding ewe in the studs. These are figures, pretty close to those for sheep in Australia. You can see that the 0.5M investment per year is easily earned big by large and cumulative value of genetic gain. For example, in year 10, the benefit from genetic improvement is \$180M whereas the annual investment is only 0.5M.

Table 15.2. Genetic mean, benefit of genetic improvement and NPV of investing in genetic improvement in each of 20 years after commencement.

year	Genetic Mean (\$)	Benefit (M)	Cost (M)	discount factor	NPV (M\$)
1	0	0	0.5	1.00	-0.50
2	1	20	0.5	0.95	18.57
3	2	40	0.5	0.91	35.83
4	3	60	0.5	0.86	51.40
5	4	80	0.5	0.82	65.40
6	5	100	0.5	0.78	77.96
7	6	120	0.5	0.75	89.17
8	7	140	0.5	0.71	99.14
9	8	160	0.5	0.68	107.96
10	9	180	0.5	0.64	115.71
11	10	200	0.5	0.61	122.48
12	11	220	0.5	0.58	128.34
13	12	240	0.5	0.56	133.36
14	13	260	0.5	0.53	137.62
15	14	280	0.5	0.51	141.17
16	15	300	0.5	0.48	144.06
17	16	320	0.5	0.46	146.37
18	17	340	0.5	0.44	148.12
19	18	360	0.5	0.42	149.38
20	19	380	0.5	0.40	150.18

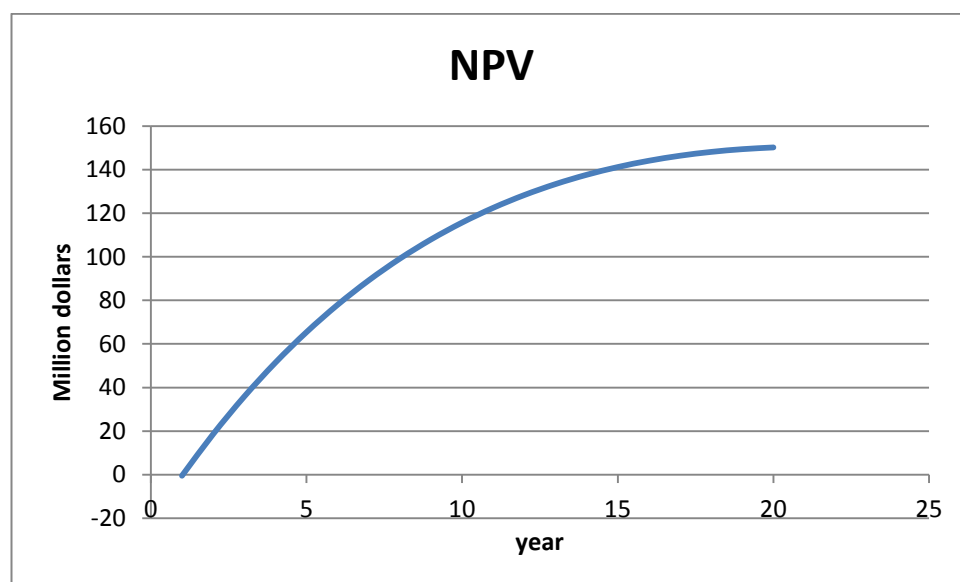


Figure 15.11 Graph showing the NPV of a genetic improvement program over the next 20 years, assuming a cost of 0.5M/year, a rate of improvement of \$2 per year and improvement expressed in 20M sheep

We can follow the same principles when comparing 2 breeding programs. For example, one with and one without genomic selection. Suppose the extra gain due to genomic selection is 10%, i.e.

dG is now \$2.20/head. Assume the cost is now 2.5 million dollars per year. The NPV for the 2 strategies are compared in Fig 15.12

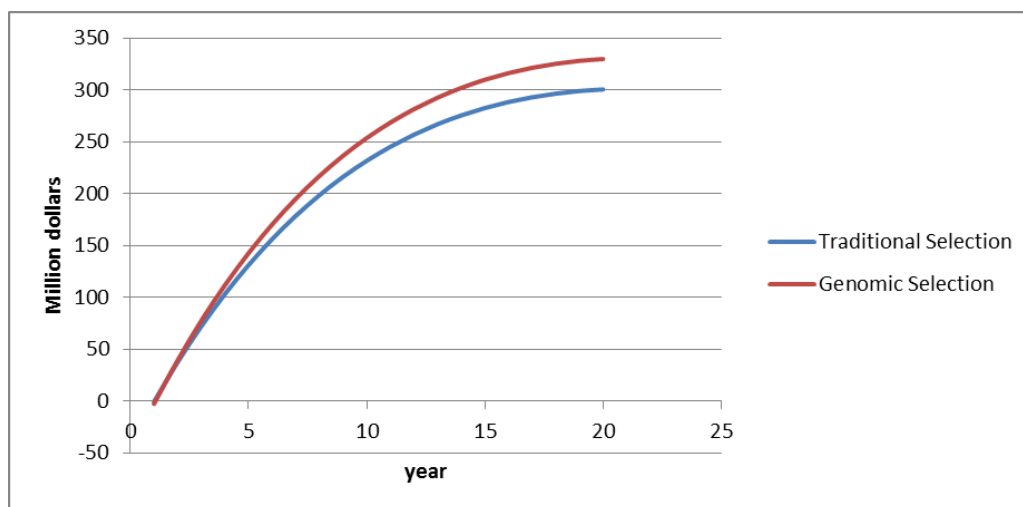


Figure 15.12. Graph showing the effect of genomic selection on industry wide NPV of a genetic improvement program over the next 20 years, assuming a cost of \$0.5M for noGS and 1.65\$M for GS, a rate of improvement of \$2 per head per year under noGS and \$2.20 under GS and improvement expressed in 20 million sheep

The example shows that investment in breeding programs is highly lucrative because 1) genetic improvement is incremental and cumulates over years, and 2) due to the multiplication factor in the 3 tier design, an investment in a small number of nucleus animals bring about benefit in many commercial animals. Even a potentially large investment of genomic selection is cost effective.

The economic assessment as presented above has a number of caveats. It is a cost-benefit analysis at an industry level, as if there was a complete integration between tiers, and the investors also reap the benefits. In reality this is not the case. It is up to the breeders to invest in measurement and technology, whereas the commercial producers reap the benefit. There would be a sharing of benefit if the breeders increase the price of seed stock according to the increased value of genetic improvement. In reality, that may be difficult. In the example, where stud breeders sell a total of 10,000 rams per year, the increase in ram price would have to be thousands of dollars over the next 20 years. So for an individual breeder, cost benefit considerations could be quite different than those at a whole-of industry level.

A more conservative approach could be to only value benefits in the second tier, i.e. for the direct clients of the stud breeders. In that case, the genetic improvement of stud rams is only valued in its direct offspring. The multiplication factor would be much lower. For example, consider a commercial operation with 10,000 ewes, needing 100 rams per year. This could be supplied by a stud breeder using 500 rams (selling 40% of his stud born males as rams to the commercial). Figure 15.13 shows the NPV for the stud breeder, assuming he shares the benefits equally with the commercial level (hence the graph would look the same for the commercial operation). It will take at least 10 years before the initial investment in genomic testing pays off and becomes more profitable than traditional measurement of phenotype. In the GS scenario he would have to increase his ram price with about \$200 more over 20 years. If the stud breeders captures less than 50% of the benefit, his perspective to invest in a relatively expensive technology such as genomic selection would look even more bleak, even though the technology delivers a clear industry wide benefit..

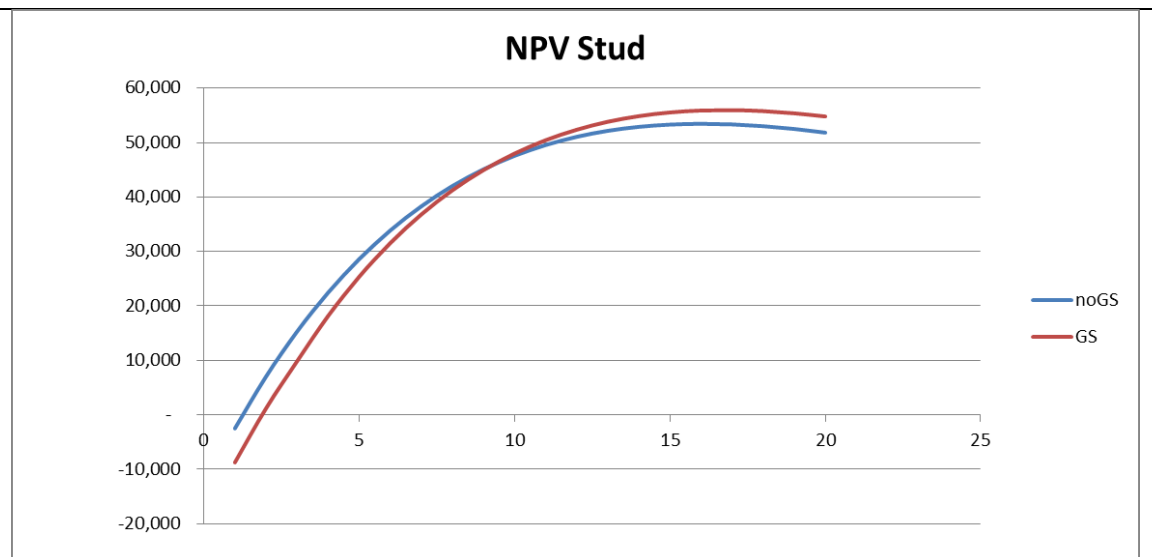


Figure 15.13. Graph showing the effect of genomic selection on NPV for an individual stud breeder of a genetic improvement program over the next 20 years, assuming a cost of \$5k for noGS (\$10/head) and \$16.5k for GS (only males genotyped for \$50/head), a rate of improvement of \$2 per head per year under noGS and \$2.20 under GS and improvement expressed in 10,000 sheep

Gene Flow

H.-U. Graser, AGBU, Armidale

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 as 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).

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 replacement 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

Receptors	Donors Age Classes													
	Males				Females									
	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 \mathbf{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 $\mathbf{m}'_{(1)} = (0 \ 0 \ 0 \ 1 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0)$

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

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

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 \mathbf{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 \mathbf{m} vectors nor in the \mathbf{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 \mathbf{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 .

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

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

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

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

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.

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.

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

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

and

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

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

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
0	0	0	0	..	0
0	0	0	0	..	0

As can be seen from these vectors, $n(t)$ 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 $m(t)'$ for years 2 to 10, 15 20 25 30 and 50 are presented in table 3:

Table 3. Vector 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

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

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 RSD in [3] and is presented in Table 4.

To calculate the genetic superiority of animals born in later generations $\mathbf{r}_{(t)}$ 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 ΔG = selection differential.

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

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

or

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

Table 4. Vector \mathbf{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	.059	.058	.062
50	.060	.060	.059	.060	.060	.060	.060	.060	.060	.060	.060	.060	.060	.060

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:

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

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.

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

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

Discount rate	Pathway					
	Sire to sire			Sire to dam		
	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 ΔG , otherwise it would make no sense to breed young bulls from 4 year old sires.

Note while the vector \mathbf{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 animal's life, e.g. milk yield. For further discussion on this method read Hill, 1974.

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