Chapter 10

Principles of Estimation of Breeding Values

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Key Terms and Concepts

- Estimated Breeding Value (EBV)
- Accuracy of EBV
- Prediction Error Variance
- Variance of EBV
- Predicting Response to Selection on EBV

Introduction to the Topic

Within animal breeding systems, we would like to rank and select animals based on their true breeding values (TBV or “A”: additive genetic value). Unfortunately we don't have this perfect knowledge - we cannot see genes and breeding values, and so we must use observed phenotypes to obtain estimated breeding values (EBV's or Â).

Genetic change due to selection based on EBV will be lower than if selection had been on true breeding value. The relative response is proportional to accuracy of EBV, and accuracy is between 0 and 1.

The most obvious piece of phenotypic information we can use to estimate an animal’s breeding value is the animal’s own phenotype. But we can also use information from relatives, such as the sire, the dam, siblings and progeny. Commercial genetic evaluation systems produce EBVs for each animal for all traits of relevance. Such an evaluation is based on a statistical procedure leading to Best Linear Unbiased Prediction (BLUP) of breeding values. Inclusion of information from relatives is automatically taken care of in the BLUP method, provided such information is available in the database through the knowledge of pedigree. We will discuss the BLUP procedure in greater detail in later topics.

In this topic we will discuss the principle of estimation of breeding value. First we present how phenotypic information is turned into an EBV. The heritability of the trait is important here. Second, we discuss the accuracy of EBV, how it is calculated, and why it is important. Basically, the higher the accuracy, the higher the response to selection based on EBV. Closely related to accuracy are the variance of the EBV and the Prediction Error Variance of EBV. The variance of the EBV indicates how much difference in EBV values we can expect. This is relevant if we want to predict the EBV of a selected group of individuals. The Prediction Error Variance gives information about the uncertainty of an EBV. It is used to predict how much an EBV can still change when more information becomes available. The higher the accuracy of an index, the smaller the change when more information comes in. This change has great practical importance, e.g. when determining the price differences between top breeding animals based on EBV.

Principle of Estimating Breeding Values

Components of Variation

Breeding Values are estimated based on phenotypic differences between animals. It is based on the notion that part of these phenotypic differences is due to genetic components. Quantitative genetic theory is used here, and one of the key principles is that phenotypic differences occur due to genetic as well as non-genetic differences. Differences are measured as variance, and therefore, phenotypic variance is the sum of genetic and non-genetic variance. Not all genetic differences between individuals are passed on to progeny. We are only interested in additive genetic variance as

- it is the variance in breeding value, i.e. that part of the genetic differences that are passed on to progeny
- it can be more easily estimated, e.g. differences between progeny groups of different sires are a reflection of additive genetic differences.

The non-additive genetic effects are due to dominance effects as well as (some) epistatic effects. These effects are not unimportant in real life, e.g. they could explain why some sires make particularly good combinations with certain cows (farmers call this 'nicking'), but these effects are hard to estimate (because the same sire is not often used to the same cow), they are relatively small and therefore non-additive effects are hard to utilise in breeding. Non-genetic effects are therefore put in the basket of 'residual effects' together with non-genetic effects due to environmental differences. Therefore

Phenotypes are made up of breeding values and residual effects:

$$P = A + E$$

We use "E" for 'environmental effect, although this is actually a residual effect, also containing non-additive genetic effects

Phenotypic differences are due to differences in breeding values plus differences in residual effects

$$VP = VA + VE$$

where: VP = Phenotypic Variance
VA = Additive Genetic Variance
VE = Residual (or Environmental) Variance

Table 1 gives an illustration of these concepts, by considering the differences between 5 bulls for yearling weight

Table 1. Performance of 5 bulls and underlying true effects

served Phenotype Yearling Weight)	P Phenotypic Deviation	A Additive Genetic Value	E Residual Effect
314	+14	+3	+11
306	+6	+7	-1
302	+2	-3	+5
293	-7	+4	-11
289	-11	-7	-4

Table 2.1 is hypothetical, as in real life we are not able to observe A and E, but it illustrates a number of things

- Phenotypic differences are due to differences in both breeding value (A) and residual effects (E)
- Differences in A and E are unrelated, i.e. animals with positive A do not have more chance to have a positive (or negative) E.
- Differences in E are generally larger than differences in A
- Animals with the best phenotype do not necessarily have the best breeding value, but…
- Selecting animals on phenotype will provide animals with on average positive breeding values (there is a correlation between P and A)

It is common that differences in E are larger than differences in A. A measure for difference is variance. Variance is formally calculated as the sum of the squared deviations. The mean values for P, A and E are zero. The variances and standard deviations in the example of Table 2.1 are

VP = 101	$SD_P = 10$
VA = 32	$SD_A = 5.7$
VE = 71	$SD_E = 8.4$

Hence, about 30% of the observed phenotypic differences are due to breeding value (A). This figure is called *heritability.*

Heritability = Additive genetic variance/ Phenotypic variance = VA / VP

In our example, the exact heritability is 32 / 101 = 0.32

It is important in quantitative genetics to have a good understanding of distributions. Taking Table 2.1 as an example: the phenotypic SD = 10. In a larger population we would expect the extremes to be about 3 SD deviating from the mean, so ranging from about -30 to +30. (Note 1: the example is only a small population so the extremes are closer to the mean. Note 2: In reality yearling weight has a larger SD: about 30Kg. If we sampled many animals, the range of values would be roughly between 200 and 400 Kg). The variance in true breeding value is smaller. If many were sampled we would expect values between -15 and +15.

Estimating Breeding Value

Without the knowledge of true genotypes, the only information that can be used to estimate breeding value is the phenotype. For this purpose we use phenotypic differences between animals, or more specifically, phenotypic deviations. The breeding value is now estimated as a proportion of this deviation, being the proportion of total variation that is due to variation in breeding value. This proportion is equal to heritability, i.e. in our example, the proportion is equal to 0.32. Hence, when the information used is an animal's own phenotypic deviation, the breeding value is estimated as

$$EBV = h^2.P$$

Where h^2 is the symbol for heritability and P is the phenotypic deviation. The heritability is a population parameter, i.e. the value is constant. It can only vary between traits or between the same trait in distinctly different environments.

The reason why we use h^2 rather than h is statistical. The correlation between breeding value and phenotype is equal to h. The proportion of variation explained by breeding value is h^2. This notation is equivalent to statistical modeling, where we use r^2 for the proportion of variance explained by the model, and r for the correlation between observed values and predicted values.

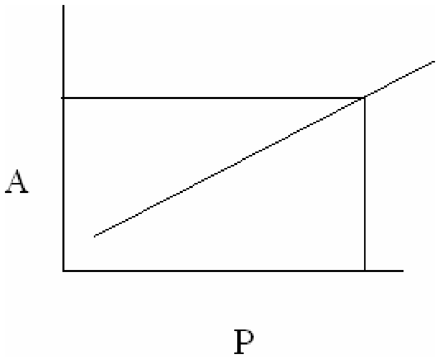
Notice that we don't use the absolute phenotypic value, but we use it as a deviation of a mean, since we are only interested in differences between animals (variation). The larger the heritability of a trait, the more we believe that observed phenotypic differences are due to breeding value.

The principle of breeding value estimation is based on regression. We want to know differences in breeding value based on observed differences in phenotype. Regression is illustrated in Figure 2.1. If we regress breeding values on the phenotypic observations, the slope of the regression line tells us how much difference we have in breeding values per unit of difference in phenotype. This slope is equal to the heritability. This can be derived from quantitative genetic theory, since the slope of a regression line is

$$b_{xy} = \frac{\mathrm{cov}(x,y)}{\mathrm{var}(y)} \text{ which is now equal to } \frac{\mathrm{cov}(P,A)}{\mathrm{var}(P)} = \frac{\mathrm{var}(A)}{\mathrm{var}(P)} = h^2$$

recalling that cov(P,A) = cov(A+E, A) = cov(A,A) = var(A). This is a theoretical derivation, as in practice we can not observe true breeding values (A). However, we can estimate heritability (see in later lectures) and therefore, with the knowledge of h^2 and phenotypes, we can estimate breeding values.

Figure 1: Estimation of breeding values is based on the principle of regression of true breeding values (A) on phenotypes (P)



<u>Example</u>

In Table 1, the best bull had a yearling weight of 314 kg. The mean of his contemporaries is 300 kg. The heritability of yearling weight is 0.32. What is the bull's EBV?

$$\text{EBV} = h^2.P = 0.32 \; . \; (+14) = +\,4.5 \text{ kg}$$

Table 2. Performance of 5 bulls, underlying true effects and EBVs

Again, Table 2.2 illustrates some important aspects of EBV

Observed Phenotype (Yearling Weight)	P	A	E	EBV
314	+14	+3	+11	+4.5
306	+6	+7	-1	+1.9
302	+2	-3	+5	+0.6
293	-7	+4	-11	-2.2
289	-11	-7	-4	-3.5

- The ranking based on EBV is not exactly the same as the ranking based on true breeding value (A), but……..
- Animals with the highest EBV have on average a higher true breeding value
- There is a prediction error on each EBV (being the difference between A and EBV).

The estimation of EBV might seem very poor for individual animals, but as a criterion for achieving genetic change the EBV is the most efficient, as will be discussed later in this topic. Also realise that with more information, especially information on progeny, the EBV will be closer to A.

In reality, we cannot see A, and therefore we will not know prediction error. The expectation of prediction error is zero (meaning that they are zero – on average). The size of the prediction error depends on the accuracy (see later in this topic). With more information available the prediction error becomes smaller, and the EBV will slowly move toward the true breeding value. With an accuracy of 1, the prediction error will be zero.

An important thing to note is that the animal with the best EBV has no more chance to have a negative prediction error that the animal with the worst EBV, i.e. each animal has just as much chance to change upward than downward if more information becomes available.

Correcting for Fixed Effects

Estimation of breeding values has two aspects to it. This first is about deriving regression coefficients, i.e. how much about a piece of information do we attribute to breeding value. This will be discussed in more detail in the next topic. The other aspect is that breeding values should be based on fair comparisons between individuals, i.e. they should not be biased by the fact that some animals had more chance to realise a good phenotype than others. Systematic effects that affect phenotypes are called *fixed* effects, e.g. the effect of the animals' sex, its herd (flock) or management group, the season it was born in, whether it was born as a single or twin, etc. For those fixed effects that are observable we can do a correction. This is in contrast to the *random* environmental effects "E" which we cannot observe, and cannot correct for.

Correction for fixed effects will be discussed in more detail when we discuss linear models and BLUP. However, the principle is that for a fair comparison among animals, we need to consider their observed phenotype as a deviation of an expected mean, i.e. as a deviation of a contemporary group mean.

A simple example can illustrate this concept.

Bull	**Phenotype**	**Herd Mean**	**P**	**EBV (h^2 = 0.30)**
Bert	330	300	+30	+9
John	300	260	+40	+12

So although Bert is a bigger bull, its EBV is lower. He was bigger mainly because of being in a good herd. Correcting for fixed effects makes sense, and is the main reason why selecting on EBV is more sensible than selecting on phenotype. However, at the same time this creates a lot of confusion as breeders might wonder why their best looking animals do not have the best EBV.

Note that it is possible that Bert's herd used better bulls, and in that case the correction would be unfair. However, in the BLUP procedure, there is a joint correction for herds and bulls used in these herds, and BLUP would take such a thing into account (this was one of the main reasons why BLUP was introduced in dairy cattle evaluation in the 1970s).

Besides correcting for fixed class effects, as above, we can also correct for continuous effects such as age. In the example below, we use a correction for weight of 12 kg/month (assume we we have first estimated from data that growth per month is 12 kg). Each animal is adjusted to yearling weight, by adjusting their weight according to age. For example, Frank was measured at 11 mo, and we expect it would be 12 kg heavier if it had been measured at 12 months. Therefore, it gets 12 kg extra credit, and we put his corrected 12 mo weight at 302 kg.

Bull	**Phenotype**	**Age (mo)**	**Corrected Phenotype**[1]	**P**	**EBV (h^2 = 0.30)**
Frank	290	11	302	+2	+0.6
Ben	305	13	293	+7	-2.1

[1] assuming that growth per month is 12 kg.

Properties of Estimated Breeding Values

Accuracy of EBV

The accuracy is defined as the correlation between true and estimated breeding value. The symbol for accuracy is r_{IA}

Since the EBV is often indicated as an Index (I), - see Topic 3- the true breeding value has symbol A and r is a common symbol for correlation.

The accuracy is between 0 and 1 (or 0% and 100%). In the extreme case of no information, the accuracy of a breeding value is 0, and with a very large amount of information, the accuracy will approach 1. Table 2.3 shows examples of accuracy. It illustrates that:

- Accuracy is higher when more information is used, e.g. from relatives and progeny
- The accuracy is higher for traits with a higher heritability, but the effect of heritability becomes smaller with more information used
- The accuracy of parent average depends on the parent EBV accuracy and not on heritability (but note that with low heritability it will be harder for a parent to achieve a certain accuracy)
- The accuracy of information from collateral relatives (i.e. siblings) is limited to 0.5 for HS and 0.71 for FS. A progeny test is required to obtain higher accuracies

Table 3. Accuracies of EBV depending on source of information used

Information used	$h^2 = 0.10$	$h^2 = 0.30$
Sire EBV (r_{IA}=0.5)	0.25	0.25
Sire EBV (r_{IA}=0.9)	0.45	0.45
Sire EBV (r_{IA}=0.5) + Dam EBV (r_{IA}=0.5)	0.35	0.35
Sire EBV (r_{IA}=0.9) + Dam EBV (r_{IA}=0.5)	0.51	0.51
Own Performance only	0.32	0.55
OP+ Sire EBV (r_{IA}=0.9)+ Dam EBV (r_{IA}=0.5)	0.57	0.66
Mean of 5 full sibs	0.32	0.48
Mean of 10 half sibs	0.23	0.33
OP + 5 FS + 10 HS	0.43	0.65
Mean of 1000 half sibs	0.49	0.50
Mean of 1000 full sibs	0.70	0.71
Mean of 20 progeny	0.58	0.79
Mean of 100 progeny	0.85	0.94
Mean of 1000 progeny	0.98	0.99

Accuracies can be derived using selection index theory. Here we only give a simple example for the derivation of accuracy of an EBV based own performance

EBV = I = h^2P giving $r_{IA} = r_{h2P,A}$

$$r_{h2P,A} = \frac{Cov(h^2P, A)}{\sqrt{V(h^2P)VA}} = \frac{h^2V_A}{\sqrt{h^4V_PV_A}} = \frac{h^2V_A}{\sqrt{h^2V_AV_A}} = \frac{h^2}{\sqrt{h^2}} = h$$

If the heritability is higher, EBV's based on own performance records become more accurate.

Variance among EBV

The variance among EBVs is of practical value because:

- it can give us an indication of the difference in EBV between the highest and lowest animals
- It is used to predict selection differential, e.g. the average EBV of the best 10% of animals

In general:

$$Var(EBV) = r_{IA}^2 VA \quad \text{and} \quad \sigma_{EBV} = r_{IA}\,\sigma_A$$

where r_{IA} is the accuracy of the EBV. Hence, the variance of the EBV's is equal to the accuracy-squared multiplied by the variance of the true breeding values (additive genetic variance).

It is useful to consider the following

If $r_{IA} = 0$ then Var(EBV) = 0:	all EBVs have the same value (=0)
If $r_{IA} = 1$ then Var(EBV) = 1:	the variance of EBV is equal to the variance of breeding values. All EBV should be equal to the true BV with this accuracy, and there is no prediction error.

Var(EBV) is generally smaller than VA
Var(EBV) becomes larger when accuracy is higher. i.e. the EBV of older animals will be more apart than those of young animals. The same holds for EBV of intensely measured nucleus animals compared to the EBV of base animals that have less information and therefore EBVs closer to each other.

Example: Single trait/own performance case:

$Var(EBV) = Var(h^2P) = h^4 VP = h^2 VA$

[... as $h^2 = VA / VP \quad VP = VA/h^2$]

In Table 2.2, the heritability is equal to 0.30, and the accuracy based on own performance EBV is $\sqrt{0.30} = 0.57$.

We expect Var(EBV) = 0.30 VA and $SD_{EBV} = 0.57\ \sigma_A$.

Using the numbers from Table 2.2 we obtain Var(EBV) = 10.3 and $\sigma_{EBV} = 3.2$. Remember that $\sigma_A = 5.7$ and VA = 32.2

Prediction Error Variance

The Prediction Error Variance (PEV) gives insight into the amount of error, and therefore the distribution of the true breeding value – see Figure 2. For this distribution we use the standard deviation, which is the Standard Error of Prediction (SEP). This distribution can be used when assessing a change in an EBV when more information becomes available – how much can they still change?
The prediction error variance (PEV) is calculated as:

$V(A - EBV) = (1 - r_{IA}^2)V_A$

And the Standard Error of Prediction (SEP) is $\sqrt{(PEV)}$

$$=\sqrt{(1-r_{IA}^2)V_A}$$

<u>Example:</u> Single trait / own performance case:
V(prediction error) = $V(A - EBV) = Var(A) + Var(EBV) - 2cov(A, EBV)$

$= V_A + h^2V_A - 2Cov(A, h^2P)$

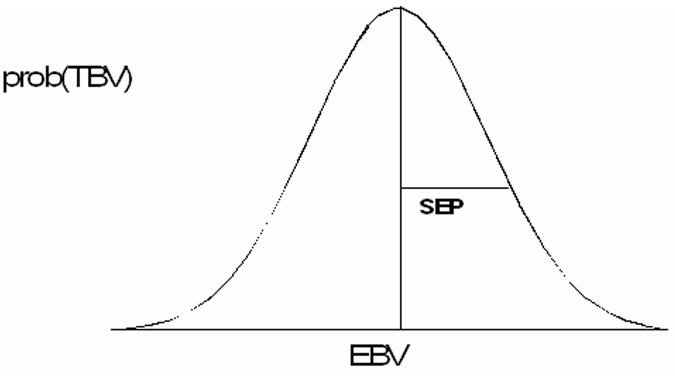
$= V_A + h^2V_A - 2h^2V_A \quad = V_A - h^2V_A = (1-h^2)V_A$

It is useful to consider the following:

- when there is no information, and accuracy is 0: all EBV's will be 0 and the variance of the prediction error is equal to V_A.
- when there is full information, the EBV will be equal to the true BV and the variance of the prediction error will be 0.
- PEV becomes smaller with higher accuracy
- Var(EBV) + PEV is equal to VA: $r_{IA}^2 V_A + (1 - r_{IA}^2)V_A = V_A$.

The prediction error of an EBV is important as it gives us an indication of the difference between the TBV and the EBV. This is important for example to answer questions like: how much could an EBV still change if we obtain more information on the animal. Changes in EBV's are not good for the industry's confidence in the genetic evaluation system. However, we have to realise that an EBV is never exact, unless the accuracy is 100%. We expect the TBV to be the same as the EBV, but there is a certain probability that it will be a bit different. The probability distribution of the TBV, given an EBV looks like Fig. 2.

Figure 2 The distribution of true breeding value (TBV), given the estimated breeding value (EBV). The SD of the distribution is equal to the standard error of prediction (SEP)



Take again the example where the best bull had an EBV for yearling weight of +4.5.

VA = 32.2 kg^2; $\sigma_A = 5.7$; $r_{IA} = 0.57$ and $r^2_{IA} = 0.32$. Then the SEP = $\sqrt{(1-0.32)}.5.7 = 4.7$.

If we would take a 95% confidence interval for the TBV we would take EBV± 1.96 SEP
SEP is +4.5 ± 1.96*4.7 is a range from -4.7 to13.7.

We see that even with a high heritability (and with r_{IA} = 0.57), the TBV can deviate still quite a bit from the EBV and it is not surprising that EBVs still change as more information becomes known about an animal. Such information can come from relatives such as the sire, the dam, half and full sibs or progeny (and possibly even more distant relatives). Using information from progeny is the only way to obtain EBV's with a very high accuracy. For example, dairy bulls often have thousands of progeny, and the accuracy of their EBV is close to 1. Such EBV's are not expected to change anymore in subsequent genetic evaluations. In fact, if EBV's are changing more than expected based on the PEV, this could be a sign that something is wrong with the evaluation procedure, e.g. a wrong model is used. However, Table 4 and Figure 3 below show that even accurate EBVs can still change.

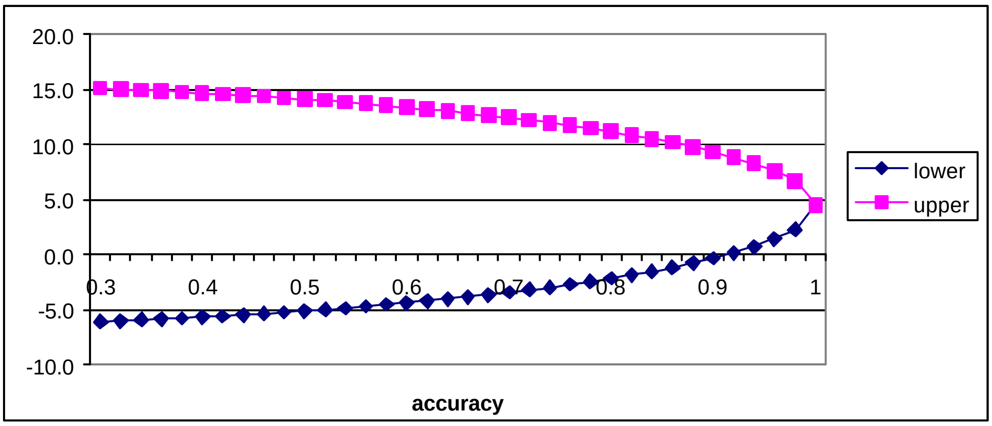
Table 4 gives confidence intervals about the best bull breeding value for different accuracies. It illustrates that, even with high accuracy, confidence intervals are still quite large. However, one always needs to take Fig. 2. in mind, showing that the highest probability about TBV is around the EBV.

Table 4. 95% Confidence interval of TBV of the best bull (EBV = +4.5) for different accuracies (s_A = 5.7)

Accuracy	SEP	lower thresh.	upper thresh.
0.51 (parent average)	4.88	-5.1	14.0
0.67 (PA + Own Performance)	4.21	-3.8	12.7
0.85 (PA + OP + 20 progeny)	2.99	-1.4	10.3
0.95 (PA + OP + 100 progeny)	1.77	1.0	8.0
0.99 (PA + OP + 600 progeny)	0.80	2.9	6.0
0.999 (PA + OP + 6000 progeny)	0.25	4.0	5.0

Table 4 might suggest that it is not very useful to have a high accuracy. Also Figure 3 shows that we can only have a very high confidence about EBV when accuracies are extremely high. However, it is wrong to conclude that only breeding animals with the highest accuracy should be used. In the next section we will see that response to selection depends linearly on accuracy. In optimising breeding programs, where we need to balance accuracy versus generation interval, it is often efficient to select younger animals and reduce generation interval while accepting lower selection accuracy.

Figure 3. 95% confidence interval of TBV (Y-axis, kg) of the best bull (EBV = +4.5) for different accuracies (s_A = 5.7).



Response to Selection

Ultimately the main issue about EBVs is the response we may expect from selecting on them.

The expected value of a selected group of animals - when selecting on EBV:

Expected average EBV: $i.\sigma_{EBV}$

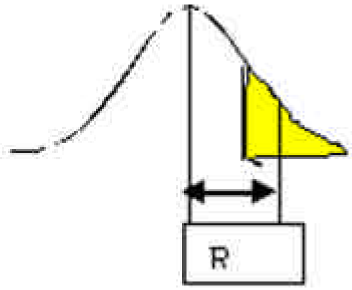
Expected average true BV: $i.\sigma_{EBV} = i.r_{IA}.\sigma_A$

Because the expected value of an EBV is equal to the true BV, see Fig. 2.2.

The expected breeding value of a selected group is equal to selection response.
Note that selection response depends directly (linearly) on accuracy

The response is equal to the selection intensity multiplied by the SD of the EBV.

$R = i.\sigma_{EBV}$



More generally:

Response = i r_{IA} σ_A

Intensity * Accuracy * Genetic SD

Often there is more information available on the selection candidates of one sex, and the accuracy of EBV's may differ between sexes. Also, the selection intensity will differ. Furthermore, we are interested in a response *per year* rather than per generation. A more appropriate formula to predict selection response is therefore:

Response per year

$$R_{yr} = \frac{i_m s_{EBVm} + i_f s_{EBVf}}{L_m + L_f} = \frac{i_m r_{IA-m} + i_f r_{IA-f}}{L_m + L_f} s_A$$

Note that with a lot of information on each animal, σ_{EBV} increases and so response increases. In other words, the response to selection is directly linked to the accuracy of EBV. It makes sense therefore, to increase the accuracy of EBV by including relatives' information. This is particularly important if we select on traits with low heritability, since selection on own phenotype only (mass selection) is not very accurate in that case. Also, the use of family information can be very useful for traits which can be measured on one sex only, or they are measured very late in (or even after!) life (e.g. longevity, carcase traits).

Predicted Progeny Performance based on Parental EBV

Expected breeding value of offspring:

$EBV_{offspring} = ½EBV_{sire} + ½EBV_{dam}$

Note that $\hat{P}$ and $\hat{G}$ are equal to $EBV_{offspring}$, as progeny dominance deviation and environmental deviation are unknown and have 'expectation' zero.

Sometimes it is stated that the heritability of an EBV is equal to 1.
This depends on the definition of heritability. The relevant definition in the context of selection response is:

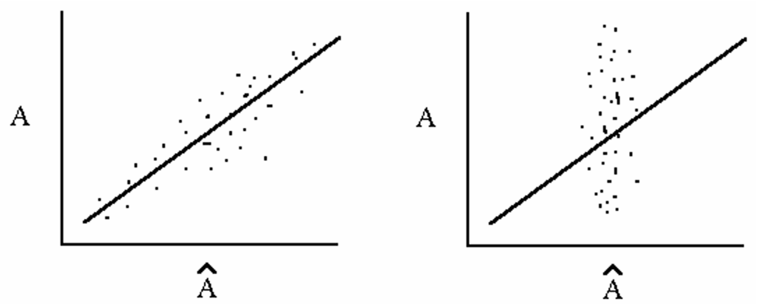
"Proportion of parental superiority (in EBV) transmitted to progeny"

This is equal to the regression of true breeding value on EBV (how much difference do we expect between progeny for a certain difference of EBV) (Fig. 2.4)

$$b_{A,EBV} = \frac{\operatorname{cov}(A, EBV)}{\operatorname{var}(EBV)} = \frac{r_{IA}VA}{r_{IA}VA} = 1$$

A selected animal is expected to pass half of this EBV superiority on to its progeny independent of the accuracy of that EBV.

Figure 2.4. Regression of true breeding value A on EBV with high accuracy (left graph) and low accuracy (right graph).



Note that $b_{A,EBV}$ (the slope) is the same for high and low accuracy. The variance of inaccurate EBV's is very low, and therefore the selection superiority based on inaccurate EBV's will not be very high.

An interesting problem is the following. Suppose that two bulls have the same EBV, however, bull A has an accuracy of 95% (based on a progeny test) whereas bull B has an accuracy of 50% (based on parent average). Which bull should be selected?

Most people would vote for animal A. However, both animals have the same expected value for their progeny. The range around this expected value is higher for animal B. However, progeny have just as much reason to be better than their expected value than to be worse. Therefore, whether you choose A or B depends on your attitude towards risk. A breeder that is interested in breeding the very best bull might be more interested in animal B, as he has more chance that his best son will be high. A commercial producer might be more interested in reducing risk and go for animal A.

Table 5 Confidence interval of a son's breeding value and progeny performance of two bulls with equal EBV(+4.5) and with different accuracy.

		Son's BV		Individual Progeny		Mean of 50 Prog	
	Accuracy	LL	UL	LL	UL	LL	UL
Bull A	0.50	-8.5	+13	282	322	297	308
Bull B	0.95	- 7.5	+12	283	321	299	306

LL, UL = lower/ upper limit of 95% confidence interval, $\sigma_P = 10$; $\sigma_A = 5.7$

Again, it might seem that EBV are not of much value, as the confidence intervals about any prediction based on the EBV seems so large. However, again you should be reminded that ultimately, selection response depends linearly on selection accuracy. Table 2.6 illustrates a small simulation, where 10 bulls are ranked on their EBV based on parent average. It shows their actual realised 400-d weight as well as true BV and EBV based on own performance. For individual cases, there seem to be huge discrepancies. However, when selecting the top 50% (best 5), we see indeed that selection response depends on selection accuracy, but even inaccurate EBVs provide a worthwhile response (Table 7).

Table 6. EBV based on parent average, realised phenotype, true breeding value and EBV based on own performance for 10 bulls for 400-d weight.

EBV_PA	Phenotype	EBV_OP	True BV
9.7	433	13	34.4
5.9	378	-8.7	1.9
4.4	423	9	12.2
4.2	391	-3.7	0.4
4	378	-8.6	-23.5
-3.1	395	-2	-6.6
-4.8	415	6	17
-8.8	345	-22.2	-22.9
-9	379	-8.4	21.3
-11.5	391	-3.5	1.4

Table 7. Selection response based on EBV based on parent average (EBV_PA), EBV based on own performance (EBV_OP) or true breeding value (TBV) for top 50% of 10 bulls for 400-d weight (s_A = 19; h^2=0.4)

Selection On	Accuracy	Predicted Response[1]	Realised Response
EBV_PA	0.45	+6.8	+5
EBV_OP	0.63	+9.5	+11
TBV	1.00	+15	+17

[1] Response is calculated as the average TBV of the top 50% when ranking is based on each of the selection criteria.