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## Genetic Improvement of the Horse

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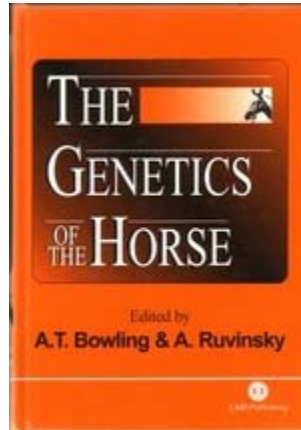
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# Genetic Improvement of the Horse 17

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## Introduction

From the time man domesticated horses some 5000–6000 years ago, horses have been subject to many forms of artificial selection that have resulted in gradual genetic changes. Differences found among breeds of horses are due to forces of artificial as well as natural selection, in addition to random change. Today there is growing interest in application of scientific animal breeding

theory to accomplish genetic improvement of valuable traits in many existing horse populations. This chapter will briefly introduce the tools available from animal breeding theory for the utilization of genetic variability within horse populations for genetic improvement. Successful application of modern knowledge of genetic improvement in animals, however, presumes that breeders have clearly defined breeding goals, that breeding populations are relatively large and, last but not least, that breeders are willing to accept scientific methods and to cooperate in a breeding programme. The same genetic principles, of course, are applicable for breeding of horses as for other farm animals. Some structural and demographic advantages and disadvantages specific to horse breeding compared with breeding of other livestock species should be highlighted:

- Thorough pedigree registration, often spanning many generations.
- Important traits are recorded on both males and females (often on a large proportion of the population).
- Low rate of reproduction.
- Long generation intervals.
- Wide overlapping of age groups among breeding candidates.
- Considerable non-random mating practised.
- Extremely large differences in economic value depending on assumed genetic merit.

Together, these factors support the application of the best available methods for accurate evaluation of breeding values for valuable traits including optimal use of all pedigree information. These factors are the main reasons for the early and widespread implementation of the animal model (AM) to obtain best linear unbiased predictions (BLUP) for genetic evaluation of horses in several European horse populations. The main aim of this chapter is to highlight some aspects of the basic theory behind the use of genetic evaluations, and the BLUP method in particular, for genetic improvement of horses. Several examples will be given for clarification. References will be given to basic sources and sometimes to suggest further reading. No attempt will be made to provide a complete review of literature of all the aspects of genetic improvement as related to horses.

## **Breeding Goals**

### ***General formulation of breeding objectives***

The prerequisite for any rational breeding scheme with the goal of genetic improvement of quantitative traits is a clear definition of breeding goals. The breeding objectives are a statement of the relative values of genetic change in all of the desired traits that are included in a breeding plan. Breeding objectives traditionally are expressed in monetary terms as economic weights to be applied to each trait of commercial importance. The most common way

of calculating these weights is an economically rational approach, such that the economic weights reflect the costs and returns in a production system without any consideration of the genetic parameters. An alternative means of developing breeding objectives is the desired gains approach, where the relative economic weights depend on the genetic parameters.

Basically, the economically rational approach involves determination of the relative economic weight,  $\alpha_i$ , of the  $i$ -th of  $n$  different traits included in the overall objective (H). The overall objective, also termed aggregate genotype, is expressed as:  $H = \alpha_1 A_1 + \alpha_2 A_2 + \dots + \alpha_n A_n$ , where  $A_i$  is the animal's breeding value for the  $i$ -th trait. In the most simple form, the  $\alpha_i$  values are obtained by defining profit = return - cost, and then taking the partial derivatives of the profit function with respect to the  $n$  traits in the aggregate genotype (Hazel, 1943). This approach assumes that the vector of the relative weights is linear in H. Extensions and modifications of the economically rational approach to fit more complex economical models in other species are found widely in the literature (e.g. Amer *et al.*, 1994).

Until now, little scientific effort has been made to derive economic weights of traits which are included in the breeding objectives for horses. The use of *ad hoc* methods, at best based on empirical experience and some biological considerations, in combination with intuition, have predominated. There may be several reasons for this. A major reason may be the failure to devote enough effort and investment to resolve these issues by scientific means. Often the value of one unit of expression of a certain trait to the total value of the horse can be difficult to determine. The long time elapsing from time of mating until the traits are expressed in the progeny, and thus resulting in saleable products, add to the difficulties in determining a proper profit function. This time lapse pertains especially to riding horses, where important traits may not become expressed until 8–12 years after the mating took place. Another problem is that relative economic weights can be non-linear in the breeding objectives. The value of an increment of one unit in the genotype for a certain trait may be highly dependent on the genetic values of one or more of the other traits. For example, for a riding horse with outstanding jumping ability the additional value of genes affecting its dressage capability is presumably negligible or even negative, while for an inferior jumper a corresponding genotype for dressage traits may considerably increase its value.

Clearly, much more research is needed for determining economic values of genetic improvement of individual traits and, more generally, for determining the breeding objectives in horse breeding schemes. Meanwhile, breeders should be provided with genetic evaluations for all the different traits that might be included in the breeding goal. Breeders would then have the opportunity to evaluate overall genetic worth using their own objectives. Breeders' knowledge and predictions of marketing trends are usually good. The correct general direction of the breeding goal in a population is of course of greatest importance, while slight deviations of economic weights from the correct ones have a limited impact on selection efficiency (Vandepitte and Hazel, 1977).

In situations where the relative economic values of genetic changes are difficult to determine, economic weights can be constructed that result in pre-chosen relative amounts of genetic change in each of the traits included in the aggregate genotype. This method is the desired gains approach. The weights for desired gains are influenced by the genetic parameters. Compared with the economical rational approach, traits exhibiting less genetic variation may receive higher economic weights in the desired gains approach. The total rate of genetic response in the linear function  $H$  will be less with the desired gains approach, but sometimes it is logical to expect that the traits that respond slowly to selection may increase in value relative to those changing more quickly. An example is the case in breeding of racing and riding horses where the traits interact in a non-linear manner in such a way that the more slowly responding traits may eventually critically suppress the horse's total value. As a specific example, the relative value per unit of genetic improvement in the constitution of legs may increase compared with the more pure criterion of racing performance as the genetic level of racing capacity emerges, thus causing more strain on pasterns, tendons and hooves. According to economic rules for markets, breeders will automatically change the weights empirically. Brascamp (1984) gives an excellent description of methods of selection for restricted and desired genetic gains.

### ***Racing horses***

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At first glance, the breeding goal for racing horses may seem simple, i.e. the genetic ability to win races and thus earn prize money. However, the genetic components of racing performance may be quite complex and involve a complicated function of anatomical, physiological, neurological and endocrinological factors. Measures of racing performance generally are competition traits where the record of racing performance is always evaluated relative to that of competitors. Thus, for any single racing horse, the genetic level of the competitors acts as an environmental effect. Genetic improvement in the population as a whole also means that the level of competitors will have increased. Increased genetic value for racing ability within the population is also likely to alter the relative importance of various biological factors which affect racing performance.

The history of breeding of Thoroughbred horses serves as an illustration of some of the problems encountered. The horse has an evolutionary history as a retreat animal which survived by escaping from its enemies at a full gallop (see Chapter 2). Speed at the gallop has certainly been an important fitness trait for horses. Selection for speed may therefore be looked upon as a continuation of a long history of natural selection. The Thoroughbred also has a long history of artificial selection for galloping speed, while being ridden by a jockey. Initially, the genetic ability for racing speed undoubtedly was an important factor for discriminating between winners and losers in Thoroughbred racing. Selection for winners in the major classic races efficiently yielded correlated

improvement in racing time for the whole population (Cunningham, 1976). As the level of the population improved for racing speed, the rate of improvement in winning times of the classic races levelled off, gradually leading to an apparent plateau. The population seemingly also became more uniform, in terms of speed, at least on the untransformed natural scale of racing time. Slight differences in racing speed between horses raced against each other became less important relative to other factors determining racing success. The likelihood of winning against equally fast horses is dependent on the mental and physical ability of the horse to react successfully to the environment, such as competitors, signals of the jockey and variations in speed at different phases of the race. The capability of mobilizing an anaerobic muscular metabolism and a 'fighting' spirit have become essential for successful Thoroughbred racers. In breeding schemes for the modern Thoroughbred, little emphasis is put on speed as part of the declared breeding goal. Sufficient genetic value for speed is assumed to exist in the upper level of the population so that the keys to success in longer stakes and in major classic races are assumed to be other factors (Langlois, 1994).

Robertson (1976) somewhat provocatively raised the question of whether the real goal in Irish and English Thoroughbred breeding was in fact high auction prices for yearlings. Variations in prices according to assumed differences in genetic merit of individual horses are tremendous. Many people would argue that this is an argument for rational use of available scientific methods for accurate and realistic genetic evaluations. However, the highly non-linear return function for racing performance may require skilful definition of the aggregate genotype and complex procedures for genetic evaluation of breeding animals. Some breeders and people in the racing industry may want to avoid rational evaluation of the breeding values as such evaluations might counteract the unrealistic expectations of gamblers on the value of slight presumed genetic differences. After all, the human desire to gamble is a prerequisite for the worldwide established marketing system for the Thoroughbred horse.

In several European countries, trotters are genetically evaluated routinely for traits measuring racing performance by the BLUP method. Verbal formulations of the breeding goals usually include terms such as: racing speed, ability to win, temperament, conformation, precocity, endurance, health and regularity of gait. In reality, the aggregate genotype can be expressed simply in monetary terms as a strictly monotone increasing function of earnings over a given age span, as the cost of input is practically invariant for all horses.

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### ***Riding horses***

Breeding goals for riding horses are usually not as strictly related to performance in competition as for racing horses. The usage of riding horses can be divided into three categories: (i) leisure riding; (ii) competition at lower (amateur) levels; and (iii) competition at higher (Grand Prix) levels. The

majority of riding horses are used in the first two categories, while the third category receives the most public attention. The traits representing Grand Prix level performance presumably dominate in the definition of official breeding goals. Such a definition is understandable because of: (i) the competition in the international market between breeders, (ii) the great difference in price between 'high' and 'low' level horses and (iii) the advertisement value related to Grand Prix champions. On other hand, most of the potential market is for the production of horses well suited for the average rider. Whether the same aggregate genotype is ideal for all classes (categories) should be considered by breeders. Studies to detect such genotype  $\times$  environment interactions in riding horses are scant.

A primary consideration when defining breeding goals in riding horses is to decide whether the goal should be a composite genotype for both dressage and jumping traits, or the goal should be for success in only one of the events. Estimates of genetic correlations between dressage traits (gaits) and jumping traits that have been published have been somewhat contradictory. Some estimates have indicated rather low, but positive genetic correlations, while other estimates have shown clearly negative genetic relationships. Some evidence suggests that the negative genetic relationships are more prominent in analyses of competition results, while the positive correlations have been found mainly in analyses of field performances. Results showing positive correlations have been claimed to be based on data where the requirements for the level of performance in each event of the test have been low. On the other hand, results showing negative correlations may be criticized for possible confounding of genetic and environmental effects in the data. For example, progeny of a stallion which has proved to be an outstanding individual in one of the events are more likely to be trained for and competed in the same event, and thus would not be given the opportunity to express their ability in other events.

When the breeding goal involves an aggregate genotype suited for lower level competitions and leisure riding, a tempting conclusion would be that both dressage and jumping traits could be included in the same objective for maximum success, with little or no cost, in terms of genetic progress, for either event. On the other hand, breeding schemes for higher levels such as Grand Prix horses would require specialized breeding populations where the breeding goals would include traits representing either jumping or dressage ability.

The so-called 3-day events include dressage, jumping and a cross-country ride so that successful horses in 3-day events have to have all-round ability. Horses competing at higher levels in 3-day events frequently are the result of crossbreeding (often with Thoroughbreds), which seems to be a viable alternative to specialized breeding because the market for superior 3-day event horses is rather small in comparison with the market for specialized jumpers and dressage horses.

Traditionally, body conformation traits reflecting type, function, soundness and grace have had a large place in the breeding goals for riding horses. More recently, health traits and longevity have received increased attention as



a part of the breeding goals (Ricard and Fournet-Hanocq, 1997; Philipsson, *et al.*, 1998).

### ***Other horse breeds***

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Most European horse breeds are able to perform the three fundamental gaits: walk, trot and gallop. Horses that are capable of performing the lateral four-beat movements called toelt, rack or slow gait, are called gaited horses. Gaited horses are quite common in many parts of the world. In North America, breeds such as the American Saddle horse and the Tennessee Walking horse are probably best known. In South America, several gaited horse breeds are represented, e.g. the Paso Fino horse. In the highlands of Ethiopia and in South Africa, many gaited horses are found. The Icelandic horse (sometimes called the Icelandic Toelter horse) is a good example of the so-called five-gaited horse, which can perform the two gaits, toelt and pace, in addition to the three fundamental gaits.

The official breeding goal (H) of the Icelandic horse consists of a linear function of seven conformation traits and seven riding performance traits which are scored in special field performance tests. The estimated breeding values (EBVs) are obtained by a multiple-trait animal model BLUP procedure. In addition to a weighted EBV for the aggregate genotype consisting of the 14 traits, the breeders are provided with EBVs for each trait and also EBVs for two additional traits (withers height, and mane and tail hairiness). The EBVs are included in a database program that allows breeders to search for information on all registered animals in the population and to obtain predictions for the outcome of any possible mating within the breed based on the parental EBVs. The breeding goal for the Icelandic horse is to breed small but powerful four- and five-gaited horses which are well suited for participation in special gait competitions as well as for leisure riding by adults and teenagers.

The Arabian horse has been divided into several subpopulations according to usage and, consequently, has several different breeding goals. In some countries, Arabians are used for races on a large scale. The common and successful participation of the Arabian horse in endurance competitions is well known. Nevertheless, a large portion of the breeding effort in the Arabian horse is directed to the imaginary perfection of the noble exhibition animal.

Production of horses to be used as draught animals in agriculture and forestry may require breeding goals including pulling power, pulling technique and temperament. An appropriate breeding goal for hackney horses (drawing carriages) should include movement, temperament and elegance as a part of the aggregate genotype. The breeding goal for small horses (ponies) which are to be used by children for riding should have more emphasis put on temperament and suitability for their intended purpose as reliable companions for children and teenagers, with less emphasis on conformational details than seems to be a common practice in many countries. The general rule is that the breeding goal should include the traits which are of real functional importance for

the breed, and should avoid wasting selection pressure on redundant traits. The breeding goals in many small horse populations of the world are often unique. Horses are bred for cutting performance and 'cow sense' for use on ranches and in rodeo shows. In Pakistan, some horses are even bred for dancing ability. The establishment of scientific breeding schemes for genetic improvement of such traits is a challenge that will continue in the future.

## **Genetic Evaluations**

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### ***Genetic background and basic theory***

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Most traits included in breeding objectives for horses are influenced by many genes and many environmental factors and thus are termed quantitative traits. Animal breeding theory for such traits traditionally has assumed an infinitesimal model developed by R.A. Fisher more than 80 years ago. The model is illustrated by the following points:

- The traits are controlled by the effects of an infinite number of genes.
- The effect of each gene is infinitely small and is equal for all genes.
- The environmental effects are randomly distributed and are independent of the genes and their effects.

The infinitesimal model obviously is only an approximation. More correctly, the traits are affected by (very) many genes, some of the genes are associated through linkage on the same chromosome (at least for several generations) and the effects of the genes on the traits vary in magnitude (major genes have been found to affect some quantitative traits in livestock). Nevertheless, the infinitesimal model has proved to be generally a good and robust approximation for modelling genetic variation and to use for genetic evaluation and for design of breeding plans.

The main consequences of the infinitesimal model can be summarized:

- Selection does not lead to any measurable changes in gene frequency within sufficiently large populations.
- Sums of gene effects (breeding values) are normally distributed within the population.
- The phenotypic values are sums of normally distributed breeding values and normally distributed environmental effects and, therefore, are also normally distributed.
- The covariance between breeding values of pairs of members of the population is proportional to the coefficient of relationship.
- The covariance of phenotypic values between pairs of members of the population is proportional to the coefficient of the relationship (i.e. phenotypic covariance between individuals is equal to the covariance between their breeding values).

The phenotypic value ( $P$ ) of any individual can be described as.

$$P = \sum g_i + \sum e_j + \mu$$

where:  $g_i$  = average effect of gene  $i$ , which affects a particular quantitative trait,  $i = 1, \dots, n$  and  $n$  is the total number of genes affecting the trait (i.e. twice the number of loci). Usually  $n$  is large, and in fact with the infinitesimal model  $n = 64$ .

$\sum g_i = A$  = the true breeding value (BV),  $e_j$  = environmental effect  $j$  affecting the quantitative trait. The effects are expressed as deviations from population means.  $j = 1, \dots, m$  and  $m \rightarrow \infty$ .  $\sum e_j = E$  = randomly distributed environmental deviates and  $\mu$  = a general form of the phenotypic population means (fixed effects in the statistical models).

According to the infinitesimal model, the environmental deviates are assumed to be independent of the effects of the genes. Therefore, the variance of the phenotypic values in the population can be expressed as the sum of the additive genetic variance and the environmental variance:

$$\sigma_p^2 = \sigma_A^2 + \sigma_E^2 = h^2 \sigma_p^2 + (1 - h^2) \sigma_p^2$$

where heritability,  $h^2 = \sigma_A^2 / \sigma_p^2$ .

The purpose of genetic evaluations is to estimate  $A$ , the breeding value of each individual animal. Breeding value is defined as the sum of average effects of the genes affecting a particular quantitative trait (or a function of several traits). Estimated breeding values always refer to a specific population.

The breeding value of an individual  $i$  can be expressed as a function of the breeding values of its parents (S and D) plus a Mendelian sampling term, i.e.

$$A_i = 1/2 A_S + 1/2 A_D + \theta_i$$

With the infinitesimal model, the Mendelian sampling terms follow a normal distribution with variance:

$$\sigma_{\theta}^2 = 1/2 (1 - F_S/2 - F_D/2) \sigma_A^2 = 1/2 (1 - F_S/2 - F_D/2) h^2 \sigma_p^2$$

where  $F_S$  and  $F_D$  are the inbreeding coefficients of the parents.

The breeding values of the parents can be decomposed further into their Mendelian components plus the average of the breeding values of the grandparents. This decomposition can be repeated recursively through the pedigree all the way to an unselected base population. Thus, an individual's breeding value is the weighted sum of the Mendelian components of all its ancestors traced to the base population (Kennedy *et al.*, 1988; Woolliams and Thompson, 1994).

### ***BLUP – the current standard method for obtaining EBV***

Unfortunately, true breeding values are never known. They can be estimated with varying degrees of accuracy depending on the amount of available information, heritability and genetic correlations among the traits. Rational methods for estimation of the breeding values with real data are based on a weighted

sum of phenotypic values of related animals deviated from corresponding population means. The magnitude of the weights (regression coefficients) are inversely proportional to the amount and accuracy of the information. BLUP has become the standard method in animal breeding for combining such information in an optimal way. One important property of BLUP is that it yields an EBV which is the unbiased linear function of the phenotypic variables that has the highest possible correlation with the true unknown breeding value ( $A_i$ ). The EBV of animal  $i$  can be expressed as:

$$\hat{a}_i = 1/2 \hat{a}_S + 1/2 \hat{a}_D + \phi_i$$

This formula shows that the EBV of animal  $i$  is average of the parents' EBV plus a deviation  $\phi_i$ . The estimate of the Mendelian sampling term can be expressed as (ignoring possible inbreeding for simplification):

$$\phi_i = d_i/(d_i + \lambda) (y_i - \mu_i - 1/2 \hat{a}_S - 1/2 \hat{a}_D)$$

where  $d_i = 1/2$  if both parents are known (have EBV),  $3/4$  if only one parent is known and  $1$  if neither parent is known;  $\lambda = \sigma^2_E/\sigma^2_A = (1 - h^2)/h^2$ ;  $y_i$  = phenotypic value; and  $\mu_i$  = phenotypic (sub-) population mean (correction for fixed effects with best linear unbiased estimates, BLUE).

The decomposition of both the true and the estimated breeding values provides a key to understanding the nature of genetic improvement over successive generations. Selected animals become the parents of the next generation. When those parents are selected intensively on the basis of their EBV ( $\hat{a}_i$ ), the level of the true breeding value of the selected individuals, which now become parents ( $1/2 A_S + 1/2 A_D$ ), is raised compared with that of the parents of the previous generation.

The Mendelian sampling term,  $\theta_i$ , is not affected by selection in the parental generation, which means that its variance remains practically unchanged even after many generations. In the first round of selection counted from an unselected base population, the main source of information contributing to the EBV ( $\hat{a}_i$ ) comes from  $\phi_i$  since the average breeding value of the parent generation is 0. In a successful breeding scheme, the level of EBV will be raised for each generation due the increased values of parental EBV. The accumulated information from the whole pedigree will always be included in  $1/2 \hat{a}_S + 1/2 \hat{a}_D$ . The additional information on the size and direction of the Mendelian deviation from the family mean, which is based on the adjusted record of the individual itself and, if it is a parent, also on the adjusted records of its descendants, is captured by the Mendelian sampling term,  $\phi_i$ .

With animal models, animals without identified parents build the base population. If the base animals cannot reasonably be assumed to belong to a single common population, but must be considered to be sampled from populations with different genetic means, a genetic grouping strategy must be applied to allow for the different expected genetic values of groups of base population animals (Westell *et al.*, 1988). Animal genetic models used for genetic evaluation of horses with the BLUP method usually assume one common base population. If the breeding population is homogeneous and most

pedigrees are well filled, tracing the majority of the younger animals to a common population of base animals is legitimate. If, on the other hand, the breeding population is a mixture from many base populations, there is importation of breeding stock from other countries or populations or there are many animals with incomplete pedigrees, an appropriate genetic grouping becomes essential in order to avoid serious errors in genetic evaluation.

***BLUP with the animal model – an effective tool for genetic evaluation of stallions and mares***

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Estimation of breeding values begins with definition of a linear model which should describe reality as well as possible in as simple a way as possible. The model should account for all major factors affecting variation in the data in a systematic way. In the simplest form, the model may be written for a single trait as:

$$y_{ij} = \mu + b_i + a_j + e_{ij}$$

where the  $y_{ij}$  is the phenotypic observation on the  $j$ -th horse belonging to the  $i$ -th class of fixed (systematic) effects affecting the trait;  $\mu$  represents the overall mean of the (base) population;  $b_i$  represents the deviation from the population caused by the  $i$ -th class of fixed effects; and  $a_j$  represents the breeding value of the  $j$ -th horse. The breeding values,  $a_j$ , according to the infinitesimal model, are random normally distributed deviations from the genetic mean of the base population. Finally  $e_{ij}$  denotes the remainder of the model, which is assumed to include randomly distributed environmental effects pertaining to the  $j$ -th horse.

With the BLUP method, the effects of fixed factors and the breeding values are estimated simultaneously by solving a large set of equations with equally as many unknown solutions. In this way, the estimated breeding values are adjusted for fixed effects and the estimates of fixed effects are correspondingly adjusted for differences in breeding values of the horses with records in the various fixed effect subclasses. The relative magnitude of the random effects ( $a_j$  and  $e_{ij}$ ) in the model depends on heritability of the trait. The elements of  $e_{ij}$  are assumed to be independent and distributed normally (if not, then a bias will be imposed into the estimated effects). In any practical case, the  $a_j$  elements are not independent as horses are related to each other. The additive genetic relationships among all animals in the population are accounted for by use of the (numerator genetic) relationship matrix.

Statistical models for practical applications of BLUP are usually far more complicated than that shown above. The model may include many fixed factors, many traits (multiple trait model), additional random factor(s) and also allow for repeated observations for some animals. The BLUP method assumes that the correct genetic parameters (i.e. variances, heritabilities, genetic correlations and environmental correlations) of the base population are known. In practice, this means that good estimates are needed.

Studies have shown that the BLUP method is robust even for situations where the assumptions of the infinitesimal model do not apply. Simulations have proved that in situations where traits are controlled by few loci, the BLUP method with an animal model still provides a good approximation (e.g. Maki-Tanila and Kennedy, 1986). Most of the properties of the BLUP method as an optimal predictor of breeding values remain true even if the traits and the breeding values are not distributed normally in the population (Henderson, 1975).

A comprehensive description of the BLUP procedure cannot be accomplished, even for the most simple models, without the help of matrix algebra. In fact, matrix algebra has become an essential tool for anyone seriously interested in quantitative genetics and in thorough understanding of the BLUP method. A technical description of the methodology is therefore outside the scope of this book. Interested readers are referred to Kennedy (1981), Van Vleck *et al.* (1989) and Mrode (1996) for comprehensible descriptions of BLUP techniques.

The well proved genetic and statistical properties of BLUP as a selection criterion (Henderson, 1975; Kennedy *et al.*, 1988) for quantitative traits have led to the use of BLUP for genetic evaluations in most livestock populations. The properties of BLUP for the animal model for obtaining EBVs are of great benefit in horse breeding and lead to the following practical consequences:

1. EBV based on full use of information from all relatives can be obtained for any member of the population. EBVs of potential progeny are easily obtained for any potential mating between any stallion and mare in the population by simply averaging the EBVs of the parents. This property can be used to assist breeders in planning of matings.
2. The EBVs are corrected for all fixed factors included in the model. The models used for genetic evaluation of horses may include effects of sex, age, year, birth-year, herd (stud) and others.
3. The EBVs of parents are corrected for EBVs of their mates. This property is particularly important in horse breeding, where the allocation of mares to breeding stallions is generally not random in terms of genetic merit.
4. The EBVs of later generations incorporate the genetic changes (progress) resulting from the effects of selection accumulated from the base population. That property means that animals from different generations can be fairly compared according to EBV. Genetic trends can be obtained easily by computing the mean EBVs for each birth-year. When year is included in the model, environmental trends, adjusted for genetic changes, can also be obtained from the corresponding solutions for year effects.

A common characteristic of most horse populations is widely overlapping generations. The amount of information pertaining to the EBVs of individual animals is quite variable. When EBVs are published, estimates of their accuracy should be attached. A horse breeder often is faced with the decision of mating

his mare with either an old or a young stallion. The EBVs from a correct model provide breeders with information for objective decisions. If the breeder is neutral concerning risk, the breeder will choose the stallion having a higher EBV irrespective of the amount of information included in the genetic evaluations of either stallion. Usually the older stallion will have an EBV with higher accuracy. If the stallions have equal EBVs, a risk-prone breeder would select the younger stallion which would have a larger variance of prediction for his EBV. In the same situation, a risk-adverse breeder would select the more accurately evaluated stallion. Unfortunately, there is often a conflict between the short-term risk considerations of the practical breeder and the risk aspects concerning the long-term breeding scheme for the whole population. This issue needs further investigation.

### ***Applications of BLUP for genetic improvement of horses***

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The use of selection index (BLUP) principles for genetic evaluation of horses started in the mid-1970s with Langlois (1975) for French riding horses and with Minkema (1976) in The Netherlands for racing trotters. The BLUP method was first introduced to horse breeders with a simple example by Van Vleck and Hintz (1976). The first applications of the BLUP method with real data appear to have been in the Icelandic horse (Arnason, 1980) and in German trotters (Distl *et al.*, 1982). The first BLUP applications in horses were based on sire models (progeny tests). The implementation of BLUP with the animal model in horse breeding was initiated by Arnason (1984) for the Icelandic horse. The application of animal models for estimating breeding values in horses has been reported for various breeds in at least ten European countries and for the Quarter Horse in the USA. Large-scale genetic evaluations are run routinely for trotters, riding horses and Icelandic horses in several countries. Breeders have access to the EBV through publications and computerized databases. A recent review of methodological developments in the genetic evaluation of performance traits in horses was given by Ricard (1998). A major problem has been to find good normally distributed measures of performance, which are appropriate for use in the framework of linear models. Various mathematical transformations of records have been used to approximate normal distributions. The alternative but computationally demanding non-parametric ranking methodology for genetic evaluation of competition traits developed by Ricard has potential for practical applications in horse breeding, due to the dramatic improvement in computer technology (Tavernier, 1991).

The increase in international trade of sport horses and breeding stock has created a need for genetic evaluation of breeding horses across countries. Therefore, there is growing interest in the development of international genetic evaluations of horses. Inter-Nordic genetic evaluation of Nordic trotters and Icelandic horses (Arnason *et al.*, 1994; Arnason and Sigurdsson, 1997) has already begun.

### ***Use of non-additive genetic effects in horse breeding***

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Selection based on BLUP EBVs with the animal model is by far the most effective way of changing genetic merit of horse populations. The use of EBVs for planning matings and to predict potential genetic and phenotypic values of the candidate progeny are also of great value to the individual breeder. However, if non-additive genetic effects (dominance, epistasis) are important, then estimates of such effects would be useful for breeders as additional information for planning of matings. Both theory and experience show that traits closely connected to evolutionary fitness, or traits otherwise subject to long-term selection pressure, are more likely to show significant effects of dominance and epistasis. Traits connected with racing performance, especially in Thoroughbreds, are particularly likely to show such effects. No genetic analyses aimed at estimation of dominance effects or epistasis in performance traits of horses have yet been published. However, many practical horse breeders claim the existence of profound nicking effects, whereby mating of individuals from pairs of lines having certain relationship structures is supposed to be successful. Even if such effects as nicking have not been confirmed scientifically, that area is in need of more research. If reliable estimates of both the additive genetic effects (EBV) and of non-additive genetics effects for individual horses were available, they could be used in mate selection.

Crossbreeding involving different breeds frequently is used for production of riding horses. Many outstanding show-jumpers and 3-day event horses have resulted from successful crosses. Crossbreeding, as generally applied in horse breeding, is an efficient way to utilize available specialized genetic resources to obtain economic heterosis through complementarity without creating permanent genetic improvement. In international competitions among riding horses at Grand Prix level, the traditional crossbred riding horses are generally losing ground in comparison with specialized synthetic horse breeds which are making rapid genetic progress. Progressive crossbreeding schemes in horses, involving selection for general or specific combining abilities, have not been implemented.

## **Selection – Genetic Response**

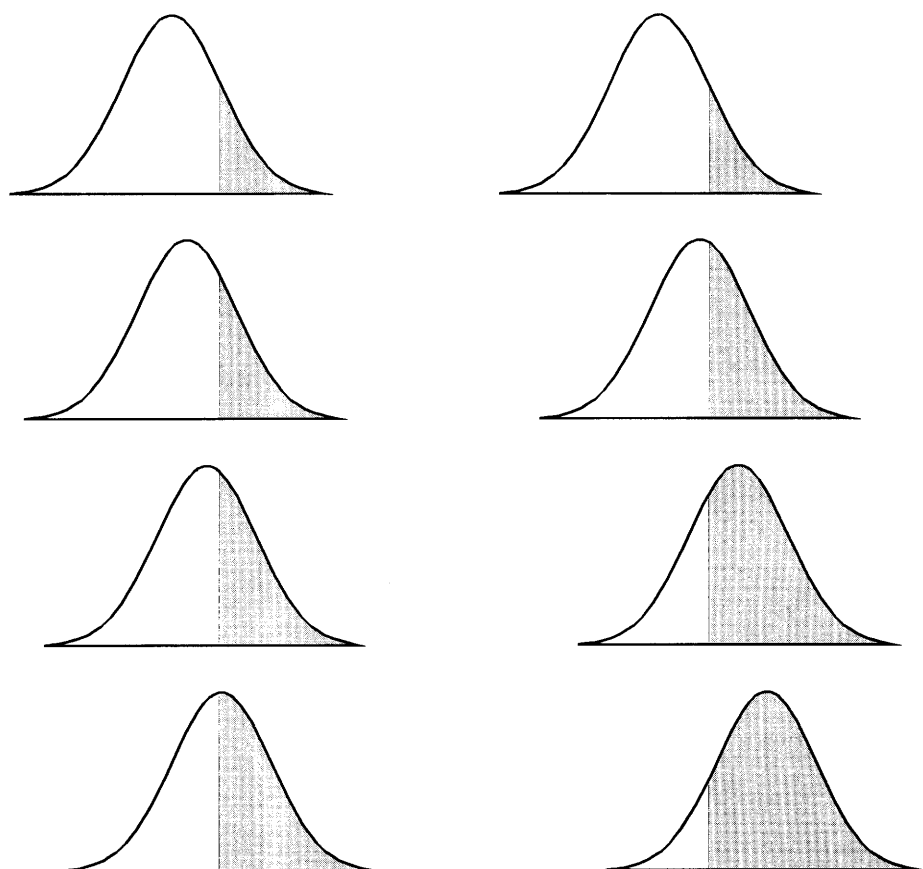
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### ***Factors determining genetic progress***

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Successful selection in a population leads to gradual transmission of average breeding values. The changes can be mapped on the horizontal scale of a normal distribution in the desired direction according to the defined breeding goals as illustrated in Fig. 17.1. Genetic response is usually measured in units per year rather than units per generation, as the intention usually is to increase the mean as quickly as possible in the favoured direction. Genetic response depends on: intensity of selection ( $i$ ); additive genetic variation in the aggregate genotype ( $\sigma_H$ ), the correlation between the selection criterion and the





**Fig. 17.1.** Effect of two different breeding schemes on accumulated genetic response over four generations. This difference in rate of response corresponds to what has been realized in horse populations implementing BLUP with animal model EBVs.

breeding goal ( $R_{IH}$ ); and the generation interval ( $L$ ). In the simplest case, this relationship is expressed in the well-known formula (e.g. Falconer, 1989):

$$\Delta G = (i\sigma_H R_{IH})/L$$

Because selection intensity, generation interval and accuracy of selection are not the same for males and females, the formula is modified to include two or four paths (Rendel and Robertson, 1950). Figure 17.1 illustrates the difference in genetic progress in two hypothetical horse populations. In one of the populations, the best 20% of the stallions according to phenotypic merit ( $b^2 = 0.3$ ) are used for breeding with no selection on the female side. In the other population, breeding animals are evaluated by the BLUP method with the animal model and the EBVs are used as a criterion for selection. On the stallion side,

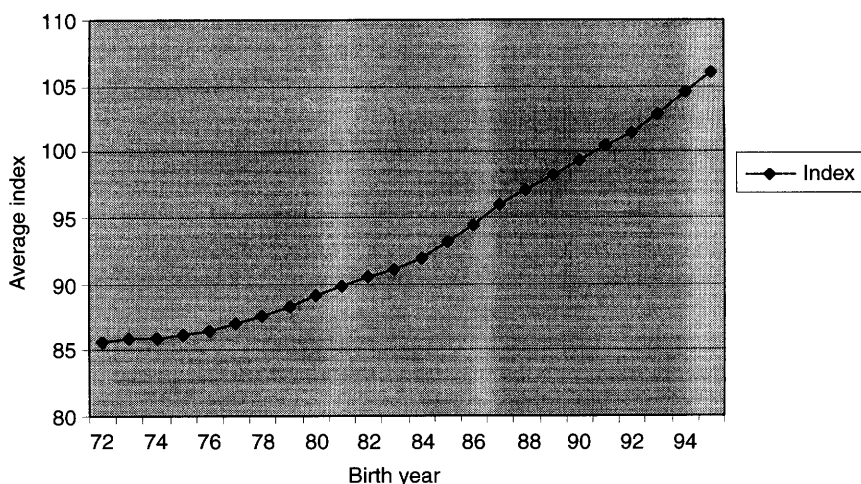
the best 2% are selected and, among the mares, the best 40% are selected. Generation intervals of 8.5 years on the male side and 11.5 years on the female side are assumed for both populations. The increased selection intensity and the increased accuracy of the selection from using BLUP is expected to result in three times faster genetic improvement in the latter selection scheme. The economic value of such an increase in progress over time would vary among horse breeds, but invariably would be equivalent to a considerable amount of money.

### ***Observed genetic progress in several horse populations***

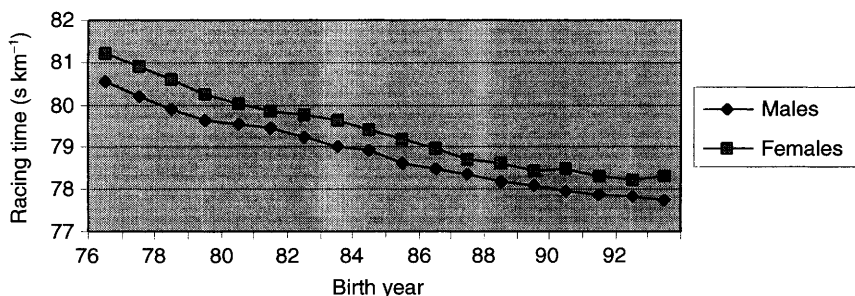
#### *Racing trotters*

Intensive selection of stallions on the basis of phenotypic racing performance has been practised in many trotter populations for quite a long time. Recently, some trotting organizations have employed BLUP methodology to provide breeders with EBVs as selection criteria for racing performance. In Sweden, index values based on a multiple trait animal model have been available to the breeders of the Standardbred trotter since 1992. The following traits have been evaluated: number of races; percentage of races ranked first to third at the finish; earnings per race; total earnings; best racing time per km; and racing status, which is denoted as one if the horse did race and zero otherwise. All traits were based on accumulated racing results as 3- to 5-year-olds. The traits were transformed in order to approximate the normal distribution before being included in the BLUP analysis (Arnason, 1994a). About 40% of Swedish Standardbred trotters do not enter races as 3- to 5-year-olds and receive a start status of zero. Start status is genetically correlated with racing performance and is therefore a correlated pre-selection criterion for performance. Ignoring such a culling process can result in substantial selection bias (Klemetsdal, 1992). As a result, EBVs of stallions with relatively few raced offspring tend to be overestimated. A practical solution has been to generate canonical variables corresponding to imaginary performance records for non-racers based on the correlation structure and genetic relationship ties within the population (Ducrocq and Besbes, 1993).

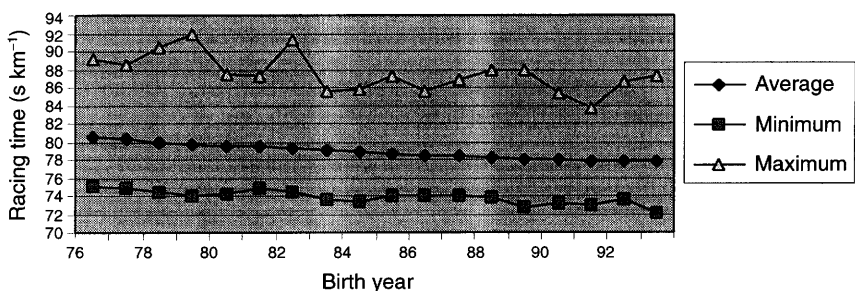
The implementation of an index based on BLUP with an animal model has increased greatly the selection intensity for both stallions and mares (Arnason, 1997). The annual rate of genetic response increased by 40% from 1988 to 1996 and corresponds to about 6% of one phenotypic standard deviation in racing performance. The trend in index values for the Swedish Standardbred trotters is shown in Fig. 17.2. For trotters, racing speed, winning ability and earnings are highly positively correlated traits. Selection for racing performance, where earnings are the main component, has resulted in substantial genetic as well as phenotypic improvement in racing time. Genetic improvement is estimated to account for about 60% of the phenotypic change. The phenotypic trends in racing time of male and female trotters in Sweden are shown in Figs 17.3 and 17.4.



**Fig. 17.2.** Genetic progress in Swedish Standardbred trotters measured by trend in BLUP EBVs. Ten units in index correspond to one  $\sigma_H$ .



**Fig. 17.3.** Phenotypic trend in average racing time in  $s\ km^{-1}$  as 3- to 5-year-olds for Standardbred trotters in Sweden for both males and females.



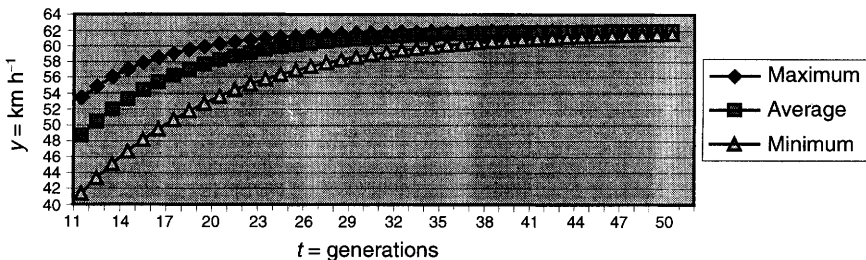
**Fig. 17.4.** Phenotypic trend for slowest, average and fastest racing times in  $s\ km^{-1}$  as 3- to 5-year-olds for Standardbred male trotters in Sweden.

### Thoroughbred horses

Gaffney and Cunningham (1988) used the BLUP procedure with a sire model to estimate genetic change in Timeform handicap ratings of Thoroughbreds in Great Britain. Timeform ratings express racing merit as weight in pounds which the compiler believes the horse should carry in an average free handicap race. Their results indicated genetic progress in Timeform ratings to be about 1% per year. This progress was not reflected in winning times of classic races, but the authors concluded that correlated genetic improvement in speed had been achieved in the Thoroughbred population as a whole. This conclusion assumes asymmetry in the distribution of racing speed. Arnason (1994b) showed how such scale effects in the distribution of racing speed might be caused by asymptotically diminishing marginal effects of gene substitutions in a genetic model with a finite number of loci. Such effects may be expected for traits where the best part of the population is approaching the physiological limit. The dilemma of lack of phenotypic progress in racing time in spite of intensive selection on racing performance traits has been discussed by Cunningham (1976), Gaffney and Cunningham (1988), Hill (1988), James (1990) and Cunningham (1998). It must be kept in mind that the selection has not been directly for racing time. The results need not be paradoxical, because the recent genetic gain may have been mainly for other traits more related to winning ability, as mentioned in the discussion about breeding objectives. A hypothetical illustration of the effects of scale on racing speed in  $\text{km h}^{-1}$  is shown in Fig. 17.5. The average value for racing speed is expressed by the graph of  $y = q_0(1 - e^{-pt})$ , which is a mirror image of an exponential function, where  $y = \text{km h}^{-1}$  in racing speed,  $q_0$  is the asymptotic limit for racing speed over a certain distance (e.g.  $62 \text{ km h}^{-1}$ ),  $p$  is a positive constant that could be estimated (e.g. by least squares) from real data, and  $t$  indicates a time scale (e.g. generations).

### American Quarter Horse

Racing performance in the American Quarter Horse was studied thoroughly in a series of papers by Buttram *et al.* (1988a,b,c). Quarter Horse races are run

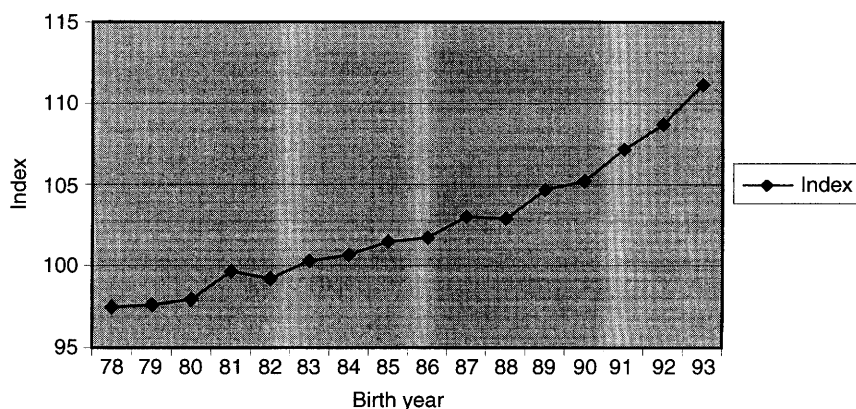


**Fig. 17.5.** Hypothetical illustration of expected trend in racing speed over the classical distances for Thoroughbred horses. The graph of  $y = q_0(1 - e^{-pt})$  is plotted for  $q_0 = 62 \text{ km h}^{-1}$  and the  $p$  constants as 0.18, 0.14 and 0.10 for the fastest, average and slowest horses in the population, respectively.

over short distances, most commonly from 320 to 402 m. A BLUP procedure with an animal model was used for genetic evaluation of racing performance based on racing time records. Genetic trend in racing time in Quarter Horse racing was estimated from solutions for breeding values (Wilson *et al.*, 1988). Annual progress of 0.004–0.009 s in the average EBV of parents was found, which corresponds to 0.06–1.8% of the phenotypic standard deviations in racing time for distances of 402 and 320 m, respectively.

### *Icelandic horses*

Since 1950, Icelandic horse breeders have had their breeding stock evaluated in field performance tests, where several riding ability and conformation traits have been scored. In 1980, a research project was initiated with the goal of implementing BLUP procedures with an animal model for routine genetic evaluations based on the scoring results. A multiple trait animal model for Icelandic horses was introduced in 1983 (Arnason, 1984) and since then breeders have been provided annually with the EBVs. The latest analyses included over 100,000 horses, of which about 16,000 have been performance tested. Annual genetic changes in the official breeding goal (total score) are shown in Fig. 17.6. The rate of genetic progress has been accelerating over the last few years, probably to a large extent due to the fact that breeders are gaining confidence in use of the EBVs to assist with selection of breeding animals. Annual genetic improvement after 1990 was five times greater than progress made before 1980 and corresponds to 6% of the phenotypic standard deviation or 10% of the genetic standard deviation of total score (Sigurdsson, *et al.*, 1997).



**Fig. 17.6.** Estimated genetic trend in total score for Icelandic horses. Ten units in index correspond to one  $\sigma_H$ .

## ***Effects of selection on genetic variation and long-term progress***

### *Selection across generations*

Additive genetic variation can be considered as the fuel for genetic response. A closer look shows what happens when this fuel is burned, i.e. breeding horses are selected on phenotypic values or functions of phenotypic values, e.g. EBVs. The additive genetic variance can be separated into variance within and between loci as shown by Bulmer (1971):

$$\sigma_A^2 = \sum_{i=1}^n \text{VAR}(g_i) + \sum_{i \neq j} \text{COV}(g_i, g_j)$$

Equilibrium	Joint disequilibrium
genetic	genetic
variance	variance

where  $\text{VAR}(g_i)$  is the variance of genetic effects at the  $i$ -th locus and  $\text{COV}(g_i, g_j)$  is the covariance between genetic effects at the  $i$ -th and  $j$ -th loci. The summations are over the  $n$  loci affecting the additive genetic variation of the trait. For the infinitesimal model, all changes in the additive genetic variance can be shown to be caused by the disequilibrium part, i.e. the part due to covariance between genes (alleles) at different loci. Variance of gene effects within loci is unchanged in the population by generations of selection provided that the number of loci affecting the trait is large. Traditional directional selection, however, results in negative covariance between loci, i.e. a negative value for  $\sum_{i \neq j} \text{COV}(g_i, g_j)$ . Directional selection, therefore, leads to reduction in additive genetic variance. If selection ceases, the additive genetic variance will rebuild, because the negative value of  $\sum_{i \neq j} \text{COV}(g_i, g_j)$  will be halved with each generation of random mating. Constant selection intensity for successive generations will lead to an equilibrium between reduction in genetic variance and the variation rebuilt due to recombination after several generations of constant selection intensity. This phenomenon (the Bulmer effect) can be compared with chemical reaction in both directions which eventually will reach equilibrium. When equilibrium is reached (steady state), the additive genetic variance will have been reduced in most breeding schemes by 10–30% depending on the selection intensity and accuracy of selection.

Most economically important traits in breeding goals for horses are affected by many genes. Selection is therefore expected to be effective for changing the population mean in the desired direction for many generations, provided that deleterious effects of inbreeding can be avoided and that the effective population size is kept large enough. Sensible animal breeding is a fantastic process for sustainable utilization of biological resources. The level of fuel may become somewhat lower in the tank, but the process should never run out of petrol.

### *Selection within generations*

The effect of selection on changes in genetic variance over generations was considered previously. The conclusion was that variance in quantitative traits

amongst the annual crops of newborn foals is reduced somewhat over time with increased intensity of selection until equilibrium is reached and that thereafter genetic variance remains unchanged. What are the effects of selection within a generation? Within each generation, the genetic variance is obviously largest before any selection is practised, i.e. amongst the newborn foals. The variation in breeding values of selected animals is reduced in direct proportion to the selection intensity and to the correlation between the selection criterion and the true breeding value. The genetic variance among intensively selected stallions would therefore be far less than the genetic variance amongst newborn foals. Multi-stage selection in breeding schemes for horses was investigated by Hugason *et al.* (1987). As shown by VanRaden *et al.* (1984), selection on EBVs across the age structure of the population is close to optimum in terms of genetic progress. However, it is important to realize that the BLUP method will account properly for the selection bias only if all the traits on which selection is based are included in the analysis and the statistical model correctly adjusts for important fixed factors.

### ***Selection in small populations***

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Many horse populations are small and animal breeding principles that are optimal in (infinitely) large populations may not apply. In small populations, gene frequencies may fluctuate randomly from generation to generation as a result of the finite sampling of gametes. This phenomenon, called genetic drift, is quantified by the term effective population size,  $N_e$  (e.g. Falconer, 1989). In a closed population, the  $N_e$  is dependent on the number of parents in each generation, the variance of parental family sizes and selection. Hill (1979) gave a formula for computing  $N_e$  from the structure of random-mating populations with overlapping generations. Several modifications of Hill's formula have attempted to account for selection as well (e.g. Wray *et al.*, 1994). An alternative way of estimating  $N_e$  is to measure the rate of inbreeding over different generations (e.g. Falconer, 1989). Then  $N_e$  for generation  $t$  can be computed as:  $N_e = (1 - F_{t-1}) / 2(F_t - F_{t-1})$ , where  $F_t$  is the mean coefficient of inbreeding for generation  $t$ . A relatively large  $N_e$  is advantageous in breeding plans in order to prevent loss of genetic variation and for accumulation of new mutations affecting valuable traits.

In small closed populations, there is a risk that intensive selection on EBVs alone will lead to a small  $N_e$ . Consequently, strict use of unmodified EBVs for selection eventually may result in reduced long-term genetic improvement due to loss of genetic variation and inbreeding depression. Breeding plans for small horse breeds have to cope with a small  $N_e$  in attaining long-term progress. Selection criteria which involve EBVs modified such that the average relationship between selected animals is restricted have been proposed by Wray and Goddard (1994) and further developed by Meuwissen (1997). Such a selection criterion was tested in a simulation exercise (Arnason, 1996). The conclusion was that the method could be used to increase long-term

response in Nordic trotters. Intense selection of males and variable family sizes may cause a surprisingly small  $N_e$  in horse populations of reasonably large actual sizes. The joint population of Nordic trotters in Norway and Sweden consists of 2000 brood-mares and 160 approved stallions. The  $N_e$  for this population has been estimated to be as small as about 30 animals (Klemetsdal, 1993; Anderson *et al.*, 1998).

In small horse populations, where there seems to be limited scope for genetic improvement, the first step to achieve improvement might be to target a market for the distinctive characteristics of the breed. One means of preserving this particular genetic resource would be to make the breed popular and to expand the breed on the basis of its special abilities, which should be strengthened with an effective breeding plan. Successful expansion of a breed sometimes follows from horsemanship associated with certain lifestyles. Interesting examples are the Western riding culture in relation to the American Quarter Horse and the global marketing of the Icelandic horse as an alternative to the traditional European riding style.

### ***Selection using genetic markers***

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In the future, interest in the possible use of marker-assisted selection (MAS) for enhanced genetic improvement in horses is likely to increase. Genetic markers are DNA sequences that can be identified relatively easily in individual animals. As the gene map of the horse becomes more complete, the chance increases of finding genetic markers closely linked to major genes affecting some important quantitative traits included in the breeding goal. The only indication of a plausible marker for a quantitative trait in horses found in literature is the report of Anderson *et al.* (1987) on an association between different alleles at the serum esterase locus (*Es*) and racing status (all-or-none trait depending on whether the horse has started in a race or not) in Swedish Standardbred trotters. MAS is likely to be a valuable complement to selection on EBVs obtained by the BLUP method, rather than as a replacement for EBVs. The use of MAS in horse breeding schemes could be particularly useful for traits that are expressed late in the horse's life because the genetic markers will become known in the foal. The effect of MAS would be to shorten the generation interval and thereby increase the rate of genetic progress.

At present, evidence for the existence of quantitative traits loci (QTL) with large effects (major genes) in horses is scarce. Traits, however, such as the lateral gaits, pace and toelt, 'cow sense' and other unusual behavioural characteristics related to special movements affecting dressage and jumping characteristics in horses could quite probably be influenced by major genes.



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