

Quantitative genetics

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Lecture notes for students of MSc courses of Nutrition and Feed Safety and Animal Science



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Quantitative genetics

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Chapter 1. Introduction to Quantitative Genetics

Quantitative genetics is concerned with the exploration of the genetic differences among the individuals of a population based on the phenotypic (detectable) differences. Development of this field began at the beginning of the 20th century.

Among the several scientists the activity of **Ronald Fisher** (1890-1962) has to be emphasized who published as early as 1918 that the metrical traits are influenced by infinitesimally many genes and the effects of the individual genes are infinitesimally small (infinitesimal model). The softwares that presently used to estimate genetic parameters and breeding values are still based on this procedure. Fisher who also was one of the most outstanding statistician of the 20th century and (among other things) he developed the generally used F-probe. The American contemporary of Fisher was **Sewall Wright** (1889-1988), whose research activity is mostly well known at the field of inbreeding.

Jay Lush (1896-1982) an American geneticist was the first who applied the quantitative genetic methods in animal breeding while in Hungary this activity was fulfilled by **Artúr Horn** (1911-2003). Artúr Horn developed the cattle breed called Hungarofríz and he also played in role in the import of the Holstein-Friesian cattle breed to Hungary. His most important work Principles of animal breeding was published in 1955. For the high quality of his scientific activity in 1970 he received the International Golden Egg Award. Probably the most well known reference book of quantitative genetics was written by **Douglas Falconer** (1913-2004) an English geneticist (Introduction to Quantitative Genetics). The book received 4 editions (1960, 1981, 1990 and 1996). In Hungary the reference book of quantitative genetics was written by János Dohy (1934-2002) (Genetics for animal breeders, 1999).

The most important quantitative genetic application of animal breeding is to improve the successive generation (for the chosen traits). To improve the generation selection has to be conducted which is based on the so called breeding value. The procedure of breeding value estimation was developed by **Charles Henderson** (1911-1989) an American geneticist who called the method as BLUP (Applications of Linear Models in Animal Breeding 1984). The procedure is part of almost every breeding programme of the domesticated species.

In order to understand quantitative genetics the definition of some terms of genetics/population genetics must be given:

Gene – A segment of DNA whose nucleotide sequence codes for protein or RNA, or regulates other genes.

Allele – Alternative form of a gene.

Genotype (G) – An organism's genetic composition.

Allele frequency – The proportion of a given allele at a locus.

Locus – The position on a chromosome of a gene.

Autosomes – Chromosomes that do not differ between sexes.

Linked to sex chromosomes – genes are located at the X chromosome.

Regulated by sex – Expression of a gene (eg. boldness) determined by sex.

Single gene inheritance – The analyzed trait is determined by a single gene (eg. colour).

Poligenic inheritance – The analyzed trait is determined by multiple genes (eg. body weight).

Dominant – An allele whose phenotypic effect is expressed in both homozygotes and heterozygotes.

Codominant – Is a situation in which both alleles are equally strong and both alleles are visible in the hybrid genotype.

Additive gene effect – The traits is determined by the combined effects of several genes where it is assumed that there are no interactions between the alleles within or among the locuses.

Epistasis – The phenomenon where the effects of one gene are modified by another gene (at a different locus).

Population – Group of individuals belonging to the same species that live at the same area and have a chance to mate with each other.

Phenotype (P) – Measurements of the analyzed trait (eg. body weight).

Hardy-Weinberg equilibrium - In a large random-mating population with no selection, mutation, or migration, the gene frequencies are constant from generation to generation, and, furthermore there is a simple relationship between the allele and genotype frequencies.

Qualitative characters – Express some quality, the trait can be shown using a nominal scale (eg. colour).

Discrete quantitative characters – The trait can be expressed using integers (eg. Litter size).

Continuous quantitative characters – The trait can be expressed using real numbers (eg. hight). These characters are determined by the combined (additive) effects of several genes.

Chapter 2. Statistical terms

Quantitative genetics relies on the knowledge of mathematical statistics. The most important terms are described below:

Arithmetic mean - Arithmetic mean is the ratio of the sum of n numbers and n .

Range - Is defined as the difference between the maximum and minimum values in a set of observations.

Variance (σ^2) - Is the average squared deviation about the mean.

Standard deviation (σ) - Is the square root of the variance.

Coefficient of variation (CV) - Is the ratio of the standard deviation and the arithmetic mean multiplied by 100 (ie. given in %). The aim of its use to compare the data where the unit of measurement is different.

Normal distribution - In many (domesticated, wild) population it is often observed that for a given trait the measurements are concentrated around a given value (arithmetic mean). The normal distribution is determined by two parameters the mean (μ) and variance (σ).

Covariance (σ_{xy}) - Calculation of covariance is similar to that of the variance. The covariance measures how much two random variables (x , y) vary jointly.

Linear regression - Linear regression measures the linear relationship between the values of two random variables. For random variables it is often supposed that one random variable can be estimated using other variable(s) through a function. Our objective is to estimate the parameters of this function based on the samples. When the relationship of the x and y variables are linear then linear model can be applied ($y = a + bx + e$).

Correlation - The correlation coefficient (r) measures the strength of the linear relationship between two random variables. Values of the coefficient of correlation range between -1 and 1 . The positive correlation means that as values of one variable increase, increasing values of the other variable are observed. A negative correlation means that as values of one variable increase, decreasing values of the other variable are observed.

Chapter 3. Variance components

One of the most important phenomena used in quantitative genetics is that the relatives show resemblance in metrical traits. The degree of resemblance can be determined at population level with simple measurements. The degree of resemblance enables us to predict the magnitude of additive genetic variance. The proportion of the additive genetic variance compared to the total (phenotypic) variance determines the methods that can be applied in order to achieve the largest selection response at population level.

The relative groups used to predict additive genetic variance are: offspring – one parent, offspring – mid parent, half sibs and full sibs.

Before starting the detailed analysis of resemblance among relative some important properties of variance and covariance has to be presented:

$$\sigma_{XX} = \sigma^2_X$$

The covariance of any variable with itself is equal with the variance of this variable.

If a is a constant then:

$$\sigma_{Xa} = 0$$

$$\sigma_{aXY} = a\sigma_{XY}$$

When both a and b are constants then:

$$\sigma_{[(a+X), Y]} = \sigma_{XY}$$

The covariance of two sums is equal with the sums of the covariances:

$$\sigma_{[(X+Y), (W+Z)]} = \sigma_{XW} + \sigma_{YW} + \sigma_{XZ} + \sigma_{YZ}$$

Concerning the variance for a given a constant:

$$\sigma^2_{aX} = a^2\sigma^2_X$$

The variance of a sum is equal with the sum of the possible variances and covariances:

$$\sigma^2_{(X+Y)} = \sigma^2_X + \sigma^2_Y + 2\sigma_{XY}$$

Based on these properties the detailed derivation of the covariance between the various relative groups can be given.

The first groups is offspring – one parent. Phenotypic value (P) can be partitioned into two components: genotypic value (G) environmental effect (E) which can be given using the following equation

$$P = G + E.$$

The phenotype, genotype of the parent and the environment affecting the parent are denoted by P_p , G_p and E_p , respectively. For the offsprings the same items are denoted by P_o , G_o and E_o , respectively. Covariance between the progeny and one parent:

$$\sigma(P_o, P_p) = \sigma[(G_o + E_o), (G_p + E_p)],$$

which is according to the property covariance of a sum:

$$\sigma(P_o, P_p) = \sigma(G_o, G_p) + \sigma(G_o, E_p) + \sigma(E_o, G_p) + \sigma(E_o, E_p).$$

Let us assume that the covariance between the genotype and environment is zero and also that the the covariance between the environments affect parent and progeny is zero,

$$\sigma(P_o, P_p) = \sigma(G_o, G_p)$$

The genotypic value of the progeny ($G = A + D$) is determined by 50 % by that of one parent (A) thus:

$$\sigma[(A + D), 0.5A] = 0.5\sigma[(A + D), A] = 0.5[\sigma(A, D) + \sigma(A, A)] = 0.5\sigma(A, A) = 0.5\sigma^2_A$$

Thus the covariance between offspring and one parent is the half of the additive genetic variance.

When the average phenotype of both parents $0.5(P_{P1} + P_{P2})$ and the phenotype of the offspring are known (P_o) then the covariance between them is:

$$\sigma[P_o, 0.5(P_{P1} + P_{P2})] = 0.5[\sigma(P_o, P_{P1}) + \sigma(P_o, P_{P2})],$$

using the same derivation as with the offspring and one parent:

$$0.5[0.5\sigma^2(A) + 0.5\sigma^2(A)] = 0.5\sigma^2_A$$

which is the half of the additive genetic variance.

Half sib group consists of individuals where one parent is the common and the other parents are different. If one individual is mated to several individuals of the other sex selecting one-offspring of each mating a half-sib group can be formed. The average genotypic value of this group is equal to the half of the breeding value of the common parent. The covariance among half sib groups is equal to the variance of the 0.5 breeding values of the common parents which is one quarter of the additive genetic variance:

$$\sigma^2(0.5A) = 0.25\sigma^2_A$$

Full sib group consists of individuals where both parents are the common, thus the average genotypic value of this group is equal to the average of the breeding value of the two parents. The covariance among full sib groups is equal to the variance of the average breeding values of the common parents, which is half of the additive genetic variance. In case of the full sib groups beside the additive genetic component the covariance contains other components.

The first of these components is the 25% of the dominance variance ($0.25\sigma^2_D$) (the derivation of the dominance variance is beyond the scope of the lecture notes). The second component is the common environmental variance (σ^2_{Ec}). In order to understand this component one has to think about the litter mates that are reared together.

As the full sibs of the same litter are generally reared together and they experience the same environment (eg. milk production of their dam). The environments can be different for the different litters. The resemblance between full sibs is therefore greater than could be attributed to their common genes and the source of this increased resemblance is the above mentioned common environmental effect.

The covariance between full sibs:

$$0.5\sigma^2_A + 0.25\sigma^2_D + \sigma^2_{Ec}$$

The phenotypic resemblance between the various relative groups can be summarized as: (see table 1.)

Chapter 4. Heritability I

Heritability is one of the most important characteristics of the metrical traits.

Heritability gives the proportion of the total (phenotypic) variance that can be attributed to breeding values of the different animals. After Wright the symbol of heritability is h^2 where

$$h^2 = b_{AP},$$

Thus heritability is the regression of breeding value on phenotypic value:

$$b_{AP} = \sigma_{AP} / \sigma_P^2$$

From which it follows that the correlation between breeding value and phenotypic value is the square root of the heritability (h)

$$r_{AP} = \sigma_{AP} / (\sigma_{PA} \times \sigma_P) = b_{AP} \times (\sigma_P / \sigma_A) = h^2 \times (1 / h) = h,$$

From the definition of heritability we see that an individual's estimated breeding value is the product of its phenotypic value and the heritability:

$$\hat{A} = b_{AP} \times P = h^2 \times P$$

Breeding values and phenotypic values both being reckoned as deviations from the population mean. The heritability has a predictive role and expresses the reliability of the phenotypic value as guide to the breeding value. For this reason the heritability enters into almost every formula connected with breeding methods. Although the predicted heritability can only be used in the population where it was predicted heritability values for some important pig production traits are given in the next table (table 2.).

The heritability is estimated from the degree of resemblance between relatives.

At the end of the previous chapter the covariance of the various relative groups are presented. Based on that table the regression (b) or the correlation (r) gives the heritability in the following manner: (see table 3.)

The estimation of the heritability from the regression of offspring on parents is straightforward. The covariance between the offspring and parents (female/male) has to be divided by the parents' variance then it has to be multiplied by two.

When measurements of both parents are available then the mid parent values has to be calculated. Using the mid parent values (instead of the parental values) the calculation is the same as previously but the regression directly gives the heritability.

See example.

Chapter 5. Heritability II

Heritability of any trait can be estimated from correlation among half-sib or full-sib groups (r_{HS} , r_{FS}) but the calculation is more complex than it was the case with parent offspring regression. In pig breeding the boars are mated to several sows and each sow gives birth to several piglets. Among the progeny groups created this way full-sib, half-sib groups and unrelated individuals can be separated. The total phenotypic variance (σ_p^2) of the progeny group can be partitioned to several components. The first variance component is the between sire component (σ_s^2), where the source of the variance is the difference among the progeny groups originating from the different boars. The second variance component is the between dam component (σ_d^2) (within the sires), where the source of the variance is the difference among the progeny groups originating from the different dams mated to the sires. The third variance component is the within dam (σ_e^2) variance component: (see table 4.)

Where σ_{HS} is the covariance among measurements of half sib groups, σ_{FS} is the covariance among measurements of full sib groups, σ_{Ew}^2 is the variance originating from the differences of individuals from their group means.

When estimating heritability using the correlation among the sib groups an important topic is the accuracy and bias of the estimated parameters. Generally the more closely related is the relationship within the group the more accurate is the estimated parameter. However, accuracy is less important than bias. When full-sib groups are used to estimate heritability the estimated parameter also contains the common environmental variance. The effect of this component is large and it is not easy to remove it even using planned experimental design. Besides the estimate is also biased with a part of the dominance variance. Therefore the heritability estimate based on full-sib groups is not reliable and its importance is that it shows the upper limit of the heritability of the analyzed traits.

Example:

The average backfat depth of the offspring groups of a pig population at 100 kg body was the following: (see table 5.)

What is the heritability of the average backfat depth at the given weight?

Solution:

Three different alternatives can be used. According the first and second alternatives the data is analyzed only by the sows and boars, respectively. In the third alternative all sources of information are accounted for.

In the first alternative only the effect of the sows is considered. The last column of the table is ignored (the between sire component (σ_s^2) is not used). The objective is to divide the phenotypic variance (σ_p^2) to the variance components between the sows (σ_d^2), and within the sows (σ_e^2). (table 6.)

The within sow component (σ_e^2) is the average of the variances calculated from the measurements of the sows. $\sigma_e^2 = (1/8) \times (1 + 2.33 + 3 + 2.33 + 1.33 + 1.33 + 0.33 + 31) = 5.33$

The means of the sows' measurements: (table 7.)

Variance calculated from the means = $3.0297616 = \sigma_d^2 + [(\sigma_e^2) / N]$,

$$\sigma_e^2 = 5.33,$$

$$\sigma_d^2 = 1.25,$$

$$\sigma_p^2 = \sigma_d^2 + \sigma_e^2 = 1.25 + 5.33 = 6.58$$

$$\sigma_d^2 / (\sigma_d^2 + \sigma_e^2) = 1.25 / 6.58 = 0.19,$$

$$h^2 = 4 \times [\sigma_d^2 / (\sigma_d^2 + \sigma_e^2)] = 0.76$$

The received heritability is overestimated.

In the second alternative only the effect of the boars is considered while the sows are ignored (the between dam component (σ_d^2) is not used). The total phenotypic variance is divided to the variance components between the

boars (σ_s^2), and within the boars (σ_e^2) from which the half sib correlation (rHS) can be calculated. The data can be sorted to the following form: (table 8.)

The way of calculation is the same. The within boar component (σ_e^2) is the average of the variances calculated from the measurements of the boars: $\sigma_e^2 = (1 / 4) \times (4.66 + 4.26 + 1.9 + 13.06) = 5.97$

To determine the between boar component first the measurements of each boar has to be averaged then using these averages as measurements their variance has to be calculated. This variance is the between boar variance component (σ_s^2) + the within boar component (σ_e^2) / N, where N = the number of measurements per boar (in this example N = 6).

The variance calculated from the means = $1.63574 = \sigma_s^2 + [(\sigma_e^2) / N]$

$$\sigma_e^2 = 5.97,$$

$$\sigma_s^2 = 0.64$$

$$\sigma_p^2 = \sigma_s^2 + \sigma_e^2 = 0.64 + 5.97 = 6.61$$

$$r_{HS} = 0.64 / 6.61 = 0.096,$$

$$h^2 = 4 \times r_{HS} = 0.38$$

The received heritability decreased. However it has to be noted that all offsprings were treated as if they were half sibs. In reality the offsprings were partly full sibs and partly half sibs.

Finally all available information is used to estimate heritability. The phenotypic variance (σ_p^2) can be partitioned to the variance components between the boars (σ_s^2), between the sows (within the boars) (σ_d^2), and within the sows (σ_e^2). From these components the full sib and half sib correlation can be calculated (r_{HS} , r_{FS}). In order to give a generalized solution let us suppose that s boars (in our example s = 4) mated to d sows (per boar) (in our example d = 2), and we have n measurements for each litter (in our example n = 3). The variance components have to be separated. The way of calculation is different than previously. (table 9.)

Where DF = degree of freedom, SS = sum of squares, MS = mean squares

$$MS = SS / DF$$

$$SS_T = \sum X^2 - CF,$$

$$CF \text{ (correction factor)} = (\sum X)^2 / (s \times d \times n)$$

To calculate SST-t the individual measurements are squared then summed from which the CF has to be subtracted (which is the square of the summed measurements divided by the number of measurements).

$$SS_T = (28^2 + \dots + 32^2) - [(28 + \dots + 32)^2 / (4 \times 2 \times 3)] = 19021 - [(673)^2 / 24] = 148.96$$

$$SS_s = (1 / d \times n) \times \sum (\text{boar's total})^2 - CF$$

In the present example we have 4 boars each with 6 measurements. The sum of the first boar's measurements is $28 + 29 + 27 + 30 + 33 + 31 = 178$. Similarly the other boar sums are 170, 165 and 160. These sums have to be squared then summed divided by the number of progeny per boar then from the received value the CF has to be subtracted.

$$SS_s = (1 / 2 \times 3) \times \sum (178^2 + 170^2 + 165^2 + 160^2) - [(673)^2 / 24] = 29.46$$

$$SS_d = (1 / n) \times \sum (\text{sow's total})^2 - CF - SS_s$$

In our example we have 8 sows each with 3 observations. The sum of the of sows are 84, 94, 81, 89, 80, 85, 82, 78, respectively.

These sums have to be squared then summed divided by the number of progeny per sow (3) then from the received value the CF and SS_s have to be subtracted.

$$SS_d = (1 / 3) \times \sum (84^2 + 94^2 + 81^2 + 89^2 + 80^2 + 85^2 + 82^2 + 78^2) - [(673)^2 / 24] - 29.46 = 34.17$$

The last variance component can be determined from the other components: $SS_e = SS_T - SS_s - SS_d = 148.96 - 29.46 - 34.17 = 85.33$

The analysis of variance table is the following: (table 10.)

$$MS_e = \sigma_e^2 = 5.33$$

$$MS_d = \sigma_e^2 + n \times \sigma_d^2 = 5.33 + 3 \times \sigma_d^2 = 8.54$$

$$\sigma_d^2 = 1.07$$

$$MS_s = \sigma_e^2 + n \times \sigma_d^2 + n \times d \times \sigma_s^2 = 5.33 + 3 \times 1.07 + 3 \times 2 \times \sigma_s^2 = 9.82$$

$$\sigma_s^2 = 0.21$$

$$\sigma_p^2 = \sigma_e^2 + \sigma_d^2 + \sigma_s^2 = 5.33 + 1.07 + 0.21 = 6.61$$

The half sib correlation:

$$r_{HS} = \sigma_s^2 / \sigma_p^2 = 0.21 / 6.61 = 0.032$$

$$h^2 = 4 \times r_{HS} = 0.128$$

The full sib correlation:

$$r_{FS} = (\sigma_s^2 + \sigma_d^2) / \sigma_p^2 = (0.21 + 1.07) / 6.61 = 0.19$$

$$h^2 = 2 \times r_{FS} = 0.38$$

From the results it is clear that when all information source was considered the heritability estimates based on half sib and full sin correlations (r_{HS} , r_{FS}) are substantially different. The results also indicate that the common environmental variance and the dominance variance is not negligible and the heritability estimate based on r_{FS} is biased.

Chapter 6. Heritability III

In the practice of animal breeding the available datasets are not balanced thus the ANOVA based methods are not suitable for estimating heritability. In order that the estimated genetic parameters would not be biased the effect of selection has to be taken into account. An appropriate method is the REML procedure developed by Patterson and Thompson (1971). Because the calculation is extremely difficult it cannot be carried out by hand. Practical application became possible since the late 1980s with the development of the following softwares: VCE, ASREML.

In order to estimate heritability we need two files. The first one is the so called data file. The data file contains the measurements of the analyzed trait and additional information about factors influencing the traits. The additional information generally gives the date (year-month) and place (herd) of measurements and the sex and body weight of the individuals. Besides there can be other information which has an effect on the measurements. The second file is the pedigree file which defines relationship among animals.

Using VCE software estimation of heritability is accomplished in two consecutive steps. In the first step the data is recoded to the required form (VCE input). Running of PEST is possible using a parameter file where the structure of the data and pedigree files are given. In the model section the traits and their influencing factors are defined. After the data is recoded the genetic parameters can be estimated using the VCE6 software, similarly to PEST a parameter file is applied. The software solves the mixed model equations in iterations. Solution is obtained when the difference between the iteration decreases to zero (convergence).

With the knowledge of the genetic parameters breeding value estimation (PEST) and selection can be carried out. Order to predict breeding values we need the variance-covariance components estimated by VCE and these components have to be inserted to a given place of the PEST parameter file. Subsequently the PEST software is used and the predicted breeding values are obtained. Selection is carried out based on the predicted breeding values.

Chapter 7. Repeatability

In animal breeding repeatability has high importance. It can only be calculated when the trait can be measured on the same individual (eg. litter size at the successive parities) several times. Such trait is for example the litter size at the successive parities. The total variance can be partitioned into variance within individuals and variance between individuals. The within-individual component is caused by temporary differences of environment between successive performances (σ_{Es}^2). The differences between individuals are both genetic and (permanent) environmental. The general environmental variance (σ_{Eg}^2) refers to environmental variance arising from permanent or non-localized circumstances. The repeatability is the correlation between repeated measurements of the same individual (r). The repeatability expresses the proportion of the variance of single measurements that is due to permanent differences between individuals, both genetic and environmental. Expressing the repeatability by an equation:

$$r = \sigma_A^2 + \sigma_D^2 + \sigma_{Eg}^2 / \sigma_P^2$$

In order to calculate repeatability the variance between individuals ($\sigma_A^2 + \sigma_D^2 + \sigma_{Eg}^2$) and within individuals (σ_{Es}^2), has to be separated then the former has to be divided by the total variance ($\sigma_A^2 + \sigma_D^2 + \sigma_{Eg}^2 + \sigma_{Es}^2$) (sum of the between and within individual variance components).

Example:

Example: litter size of 5 sows at the first three parities was the following: (table 11.)

The repeatability has to be calculated.

Solution:

First the variance components between and within individuals have to be determined.

The within individuals variance component can be calculated as the average of the variances calculated from the individual measurements.

In the present example the first sow has three measurements: 10, 11, 11. Based on our earlier studies the variance of these measurements is:

$$(1 / N - 1) \times (\sum X^2 - (\sum X)^2 / N),$$

where N = number of measurements per sow (3 in this example).

The variance of the first sow's measurements is:

$$(1 / 3 - 1) \times (10^2 + 11^2 + 11^2 - (10 + 11 + 11)^2 / 3) = 0.33$$

Similarly, the variance of the second sow's measurements is:

$$(1 / 3 - 1) \times (9^2 + 10^2 + 11^2 - (9 + 10 + 11)^2 / 3) = 1.0$$

For the third sow:

$$(1 / 3 - 1) \times (11^2 + 11^2 + 12^2 - (11 + 11 + 12)^2 / 3) = 0.33$$

For the fourth sow:

$$(1 / 3 - 1) \times (10^2 + 9^2 + 12^2 - (10 + 9 + 12)^2 / 3) = 0.83$$

For the fifth sow each measurement was 10 so the variance of these numbers is zero.

The within sow variance component is: $(0.33 + 1.0 + 0.33 + 0.83 + 0.0) / 5 = 0.498$

To calculate the between individuals variance component first the individual measurements have to be averaged. Then using these averages as "measurements" their variance has to be determined. This variance is the between

individuals variance component + the within individuals variance component / n, where n = number of measurements per individual.

In the present example the litter size averages for the 5 sows were the following: 10.66; 10; 11.33; 10.3; 10. Their variance is: $(1 / 5 - 1) \times (10.66^2 + 10^2 + 11.33^2 + 10.3^2 + 10^2) = 0.31$. From this variance the between individuals variance component can be obtained: $0.31 - (\text{within individuals variance component} / n)$. Thus the between individuals variance component is: $0.31 - (0.498 / 3) = 0.151$. The repeatability is: $0.151 / (0.151 + 0.498) = 0.232$. Litter size can be characterized as a reproductive trait which generally has low heritability. This is justified by the present result as the repeatability sets the upper limit of the heritability where the latter can only be smaller or equal than the former. The advantage of the repeated measurement is that with the increasing number of measurements the accuracy of the variance components also increases (proportionally to the total variance). The variance component (σ^2_{Es}) is reduced by repeated measurements (n). The total variance can be calculated using the following equation:

$$\sigma^2_{P(N)} = \sigma^2_A + \sigma^2_D + \sigma^2_{Eg} + (1 / N) \times \sigma^2_{Es}$$

where n = number of measurements.

From the equation it follows that when the repeatability is low and there is a large special environmental variance (σ^2_{Es}) multiple measurements may lead to a worthwhile gain in accuracy. In this case this variance component decreases substantially with the increasing number of measurements and repeatability also increases. However, when the special environmental variance (σ^2_{Es}) is small then the repeatability is large and in this case the increased number of measurements does not change accuracy substantially.

Repeatability can also be used for the prediction of future performance (when some parameters of the population are known). It is based on the fact that the repeatability is the correlation between the successive measurements. Assume that each individual has two measurements: X and Y. In this case repeatability is the correlation coefficient between X and Y. Correlation coefficient can be obtained by dividing the covariance between X and Y (σ_{XY}) by the product of the standard deviations of X and Y ($\sigma_X \times \sigma_Y$):

$$r = \sigma_{XY} / (\sigma_X \times \sigma_Y)$$

In order to predict future performance the regression coefficient of Y on X has to be calculated. The regression coefficient is the covariance between X and Y (σ_{XY}) divided by the variance of the independent (X) variable:

$$b = \sigma_{XY} / (\sigma_X^2),$$

alternatively:

$$r \times (\sigma_Y / \sigma_X).$$

For the prediction of future performance at population level the correlation coefficients between the successive measurements and their means and standard deviations have to be known.

Example:

The correlation (repeatability) between the milk yields of the first and second lactations is 0.4. The mean and standard deviation of the first and second lactations are: 4096 kg, and 696 kg; 4232 kg and 934 kg, respectively.

The second lactation milk yield of an individual has to be predicted when it is known that at the first lactation the milk yield of this cow was 5000 kg.

Solution:

$$Y - \bar{Y} = b \times (X - \bar{X}),$$

$$\text{where } \bar{Y} = 4232;$$

$$b = 0.4 \times (934 / 696);$$

$$X = 5000 \text{ kg}; \bar{X} = 4096 \text{ kg}$$

Using the equation: $Y = 4716.5 \text{ kg}$.

Chapter 8. Selection

In the previous chapters the genetic properties of a population was shown as it exists under random mating. In this chapter we will consider the changes brought about the action of a breeder. There are two ways in which the breeder can modify the genetic properties of a population. Choice of the individuals forming the next generation (selection), control the way in which the parents are mated (topic of inbreeding and crossbreeding). Selection means choosing the "best" animal. The simplest form of selection is to select individuals solely according to their own performance. In most breeding programmes the animals are selected based on predicted breeding values (BLUP) of various traits. The most important phenomenon connected to selection is the change of the population mean. This is called selection response and symbolized by "R". Selection is characterized by the superiority of the selected individuals (compared to the whole unselected population). This is called selection difference and symbolized by "S". When the selected trait follows the normal distribution, moreover selection is done by truncation then the selection differential depends only the proportion of the population included in the selected group. In this case the selection differential can be expressed in terms of the phenotypic standard deviation. Knowing the selected proportion the selection intensity can be determined from statistical tables. Selection intensity (i) = selection differential (S) divided by the phenotypic variance of the parental generation (σ_P), that is

$$i = (S) / (\sigma_P).$$

Selection differential and intensity can be different for males and females. Where S_m , S_f , i_m , i_f , are Selection differential and intensity for the males and females, respectively. Selection response (R) = selection intensity multiplied by the heritability and by the phenotypic variance of the parental generation:

$$R = i \times h^2 \times \sigma_P = i \times h \times \sigma_A.$$

So far it was assumed that in the course of selection the same trait is measured which is improved (direct selection). However in certain cases the measured and improved traits are not identical (indirect selection). Indirect selection is possible because of correlation between the traits. The question is that when X trait is selected how will Y trait change as a result of this selection?

The selection response (R_X) of the trait X (which is selected) is the average breeding value of the selected animals. Therefore the selection response of the Y trait (CR_Y) can be obtained by the regression of the breeding values of Y on the breeding values of X multiplied by the selection response of trait X. Regression is the ratio of the appropriate covariance and variance:

$$b = \sigma_{AXY} / (\sigma_{AX}^2) = r_A \times (\sigma_{AY} / \sigma_{AX}).$$

Selection response of trait X:

$$R_X = i \times h_X \times \sigma_{AX}.$$

Selection response of trait Y (originating from the genetic correlation between X and Y):

$$CR_Y = i \times h_X \times r_A \times \sigma_{AY},$$

alternatively,

$$CR_Y = i \times h_X \times h_Y \times r_A \times \sigma_{PY}.$$

Selection response of trait Y – originating from the selection of X and genetic correlation between X and Y – can only be estimated when heritabilities and the genetic correlation are known. The direct and indirect selection response (CR, R) can also be used to predict the genetic correlation (r_A). The correlated selection response raises the question if it is possible to observe higher indirect selection response for trait Y (CR_Y) compared to the direct selection response of the same trait (R_Y)? Practically we examine if $(CR_Y) / (R_Y) > 1$. Based on the previous derivations:

$$(CR_Y) / (R_Y) = (i_X \times h_X \times r_A \times \sigma_{AY}) / (i_Y \times h_Y \times \sigma_{AY}) = (i_X \times r_A \times h_X) / (i_Y \times h_Y).$$

Supposing that the selection intensities are the same the ratio is greater than zero when $r_A \times h_X > h_Y$.

The indirect selection can be more effective than the direct selection if the trait to be improved has low heritability but there exist another trait with high heritability where the genetic correlation between the traits is also high. Regardless of the value of $(CR_Y) / R_Y$ indirect selection can be applied when measuring a trait is expensive (e.g. feed conversion ratio).

Genetic correlation can also be used to characterize genetic environment interaction. Certain genotype that has a favourable performance in a given environment can exhibit low performance in another environment if there is genetic environment interaction. In order to characterize genetic environment interaction by means of genetic correlation the trait measured in different environments has to be considered as separate traits.

Let us suppose that X = average daily gain using a favourable diet, Y = average daily gain using an unfavourable diet. The objective is to examine the selection response of trait Y when selection targets trait X (compared to the direct selection response of trait Y).

This is the ratio of the indirect and direct selection response:

$$(CR_Y) / (R_Y) = r_A \times (iX \times h_X) / (iY \times h_Y).$$

The main question is the genetic correlation between X and Y . When the correlation is high and the heritability values are not substantially different then the quality of the diet will not heavily influence the results of selection.

However, when the estimated genetic correlation is low then it is advisable to select the individuals in the same environment where their production will be realized.

Chapter 9. Pedigree analysis

The most important goal of animal breeders is to create and maintain animal populations of high genetic merit. To achieve this goal the background and structure of the populations has to be known. The required information can be obtained by means of pedigree analysis or by molecular markers. From the available methods the pedigree analysis is much more cost effective. During the last years exploration of the populations' genetic variability was gaining importance. By means of the pedigree analysis population structure and its genetic variability can precisely be estimated. Pedigree analysis has an important role in conservation genetic programs of populations. By means of pedigree analysis various parameters can be calculated and the inbreeding level of the population can be kept at an acceptable level. Based on genealogy the following parameters can be estimated: breeding values and level of inbreeding, line or family affiliation, relatedness, frequency of harmful recessive genes per generations. As it was the case for breeding value estimation application of pedigree analysis is only possible with the use of specialized softwares (ENDOG, PEDIG).

The main parameters are:

Inbreeding coefficient (F): the probability that the two genes at any locus in an individual are identical by descent. Inbreeding coefficient is influenced by the length and completeness of pedigree the longer and more complete the available pedigree is the more reliable the estimated inbreeding coefficient.

The average relatedness coefficient (AR) of each individual is defined as the probability that an allele randomly chosen from the whole population in the pedigree belongs to a given animal. The average relatedness coefficient (AR) is evaluated together with the inbreeding coefficient. In case of a short and incomplete pedigree AR should be used to describe population structure.

Pedigree Completeness (CGE): the equivalent complete generations for each animal in the pedigree data is computed as the sum over all known ancestors. Comparison of average inbreeding coefficients of different populations is only meaningful when this parameter is known.

Generation intervals (GI), defined as the average age of parents at the birth of their progeny kept for reproduction. Parameters are computed for the 4 pathways (father- son, father - daughter, mother - son and mother - daughter).

Effective population size (Ne): is defined as the number of breeding animals that would lead to the actual increase in inbreeding if they contributed equally to the next generation.

Effective number of founders (fe): the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study.

Effective number of ancestors (fa): is the minimum number of ancestors, not necessarily founders, explaining the complete genetic diversity of a population (fa is smaller or equal than fe).

Founder genome equivalents (fg): the number of founders that would be expected to produce the same genetic diversity as in the population under study if the founders were equally represented and no lost of alleles occurred.

Chapter 10. Population structure

So far it was assumed that the populations are panmictic. However in most cases the populations are subdivided. Subdivision means that genetic variation exists at two levels: within local populations and between local populations.

Wright used inbreeding coefficients to describe the distribution of genetic diversity within and among population fragments. Wright partitioned inbreeding of individuals in the total population (F_{IT}) to inbreeding of individuals relative to their sub-population (F_{IS}) and inbreeding due to differentiation among sub-populations (F_{ST}).

$$F_{IT} = F_{IS} + F_{ST} - (F_{IS})(F_{ST})$$

$$F_{ST} = F_{IT} - F_{IS} / (1 - F_{IS})$$

The F statistics (F_{IT} , F_{IS} , F_{ST}) can be calculated using the relationship between heterozygosity and inbreeding.

$F = 1 - (H_i / H_o)$, where H_i and H_o the expected and observed heterozygosities

$$F_{IS} = 1 - (H_i / H_s)$$

$$F_{ST} = 1 - (H_s / H_T)$$

$$F_{IT} = 1 - (H_i / H_T)$$

H_i is the observed heterozygosity averaged across all population fragments.

H_s is the expected heterozygosity averaged across all population fragments.

H_T is the expected heterozygosity for the total population.

The population structure is characterized by F_{ST} when its value is 0 then there is no differentiation between fragments. However, when the value of F_{ST} is 1 the fragments are fixed for different alleles.

Chapter 11. BLUP

When selection index is applied there are some circumstances which have to be considered. For those factors that significantly influence the measurement they have to be precorrected (e.g. sex, year, season, herd etc.). Theoretically the procedure can only be applied when the mating is random. Taking into account the relationship among the individuals is difficult. To solve these difficulties Henderson (1975) developed a procedure called BLUP which makes simultaneously the above mentioned pre-correction (for the environmental factors) and predicts breeding values. The BLUP procedure can be used to predict the breeding values of male parents based on the performances of their offspring (sire model) or to predict breeding values for all individuals in the pedigree (animal model). Repeated measurements of the same animal (repeatability model) or additional random effects (such as the random litter effect) can also be accounted for. From the different BLUP models the sire model is the most simple which will be demonstrated through an example. (see table 12.)

Example: milk yield of 13 Jersey cow originated from two sires were registered at two farms.

The breeding value of the sires and the farm effects have to be estimated for the trait milk yield and the effect of the influencing environmental effect (farm in our case). As the breeding values of the other animals are not estimated a sire model has to be used. The significance of this model type was higher in those times when the computing capacity was low and it was impossible to predict the breeding values for large number of animals simultaneously. Therefore the breeding values of the sires were estimated as in a given population there are smaller number of sires than dams (lower demand for computing capacity), moreover the sires have much larger number of offspring which also justifies the prediction of their breeding values.

The equation of the sire model is the following:

$$y = Xb + Zu + e$$

y = vector of the n measurements ($n \times 1$)

(or a matrix having n rows and 1 column)

X = incidence matrix of fixed effects ($n \times f$)

(the matrix has n rows and f columns, where f = levels of fixed effects)

b = vector of f fixed effects ($f \times 1$)

(b = a matrix with f rows and 1 column)

Z = incidence matrix of random effects ($n \times s$)

(the matrix has n rows and s columns s = number of animals where their breeding values has to be estimated)

u = vector of s random effects ($s \times 1$)

(u = a matrix with s rows and 1 column)

e = vector of residual ($n \times 1$)

The equation $y = Xb + Zu + e$ has to be solved for b and u vectors. This is not possible directly as we have one equation with two unknowns. Solution becomes possible when both sides of equation is multiplied by X' and by Z' where X' and by Z' are transpose of X and Z (the transpose of a $n \times p$ matrix is defined to be a $p \times n$ matrix that results from interchanging the rows and columns of the matrix).

After multiplication we get:

$$X'Xb + X'Zu = X'y$$

$$Z'Xb + Z'Zu = Z'y$$

Which is equivalent to:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z \end{bmatrix} \times \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

The solution is possible thus the equation can be solved for b and u vectors.

The first step of the solution is to decide what are the fixed and random effects in our model.

As we use the sire model the milk yield is only influenced by two factors, the sire and the farm:

Milk yield = farm + sire

Which of these are fixed or random?

Any factor is treated as fixed when it has several levels and the aim of the analysis is to compare the effects of these levels. In this example farm is a fixed factor as it has two levels and the aim of the analysis is to compare the two farms which is obtained by solving the equation for vector b.

The random effect on the other hand treats the effect as a variance component which means that our objective is to find out that what is the proportion of the total variance that can be attributed to this effect. In this example the sires are considered as a random effect (solution for the u vector).

It has to be noted that categorizing any effect as fixed or random also depends from the objective of the analysis. For example if one would like to know the percentage of the total variance that is attributable to the farms then the farm is a random rather than a fixed effect.

After defining the fixed and random effects matrix X, Z and vector y are given:

X matrix [n × f] n = 13, f = 2 ie. 13 cows produce milk at either farm A or B:

$$X' = \begin{bmatrix} 1 & 1 & 1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 1 \end{bmatrix}$$

Z matrix [n × s] n = 13 s = 2 ie. the cows originated either from sire 1 or sire 2:

$$Z' = \begin{bmatrix} 1 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 1 & 1 & 1 \end{bmatrix}$$

y vector (13 × 1) contains milk yield of the cows

n = 13, ie. 13 milk yield records are available:

y' = [8 9 11 12 12 13 14 15 14 15 18 19 20]

Finally X and Z matrices have to be multiplied by their transpose.

According to the property of matrix multiplication X'X matrix has 2 rows and 2 columns and the numbers in the matrix provide the sum of the measurements in the factor's levels:

$$X'X = \begin{bmatrix} 7 & 0 \\ 0 & 6 \end{bmatrix}$$

The fixed effect of the farm has two levels A and B,

From the 13 cows 7 produced milk at farm A and 6 cows at farm B

$$Z'Z = \begin{bmatrix} 5 & 0 \\ 0 & 8 \end{bmatrix}$$

The random of the sire has 2 levels, 1 and 2.

In the present analysis 5 daughters of sire 1 and 8 daughters if sire 2 had milk yield measurements.

$$X'Z = \begin{bmatrix} 2 & 5 \\ 3 & 3 \end{bmatrix}$$

From the 7 cows produced milk at farm A 2 cows originated from sire 1 and 5 cows originated from sire 2.

Similarly, from the 6 cows produced milk at farm B 3 cows originated from sire 1 and 3 cows originated from sire 2.

$$X'y = \begin{bmatrix} 79 \\ 101 \end{bmatrix}$$

At farm A and B the total milk production was 79 kg and 101 kg, respectively.

$$Z'y = \begin{bmatrix} 61 \\ 119 \end{bmatrix}$$

The total milk production of the daughters of sires 1 and 2 was 61 kg and 119 kg, respectively.

The relationship between sires 1 and 2 has also be taken into account. For example if bull 1 is the sire of bull 2 then the relationship matrix is:

$$A = \begin{bmatrix} 1 & 0.5 \\ 0.5 & 1 \end{bmatrix}$$

thus

$$Z'Z + \lambda A^{-1} = \begin{bmatrix} 25 & -10 \\ -10 & 28 \end{bmatrix}$$

The solution is obtained solving:

$$\begin{bmatrix} 7 & 0 & 2 & 5 \\ 0 & 6 & 3 & 3 \\ 2 & 3 & 25 & -10 \\ 5 & 3 & -10 & 28 \end{bmatrix}^{-1} \times \begin{bmatrix} 79 \\ 101 \\ 61 \\ 119 \end{bmatrix} = \begin{bmatrix} b \\ u \end{bmatrix}$$

The solution vector has 4 lines and one column:

$$\begin{bmatrix} 11.1 \\ 16.8 \\ -0.3 \\ 0.3 \end{bmatrix}$$

The first 2 numbers of the solution vector gives the effect of the farm. This means that farm B increases the daily milk yield by 5.7 kg compared to farm A. The 3rd and 4th number of the solution vector gives the estimated breeding values of the sires from which it can be seen that sire 2 is superior compared to sire 1.

Appendix A. Appendix 1

Relatives	Covariance
Offspring – one parent	$0.5\sigma^2A$
Offspring – mid parent	$0.5\sigma^2A$
Half sibs	$0.25\sigma^2A$
Full sibs	$0.5\sigma^2A + 0.25\sigma^2D + \sigma^2Ec$

Table 1. - The phenotypic resemblance between the various relative groups.

Trait	h^2
Ovulation rate	0.10-0.25
Embrio survival	0.10-0.25
Litter size	0.10-0.20
Survival of the offspring	0.05-0.10
Readiness to rebreed	0.05-0.10
Milk yield	0.15-0.25
Milk quality	0.30-0.50
Longevity	0.10-0.20
Weight gain	0.30-0.60
Lean growth rate	0.40-0.60
Appetite	0.30-0.60
Backfat depth	0.40-0.70
Carcass length	0.40-0.60
Meat quality	0.30-0.50
Flavour	0.10-0.30

Table 2.

Relatives	Regression (b) or correlation (r)
Offspring – one parent	$b = 0.5h^2$
Offspring – mid parent	$b = h^2$
Half sibs	$r = 0.25h^2$
Full sibs	$r \geq 0.5h^2$

Table 3.

Let us suppose that the body weight of pigs (Y) and the average body weight of their parents (X) was measured at the same age:

N	X	X ²	Y	Y ²	X×Y
1	18	324	18.4	338.56	331.2
2	21.6	466.56	20.4	416.16	440.64
3	20	400	19.2	368.64	384
4	18	324	17.6	309.76	316.8
5	24.4	595.36	22	484	536.8
6	17.6	309.76	18.8	353.44	330.88
7	19.6	384.16	20.4	416.16	399.84
8	24	576	20.8	432.64	499.2
9	20	400	19.6	384.16	392
10	18.8	353.44	20.4	416.16	383.52

The task is to predict the heritability of the body weight at the given age.

Solution:

$$\sum X = 18 + 21.6 + \dots + 18.8 = 202;$$

$$\sum Y = 18.4 + 20.4 + \dots + 20.4 = 197.6;$$

$$\sum X^2 = 324 + 466.56 + \dots + 353.44 = 4133.28;$$

$$\sum Y^2 = 338.56 + 416.16 + \dots + 416.16 = 3919.68;$$

$$\sum X \times Y = 331.2 + 440.64 + \dots + 383.52 = 4014.88;$$

$$(\sum X)^2 = (202)^2 = 40804$$

$$\text{The covariance } (\sigma_{XY}) = (1 / N - 1) \times [(\sum X \times Y) - (\sum X \times \sum Y) / (N)] = 2.596$$

$$\text{The variance } (\sigma^2_X) = (1 / N - 1) \times [(\sum X^2) - (\sum X)^2 / (N)] = 5.876$$

$$b_{YX} = \sigma_{XY} / \sigma^2_X = 2.596 / 5.876 = 0.442 = h^2$$

Example 1.

Variance component	Estimated parameter
σ^2_s	$\sigma_{HS} = 0.25\sigma^2_A$
σ^2_d	$0.25\sigma^2_A + 0.25\sigma^2_D + \sigma^2_{Ec}$
$\sigma^2_s + \sigma^2_d$	$\sigma_{FS} = 0.5\sigma^2_A + 0.25\sigma^2_D + \sigma^2_{Ec}$
σ^2_e	$0.5\sigma^2_A + 0.75\sigma^2_D + \sigma^2_{Ew}$
σ^2_p	$\sigma^2_A + \sigma^2_D + \sigma^2_{Ec} + \sigma^2_{Ew}$

Table 4.

Sow	Progeny			Boar
1	28	29	27	1
2	30	33	31	1
3	28	28	25	2
4	30	31	28	2
5	26	26	28	3
6	27	29	29	3
7	27	28	27	4
8	25	21	32	4

Table 5.

Sow	Progeny			Variance
1	28	29	27	1
2	30	33	31	2.33
3	28	28	25	3
4	30	31	28	2.33
5	26	26	28	1.33
6	27	29	29	1.33
7	27	28	27	0.33
8	25	21	32	31

Table 6.

Sow	Measurements			Mean
1	28	29	27	28
2	30	33	31	31.33
3	28	28	25	27
4	30	31	28	29.66
5	26	26	28	26.66
6	27	29	29	28.33
7	27	28	27	27.33
8	25	21	32	26

Table 7.

Boar	Meas.			Variance	Mean			
1	28	29	27	30	33	31	4.66	29.66
2	28	28	25	30	31	28	4.26	28.33
3	26	26	28	27	29	29	1.9	27.5
4	27	28	27	25	21	32	13.06	26.66

Table 8.

Source	DF	SS	MS	Estimated Variance component
Between boars	$s-1$	SS_s	MS_s	$\sigma^2_e + n \times \sigma^2_d + n \times d \times \sigma^2_s$
Between sows	$s \times (d-1)$	SS_d	MS_d	$\sigma^2_e + n \times \sigma^2_d$
Within sows	$s \times d \times (n - 1)$	SS_e	MS_e	σ^2_e
Total	$s \times d \times n - 1$	SS_T		

Table 9.

Source	DF	SS	MS	Estimated Variance component
Between boars	3	29.46	9.82	$\sigma^2_e + n \times \sigma^2_d + n \times d \times \sigma^2_s$
Between sows	4	34.17	8.54	$\sigma^2_e + n \times \sigma^2_d$
Within sows	16	85.33	5.33	σ^2_e
Total	23	149.96		

Table 10.

Sow	Litter size		
1	10	11	11
2	9	10	11
3	11	11	12
4	10	9	12
5	10	10	10

Table 11.

ID	Farm	Sire	Milk yield
1	A	1	8
2	A	1	9
3	A	2	11
4	A	2	12
5	A	2	12
6	A	2	13
7	A	2	14
8	B	1	15
9	B	1	14
10	B	1	15
11	B	2	18
12	B	2	19
13	B	2	20

Table 12.