

Recent Advances in Animal Breeding Theory

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Abstract

Recent developments in animal breeding theory have been driven largely by computer science and molecular biology. Several of the theories designed for practical application to animal breeding are heavy computing requirements. The development of computer hardware and of many algorithms for constructing and solving mixed model equations (MME) has enabled breeding values to be estimated from data on a huge number of animals by best linear unbiased prediction (BLUP) procedures. It has also enabled genetic parameters to be estimated by restricted maximum likelihood (REML). However, because the size of the MME that can be analyzed by REML depends on the genetic model and the numbers of traits and animals, all kinds of data cannot be used to estimate genetic parameters by even the latest supercomputers. For this reason, traditional theories are still being improved and new theories studied for practical applications to animal breeding. Traditional quantitative genetics theory has been based almost exclusively on the assumption that genetic variation in quantitative traits of interest is controlled by polygenes. On the other hand, molecular genetics techniques have made it possible to estimate individual genotypes. Because DNA marker information can be obtained by using these molecular biological techniques, theoretical studies of linkage mapping, detection of quantitative trait loci (QTLs), and the potential for marker-assisted or genotype selection have been developed in the last decade. Information on QTLs with large effects will be used for the genetic improvement of animals in the near future. These new technologies will not replace existing animal breeding practices, but will be blended with them through the use of breeding program design and genetic evaluation methods that cover both known and unknown QTLs.

1. Introduction

Population genetics and quantitative genetics are

the sciences behind animal breeding theory. Fisher (1918) demonstrated that measured correlations between relatives could be explained by the contributions of a large number of Mendelian factors (now called polymorphic loci), each with a small effect. The advancement and use of animal breeding theory have been based almost exclusively on this assumption. The classical model of inheritance based on this assumption seems to be quite robust in the predicted response to selection and simulation studies. The development of computer hardware has enabled this traditional theory to be applied to actual animal breeding programs. On the other hand, molecular genetics techniques have made it possible to detect quantitative trait loci (QTLs). This information may increase the efficiency of genetic selection programs for livestock. For these reasons, computer science and molecular biology have largely driven recent advances in animal breeding theory.

The purpose of this review is to introduce the traditional and recent animal breeding theories that are widely applied to animal breeding. In addition, I will discuss the effect of including information on currently identified QTLs. Finally, I will briefly discuss the nature of animal breeding in the near future.

2. Effects of development of computer science on animal breeding theory

2.1 Application of best linear unbiased prediction (BLUP) to genetic evaluation

Figure 1 is an example of a basic system of genetic improvement by selection in livestock. In this system, genetic improvement in the population is strongly affected by selection rather than by constructing base population, mating system, or first-stage selection at weaning. The basic problem in animal improvement through breeding is to choose animals that have the greatest genetic value as parents of the next generation. To evaluate the genetic value of candidates for selection, we need to divide the

phenotypic value into component parts attributable to different causes. The simplified model for the relationship between an animal's phenotype and its genotype is:

$$\begin{aligned} \text{Phenotype} &= \text{Genotype} + \text{Environment} \\ &= (\text{Additive genetic effect} + \text{Other genetic effects}) + \text{E}. \end{aligned}$$

Before 1970s the selection index was the major tool used in genetic improvement programs in most countries for estimating individual genotypes although it is dependent on the animal species. The selection index is a tool for estimating the breeding value of an animal by combining all information available on the animal and its relatives (Hazel, 1943). The theory of restricted selection indices, whereby the aim is a genetic change of zero in one or some traits (Kempthorne and Nordskog, 1959) or predetermined relative changes in some (Harville, 1975) or all traits (Yamada et al., 1974) under selection, was developed after the introduction of selection index theory by Hazel. A detailed discussion can be found in a review by Brascamp (1984). The restricted selection index theory is still studied today and new theories are still being developed (e.g. Lin, 2005).

The application of best linear unbiased prediction (BLUP) to dairy and beef cattle breeding continued to develop rapidly during the 1970s. The theory of BLUP was originally developed by Henderson (1949, 1973) for the genetic evaluation of sires in the dairy industry. Since then, it has evolved from application to sire and maternal grandsire models for genetic evaluation in the early years to multiple-trait animal models (Henderson and Quaas, 1976) and random

regression models (Henderson, 1982), which are used to analyze of longitudinal data or repeated records on individuals over time, in recent years. BLUP has become the most widely accepted method of genetic evaluation of domestic animals.

Some of the reasons for the greater genetic gain achievable by using BLUP are summarized by Long et al. (1991), as follows:

- BLUP uses information from all known relatives of an individual and facilitates comparisons of the genetic merit of animals by using differing amounts of information.
- It facilitates comparisons of genetic merit among animals for which data have been recorded in different management regimes or over different periods of time, and it facilitates comparisons between animals from different herds.
- It allows comparisons to be made among animals that have undergone different amounts of prior selection.
- It partitions genetic and non-genetic effects on performance into their respective components, thus enabling breeders to assess genetic change over time.

We need to solve mixed model equations (MME) to obtain BLUP of breeding values. The size of the MME depends on the genetic model (Figure 2). One of the main advantages of the genetic models used lately is the fact that they increase the accuracy of evaluations. For example, although the breeding values can be predicted by solving MME with several dozen or a few hundred unknowns in a sire model, one multiple-trait, random regression model in a country with an advanced dairy cattle evaluation system led to MME with near 100 million unknowns (Lidauer et al., 1999).

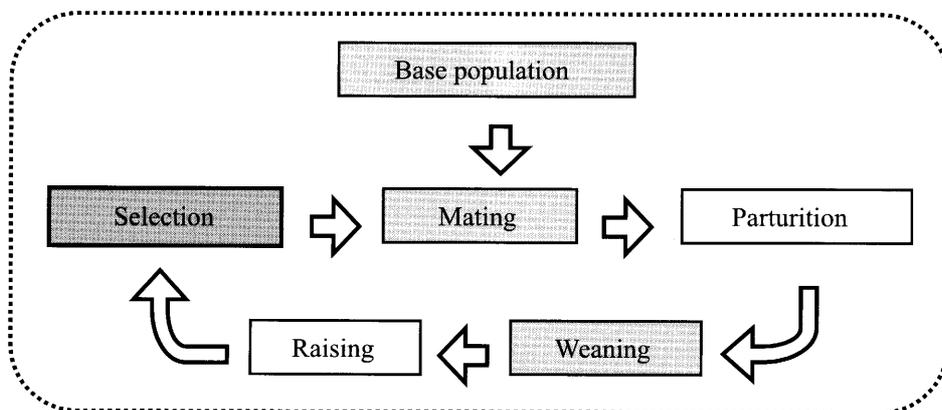


Fig.1. A basic system for genetic improvement by selection.

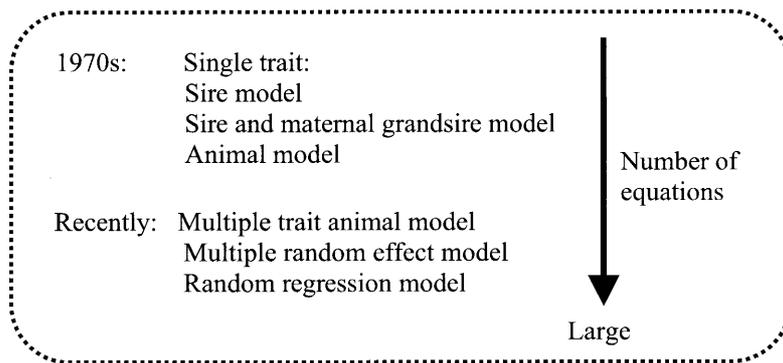


Fig. 2. Relationship between size of MME and mathematical model.

Genetic evaluation of livestock owes what its current status to increasing computer power. Currently we can solve MME with a few million unknowns by using only a personal workstation. The development of computer science has facilitated stochastic computer simulation studies for comparing genetic models or animal breeding systems by selection using BLUP. The genetic evaluation systems are supported not only by computer hardware but also by software. After the 1970s, many studies on BLUP methodologies, such as methods for computing the inverse of a relationship matrix (Henderson, 1976; Quaas, 1976), rules for calculating the coefficients associated with genetic group effects of MME (Westell et al., 1988; Quaas, 1988), or iterative algorithms and their application in solving MME (e.g. Schaeffer and Kennedy, 1986; Tsuruta et al., 2001; Strandén et al., 2002), have been developed. As a result, many programs for calculating the BLUP of breeding values are now offered worldwide. For these reasons, the development of computer hardware and software is enabling us to apply important breeding theory to practical animal breeding systems.

2.2 Problems in applying BLUP to genetic evaluation

Some basic assumptions of the linear model are demanded for predicting breeding values by using BLUP methodology. For example, the distributions of observations, breeding values, and random residual effects are assumed to be multivariate normal, implying that traits are determined by many additive genes, each with infinitesimal effects, at many infinitely unlinked loci; and the base population is assumed to be unrelated, unselected, and sampled randomly from a conceptually infinite population. However, actual data are not based on these assumptions. Several problems, therefore, arise when

breeding values are predicted by the BLUP method on the basis of actual data. Two of them—genetic parameter estimation and selection with constraints—are introduced in this subsection.

In the BLUP method, genetic parameters in the base population are assumed to be known. However, the genetic parameters are generally unknown. Accordingly, we have to estimate genetic parameters in the population beforehand. Before the 1980s, Henderson's Method III (Henderson, 1953) was widely used for estimating the variance component. A disadvantage of this method for animal breeding application is that it was difficult to estimate genetic covariances. Restricted maximum likelihood (REML: Patterson and Thompson, 1971) was then adopted by animal breeders for estimating genetic parameters. More recently, Bayesian inference via Gibbs sampling (Geman and Geman, 1984; Gianola and Fernando, 1986) and Method R (Reverter et al., 1994) have been proposed for estimating variance components.

The effects of selection (e.g. van der Werf and de Boer, 1990; Schaeffer et al., 1998), statistical models (e.g. Clément et al., 2001; Satoh et al., 2002), incomplete pedigree information (e.g. Schenkel and Schaeffer, 2000; Roughsedge et al., 2001), and different methods of estimating genetic parameters (e.g. van Tassell et al., 1995; Cantet et al., 2000) have been studied for a few decades. There have also been many studies on the empirical comparison of REML algorithms. A detailed discussion can be found in a review by Hofer (1998).

The REML technique is the most accurate method available, because it takes account of all genetic relationships between the animals and the effects of selection. Larger data sets and more complex models can be analyzed by REML, owing to the increased power of computers and advances in computing algo-

Table 1. An example of comparison with methods for calculating restricted BLUP¹

Selection method: Author and (Year)	Constraints	Number of nonzero elements ²	CPU time ³ (second)
Satoh (1998)	All animals	144,161	0.72
Quaas and Henderson (1976)	Some animals	204,561,480	6,916.91
Satoh (2004)	Some animals	17,620,448	169.97

¹ Total number of animals used for calculation is 31,650 and the number of restricted animals is 6,000.

² Number of nonzero elements in the upper triangular matrix on the left-hand side of restricted BLUP equations.

³ Central processing unit time.

rithms. However, the computational requirements for variance component estimation are still demanding, and continued efforts at improvement are still necessary.

In Japan, selection for desired change in all traits has been frequently used in swine or poultry breeding programs. At first, this selection procedure was based on a restricted selection index, achieving predetermined relative changes in all traits (Yamada et al., 1974). After that, restricted selection indices were applied to restricted BLUP (Quaas and Henderson, 1976). The original method for calculating restricted BLUP of breeding values has been improved by Itoh and Iwaisaki (1990) and Satoh (1998). More recently, Satoh (2004) derived a new procedure for estimating restricted BLUP of breeding values when constraints were imposed on the additive genetic values of only some animals in a population. This method requires several hundred times more computing power than usual multiple-trait BLUP (Table 1).

Because the population size of closed herds in swine or poultry breeding in Japan is generally small, calculation of restricted BLUP is not difficult. However, if all the animals in the whole country were to be evaluated, the computing requirement would be quite heavy. Because restricted selection includes selection with zero change in one or a few traits, if some economic trait is optimized by selection, then restricted selection with zero change will be conducted. Egg weight in laying hens and backfat thickness and meat quality (e.g. intramuscular fat content and meat color and pH value) in swine and beef cattle have optimum levels in terms of economics or consumer requirements, and these traits may reach their optimum levels in the near future. Traits that required balance, such as milk and milk fat yields in dairy cattle, body weight and leg weakness in swine, and composition of fatty acids in

meat will be also used for selection with constraints. Calculation of restricted BLUP as well as REML will require increased computing power.

3. Effects of development of molecular biology on animal breeding theory

3.1 Detection of QTLs segregation

Over the last few decades, we have developed molecular biology techniques and the associated analytical genetic tools. These advances have increased interest in using genotypic information to improve response to selection. In particular, theoretical studies on the detection of QTLs by using polymorphic DNA markers and on the use of QTL information for genetic improvement in livestock have developed rapidly in the last decade. These are a series of problems, including genetic marker linkage analysis and mapping, identification of marker loci linked to QTLs, and identification of QTLs. Interest of the next step can be divided into two directions. One is the analysis of gene function and genetic mechanisms by molecular geneticists; the other is the use of linkage associations or QTLs directly in the genetic improvement of economic merit by animal breeders and quantitative geneticists.

Dense marker linkage maps have been constructed for the most important domestic species. There are few theoretical problems in terms of yield. DNA polymorphisms are used as linked or direct markers to detect QTLs segregating in particular populations with specific allele frequencies. More recent practical studies have investigated polygenic traits with the aim of identifying QTLs for production traits such as growth, meat, milk, wool, fertility, and disease resistance, and the results of a large number of studies have been summarized in species-specific QTL maps (e.g. Bidanel and Rothschild, 2002; Khatkar et al, 2004). Finally, all QTLs with economic merits will

be identified and the location of the QTLs in the genome and the size of the QTL allele effects will be estimated.

Accurate estimation and improvement of the accuracy of estimation of QTL allele effects are most important in the use of QTL information for genetic improvement in livestock. The accuracy of this procedure depends on the number of animals and the heritability of the trait affected by the QTLs. In this respect, estimation of the genotype of the QTL allele is similar to breeding value estimation using BLUP methodology. After all, estimation of the genotype of the QTL allele is affected by the phenotype itself.

3.2 Selection efficiency of direct use of QTL information

Genetic markers can be used to identify specific regions of chromosomes where genes affecting quantitative traits are located. Marker-assisted selection (MAS) uses information about these regions in livestock selection programs to identify individuals with favorable combinations of QTL. Most researchers agree that MAS is likely to complement, rather than replace, conventional selection systems, leading to increased rates of genetic change. However, there is a risk of reduced genetic response if the marker association information is inaccurate, since MAS is a form of indirect selection. On the other hand, if assumed, error-free QTL information is used directly to predict response to selection, the genetic improvement is expected to be greater than that by using MAS and QTL information with errors. However, if the response to selection by using identified error-free QTL information is inferior to that by using conventional selection, information on the identified QTL will not be useful for genetic improvement. The potential benefit from using information on identified QTLs in selection is discussed in this and the next subsections.

The benefits of combining both the genotype and performance information have mostly been assessed in terms of the short- and medium-term genetic responses relative to traditional mass or BLUP selection. However, the benefits decrease in long-term selection (e.g. Larzul et al., 1997; Pong-Wong and Woolliams, 1998; Villanueva et al., 1999). The general conclusions are that the use of QTL information from genes with large effects or from markers linked to these genes significantly increases

the short-term genetic response but has lower cumulated gain than the use of traditional selection methods such as phenotypic or BLUP selection. Figure 3 shows the typical responses to selection using QTL information. Loss of long-term response with genotypic selection or with BLUP selection based on genetic markers linked to a QTL is caused by a reduction in the effective intensity of selection that is applied to polygenes (Gibson, 1994). The loss in polygenic response is not offset by the increased response for the major gene. Build-up of gametic-phase disequilibrium between the major gene and the polygenes is also a reason why the result of genotypic selection is less than that of phenotypic selection in the medium to long term. The most important conclusion is that there is no large difference in response to selection whether or not QTL information is used for genetic evaluation.

3.3 Selection efficiency indirectly using QTL information

Much of the breeding of commercial plants such as rice, wheat, and soybean is based on pedigree selection, by which elite inbred lines are crossed and then self-fertilized for several generations to produce a large number of recombinant inbred lines that are tested to select a new set of elite inbreds.

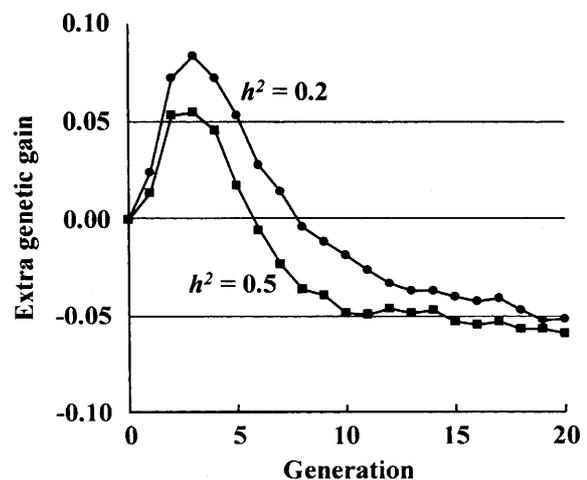


Fig. 3. Total genetic gain over 20 generations of selection using BLUP with the genotype information when selecting a performance trait with heritability (h^2) of either 0.2 or 0.5. Results are expressed as deviation from the predicted cumulated gain achieved with the conventional BLUP selection.

This breeding system may be effective in using QTL information. Furthermore, each plant species has many genetic resources that may include some important QTLs. Therefore, the advantages of using QTL information in animal breeding are smaller than in plant breeding, particularly if the allele effect of the identified QTL is not large.

Candidates for performance testing in cattle or in swine being grown for breeding stock are generally selected by information on relatives and by visual inspection. Additionally the use of information on a QTL identified in the first-stage of selection in a multi-stage selection system is more effective than the direct use of information on the identified QTL (Figure 4), even if the total genotypic variance of the identified QTL is around 20% or less of the total genetic variance of the trait. The use of QTL information may also be effective in evaluating genetic performance when it is applied to traits such as those that:

- have low heritability and/or are unmeasurable before sexual maturity
- are expressed late in life, i.e. lifetime productivity
- are sex-limited, i.e. reproductive or maternal performance
- are expensive and difficult to measure, i.e. disease resistance.

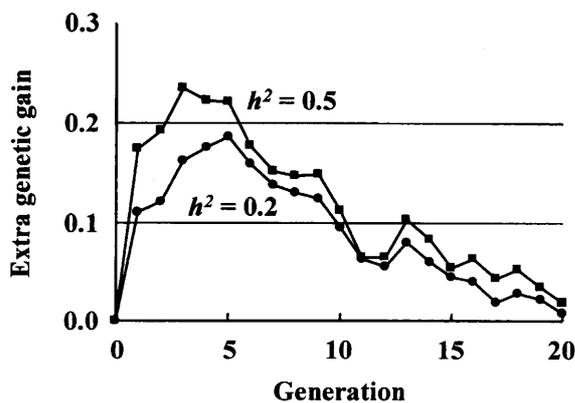


Fig. 4. Total genetic gain over 20 generations of two-stage selection using BLUP with the genotype information. First-stage selection was carried out within families on the basis of QTL information, and second-stage selection was based on BLUP selection. Results are expressed as deviations from the predicted cumulated gain achieved with conventional BLUP selection.

Little attention has been paid to research into unproductive traits, such as disease inheritance. However, owing to the high selection intensity of recent animal breeding systems, studies on disease inheritance or inbreeding depression will become important. In fact, single recessive genes that cause inherited diseases and have major negative impacts on productive traits have now been identified by using molecular genetic approaches (Raadsma and Tammen, 2005). Consequently, the design of breeding programs and genetic evaluation methods to exploit properly the benefits of major genes is urgently required.

4. Conclusions and implications

Almost one century has passed since the first step in animal breeding theory was taken. Recent advances in animal breeding theory have been driven largely by computer science and molecular biology. Conventional animal breeding systems will gradually change with these advances. The genetic model for evaluating candidates for selection will become more complex, and evaluation of combining both information on identified major genes (such as those for inherited diseases) and conventional performance in economic traits will be used in breeding systems. New molecular biological technologies will not replace existing animal breeding practices. Indeed, these new techniques will blend in with conventional methods that are used in breeding program design and genetic evaluation methods which covering both known and unknown QTLs. However, since genetic improvement of economic traits is very rapid, even if we were to continue to use traditional genetic evaluation systems, some traits would approach their selection limits in the near future. We need to consider the development of animal breeding theory aimed at genetic improvement by balancing genetic merit and genetic diversity.

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