

Genetic diversity and sustainable management of animal genetic resources (AnGR), globally

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Summary

The general trends of development imply uniformity of animal genetic resources, caused by loosing endangered breeds and increased inbreeding within commercial breeding populations. This implications lead to reduction of genetic diversity of the animal genetic resources, which may reduce the future possible utilization, when we can see at the same time a dramatic changing environmental production conditions. In order to change this trend of development, sustainable management of the animal genetic resources must be promoted, globally. The fundament for such sustainable management is put forward by the principles given by the Convention on Biological Diversity. In order to accomplish sustainable management of these resources, the following has to be fulfillment:

- A national and global responsibility for maintaining genetic diversity – policies, which will not be treated within this paper
- Develop knowledge as a fundamental concept to impose sustainable management of these animal genetic resources. This will dealt with in this paper. A more complete description of these features can be found in Woolliams, (2005). Sustainable Management of Animal Genetic Resources. Nordic Gene Bank Farm Animals ISBN 92-893-1089-8.

Keywords: Animal genetic resources, Sustainable management, Maintain genetic diversity, Optimal selection, Conservation.

Introduction

In addition to maintaining diversity, the CBD (Convention on Biological Diversity) also intends to activate GR (genetic resources) for food production, which may imply the sustainable management of all farm AnGR, including:

- Sustainable use,
- Sufficient conservation, Fair and equitable sharing of benefit, and
- National responsibility.

The objectives of the CBD can be accomplished in two ways, i.e., via political incentives and/or directives/acts on one hand, and through knowledge, analysis of future consequences and invention of technological tools to avoid damage made by insufficient breeding programmes on the other. In addition, sufficient conservation of endangered breeds must be done, such that the genetic diversity among breeds can be maintained.

The Nordic Gene Bank Farm Animals (NGH) focuses on developing the knowledge needed to accomplish sustainable management of AnGR, based on extensive cooperation with, among others:

- National ministries of agriculture,
- National gene resource committees or other bodies appointed by the national authorities to organise the national conservation of AnGR, within the scope of available budgets, and
- National breeding organisations, breed societies, etc.

NGH has directed increasing focus on the elements needed to secure sustainable management of AnGR.

Elements needed for sustainability

The following factors influence sustainable management of AnGR:

- Inbreeding, $F = 1/Ne$, a function of the efficient population size, Ne
- Maintaining alternative breeds, means appearance of a multiple breed livability
- Selection on a complete set of traits, and
- Interaction between environment (production systems) and genetic effects.

Items 1 and 2 encompass the requirement of maintaining diversity of farm AnGR and can be accomplished by the following measures:

- I. Avoidance of inbreeding:
 - ❖ Optimal selection based on the contribution theory; the needs are equal for all breeds, and
 - ❖ Maintaining sufficient number of breeds to secure between-breed diversity, which provide new genes for immigration /exchange from other breeds. This requires several alternative breeding populations.

- II. Conservation of breeds activated by:
 - ❖ Activate properties of certain breeds for developing branded food products,
 - ❖ Sufficient conservation to secure maintenance of important genes for future use, and
 - ❖ Conservation of historical/culturally important breeds.

- III. In order to maintain the population of farm animals as a healthy production unit, the breeding goal must encompass traits of both marketable products and those important for the functionality of the individuals belonging to the population. This implies:
 - ❖ Weighting factors for the traits must counterbalance the negative response via genetic correlations with vital traits of functionality, or proper trait restriction must be used as a selection tool, and
 - ❖ By using reproduction, health and survival traits in the selection goal properly, one may avoid unexpected problems caused by rapid changes in the frequency of unfavourable alleles/deleterious genes, and also reduce inbreeding depression in fitness traits.

To illustrate, the realised G for mastitis in Norwegian Red is shown in Figure 1.

Breeding programs can be designed in a way that gives a positive response to such traits as mastitis. Similar responses can be shown for non-return rate and other health problems in the breed in this example.

IV. The last important factor impacting sustainability is the occurrence of interaction between production systems and genotypes.

An international "regulation" of exchange of AnGR should focus on this interaction and its social and economic consequences for the recipient population in the long run.

It would seem appropriate to copy some of the principles of the national legislation of trade of goods in several countries, which put responsibility on the seller to sell an appropriate product. Such requirements could easily be included in a standard agreement for transferring genetic material of farm animals.

When the testing of the breeding animals and the production of the offspring are performed in the same environment or in the same production system, the interaction between genotype and environment or production system can usually be ignored. However, when the offspring is exported, the environment may be quite different from the test environment of the parents in the importing country. Besides, a lack of adaptation of the breeds to the environment in the importing country might have a negative effect on fitness traits leading to disappointing production figures. An international regulation of exchange of farm animal genetic resources should focus on the existence of possible interactions and its long-term social and economic consequences for the importing country. It might undermine the livelihood of farmers in the importing country. Such import often implies that the local livestock systems erode and often the livelihood of entire groups of people is destroyed. It has to be realized that as much as 70% of the world's rural poor (approximately 2 billion people) keep livestock to meet the food demands of their families. There, livestock diversity thus contributes in many ways to human survival and wellbeing (Drucker, 2002).

Increasing the production volume may also increase waste output. The considerable volumes of waste produced by large-scale, high-density livestock operations can cause severe soil, water and air pollution (Cunningham et al., 2003). The most important pollutants giving rise to concern are nitrogen, phosphorous, various heavy metals and greenhouse gasses such as methane and nitrous oxide. If the recycling of manure and urine in agriculture is not firmly regulated, considerable environmental damage may arise. The strong focus on environmental issues in several countries may lead to regulations that minimize the output of wastes from livestock systems. Such regulations may require other genotypes than those favoured by the present breeding goals with maximizing yield. This means that breeding programmes that maximize production volume per animal may lead to a reduction of the environmental quality for the society.

Food security and safety

Woolliams (2006) discusses the fundamental importance of farm animal genetic resources for food security and safety. The general answer is that livestock development works best when all strategies are co-ordinated and work in the same direction. For example, fertility in dairy cattle tends to decrease as milk yield increases. An established consequence of infertility is an increase in greenhouse gas emissions from the production system per litre of milk produced. The effectiveness of any management solution will be compromised when selection will increase yield without taking into account the genetic merit for fertility. Then, the overall utility of the system will not be optimised (Woolliams 2006). Genetics can play an important role in the dynamics of the populations caused by genetic selection, and one should use genetic options, where they exist, as part of the solution to improve security and safety.

To meet the challenges to food security arising from the increased global demand and the threats from global warming, livestock breeding must be included as a component of the solution. In the long term, unsustainability of managing the animal genetic resources may lead to increasing risk in failure of the food security and safety.

Knowledge as a driving force for sustainability

Since the food coming from farm animals accounts for 40-50 % of the caloric intake, and very much of this food originates from the commercial or mainstream breeds, in many countries, the maintenance of genetic diversity within these breeds becomes increasingly important. As the number of breeds used in food production is increasingly declining, there is an increasing risk of some genetic failure. The loss of breeds contributing to our food supply directly diminishes the aspect of food security inherent in maintaining a diversity of food resources. Thus, major breeds, which have “no alternative” for immigrant genes from other breeds, have to invest in tools and strategic measures to avoid the risk of genetic failure, as part of the running breeding programme. Investments in risk management measures for running breeding programmes are not well documented.

Therefore, I would like to discuss more thoroughly the importance of managing the mainstream breeds by maintaining their future genetic diversity as part of the breeding programmes.

Present status

The classic measure for genetic improvement per generation is accuracy (the square root of heritability, h) times the genetic selection differential expressed in real units of the trait (i_{-g}); $\Delta G = h i_{-g} = h^2 i_{-p}$, in which h is the correlation between genotype g and phenotype p , h^2 is the regression of g on p , i is the selection differential and $_{-g}$ and $_{-p}^2$ are genetic standard deviation and phenotypic variance, respectively. Efficient methods for registration of lineage and such traits as performance, fertility, health and survival for individuals in a population have been implemented. At the same time, efficient methods for breeding value estimation were developed, which linked the individual's traits to all relatives. These methods were based on the principle of “Best, Linear Unbiased Predictions” (BLUP), (Henderson, 1976).

Due to the above-mentioned development, a limited number of certain individuals and their relatives can easily come to dominate as parents in future generations. As a result, the breed will eventually consist of animals originating from fewer and fewer families. As time passes, the average degree of relatedness between parents increases and thus, the inbreeding rate will increase.

Developing a sustainable breeding theory

An important discovery within genetic theory was the effect of selection on genetic variation. This was developed by Bulmer (1971) and shows that systematic selection of parents results in reduced genetic variation among their offspring. After 4-5 generations with the same selection intensity, the reduction will stabilise. In practical cattle breeding work, Finland (1979) showed that this reduction could amount to 20 – 30 %, depending on the selection intensity and accuracy. Systematically, intensive selection thus leads to the stabilisation of genetic variation at about 70 – 80 % of the level of variation achieved with random mating and no selection.

The next step towards developing a more realistic foundation for breeding work was the discovery of the dynamic traits of the additive kinship matrix **A**, by Hill (1974), Henderson (1976), Thompson (1977) and Wray and Thompson (1990). The elements in the **A** matrix generate covariance or degrees of relatedness between all individuals in a pedigree for the respective population, as well as the individuals' inbreeding status along the diagonal of **A**. When determining **A** from the "base" generation, one can identify gene transfers throughout all individuals in a lineage; sires to sires, sires to dams, dams to sires and dams to dams, from the base generation to the present population. In addition, one gets an overview of the individuals that have provided a lasting genetic contribution to genetic improvement, and of those individuals that no longer are considered as contributors to genetic improvement.

The latest major step of the development was the establishment of the unique "genetic contribution" theory put forward by Woolliams and Thompson (1994), which also provided a tool to estimate values for ΔG and ΔF . The two defined factors that determine genetic improvement and inbreeding rate are:

- A factor, r , which is the additive genetic contribution from an individual in a pedigree to today's population, where the corresponding element of **A** is a function of r . When $r > 0$, the individual is a contributor to genetic improvement, but when $r = 0$, the individual has not contributed to the genetic improvement of today's population. The sum of r of all dams contributing to the present population is 0.5. The same applies to the sires contributing to the present population.
- The breeding value of an individual is comprised of: $g = g_s + g_d + s$, where g , g_s , g_d are the additive breeding values for the individual, sire and dam, respectively; and s is the individual's unique additive breeding value for the trait, consisting of the individual's unique gene combination in addition to the additive breeding value transferred by the parents. Variation of this element, s , can amount to more than half of the additive genetic variation of present populations. The expression is used because if selection is carried out in the parent generation, the additive genetic variation that is transferred from the parents to their offspring will be less than when using random mating and no selection among parents (the so-called Bulmer effect). The value of s is often called the "individual's sampling term".

It was shown that:

1. $\Delta G =$ sum of r multiplied by s for all individuals in the pedigree who pass on genes to individuals in today's population ($\Delta G = \sum r \cdot s$). This shows that genetic improvement is a direct product function of the individuals contributing genes ($r > 0$) and the corresponding value of s , which expresses the individual's unique gene combinations, i.e., the genes that are not additively passed down from the parents or from more distant relatives in the pedigree.
2. $\Delta F =$ sum of r squared for all individuals who contribute genes to individuals in today's population ($\Delta F = \sum r^2$), under certain assumptions, e.g., random mating.

Due to the dynamics of breeding work, if one goes back 5-7 generations in the pedigree, the contribution from those parents passing on genes to present-day and future individuals will be the same for each of these ancestors. This means that genetic contribution of previous 'matadors' (extensive used) breeding animals that have contributed to a large share of genes in today's population cannot be changed in a closed breeding population. In a closed population, genetic change will take place for those genes that can contribute to new gene

combinations. Such new gene combinations can only occur via the “gene base”, which is identified by the individual’s sampling term. The individual’s sampling term is the individual’s specific and unique set of genes, and thus represents the foundation for the future genetic renewal that can occur within closed populations. Fifty per cent of genetic variation is fixed through previous selection of parents and earlier relatives. Only in the most recent generations, will the genetic contributions be affected by the accuracy of the breeding value and the individual’s selective benefit. It is thus obvious that an individual contributing to sustainable improvement has a sampling term that is larger than the average of its parents’ breeding value. The characterisation of this genetic diversity shows a resource potential for the respective trait and population. Theoretically, an individual’s sampling term as an infinite resource will only exist for traits consisting of an infinite number of loci. For traits with only one locus or few loci, selection will rapidly approach fixation, and thus be depleted of its genetic variation.

In closed populations with intensive selection and the use of few sires, the long-term contribution and a large share of the genes will be provided from only a few individuals. In such cases, the effective population size, which is $N_e = 1/(2\Delta F)$, will be relatively small. Since the selection space for breeding work is $2N_e i h^2 - p^2$, breeding programmes with small effective population sizes (N_e) will result in less total improvement than breeding programmes that secure larger effective population sizes. It has been indicated that moderate selection (about 50 %), especially in the first generations, will ensure maximum genetic improvement in the long run. It should be well known that intensive selection in the start-up of a breeding programme leads to the loss of numerous beneficial genes in the first few generations, due to the effect of linkage between loci. A more moderate selection intensity early in the programme will help to “break apart” these linkages as time progresses, thus enabling more beneficial genes to be passed on to future generations, (Alan Robertson personal communication from 1974).

One way to regenerate genetic variation is to enable immigration of genes from various other populations. This is the most effective way to provide new genetic variation, especially when the external population contains more beneficial genes than the mother population. However, immigration from other, similar populations can also lead to improved genetic variation, especially for inbred mother populations. For these, genetic variance would be $(1-F) - g^2$, where F is accumulated inbreeding. In such cases, the new supply of genes can “break apart gene pairs identical by descent” that have been inherited from the same ancestor and replace these with genes that either are more beneficial or have the same functional value. In either case, inbreeding will be discontinued, thus revitalising the genetic variation within the population.

Optimised selection is the maximisation of the selection differential, with the restriction that ΔF is less than, e.g., 0.5 %, in which case $N_e = 100$ animals. Optimisation is achieved by maximising the selection differential for the potential parents by using a mating strategy that keeps the inbreeding rate in the next generation below a given value, e.g., 0.5 %. The process of optimisation implies determining which animals to use in breeding, and deciding on the relative genetic contribution of each of these, c_i . This includes, for example, determining the relative share of semen provided by each proven sire. If this value is expressed as c_i , optimised selection will result in maximised correlation between c (contribution to next generation) and r (long-term contribution).

Effect of selection

In classic breeding, genetic improvement is accuracy (h) times selection intensity (i) times genetic standard deviation for the trait. Note that 'accuracy' here is an expression for the accuracy of an individual's breeding value (g). Due to uncertainty and other factors, certain selected individuals may not contribute to future genetic gains. For example, it has been shown that some bulls selected as breeding sires generate progeny, which for various reasons do not contribute to genetic improvement.

By calculating the contribution to genetic gain ($\Delta G = \sum r \cdot s$), where r is the long-term contribution, and s is the sampling term, one sees that these bulls (with r = 0) do not contribute to genetic improvement.

This implies that:

1. Long-term contribution (r) correlates better with the breeding value of the individual's sampling term (s) than with the individual's breeding value (g). In other words, the individual's selectivity is more closely tied to the value of the sampling term (s) than to the individual's breeding value (g).
2. Additive genetic variation from g_f is less than half of the variation of s – the individual's sampling term in populations under selection.
3. Due to restrictions on ΔF , optimised selection leads to greater accuracy with regard to the contribution to genetic gain than when applying classic breeding theory, in other words, this maximises the correlation between c (contribution to next generation) and r (long-term contribution).
4. Optimal selection secures "new genes" with selective benefits from potential parents' sampling term, s, and which have not been previously expressed by animals in the pedigree. Such animals will contribute to sustainable breeding gain in future generations.

An analysis done by Avendano et al. (2004) shows the following results:

1. Correlation squared between the long-term contribution (r) and estimated sampling term (s) is 0.84
2. Correlation square between the long-term contribution (r) and estimated breeding value (g) is 0.43

This means that restricted inbreeding in the breeding programs improve the efficiency of the breeding operations.

It was also shown that the effect of selection in an optimised selection strategy was 0.92, compared to 0.50 in ordinary BLUP selection, i.e., nearly twice as much. Furthermore, optimal selection gave 20 % more genetic improvement than ordinary selection. These results confirm that, when selecting parents, restrictions on expected ΔF in the next generation rather reflect the individual's sampling term, s, than the breeding values of the individual's parents.

Several analyses have shown that restrictions on the rate of inbreeding can lead to the apparent loss of phenotypic selection differential. Restriction of inbreeding in the optimal selection scheme leads to the selection of alternative parent animals with a higher probability of contributing to the renewal of genetic variation. It is also more probable that these breeding animals will contribute to the long-term genetic gain ($r > 0$) than animals selected for ensuring a maximum "phenotypic" selection differential. When placing restrictions on inbreeding rate for the next generation, the net effect is that the product of selection differential times accuracy is maximised. This implies that optimal selection in general includes the use of

breeding animals that lead to greater selective benefits and higher probability for a long-term contribution to genetic gain. The result is more efficient genetic improvement than when selection is merely based on BLUP values.

Conclusions

Optimal selection focuses on:

1. The individual's selectivity, which is dependent on the relative share of genes (r) and a positive additive value of the individual's sampling term ($s > 0$).
2. Maximising the probability that the selection of parents gives unique, new genes that contribute to genetic improvement in coming generations, i.e., finding potential parents with a considerable probability of providing unique and new genes from their sampling term.
3. Genetic improvement requires that, new, unique and beneficial genes be introduced from the sampling term of each new generation of potential parents.
4. Selection for traits with limited number of loci will gradually reduce the genetic variance as loci become fixed. In traits with infinite number of loci the random sampling term with its genetic variance seem to be unaffected by selection. However the intense selection of parent imply that the parent contribution to the next generation of the genetic variance will be less than $\frac{1}{2}$. Thus, the sum of the random sampling term of genetic variance and the part coming from its parent will be less than the original genetic variance with no directional selection of the parents. The Bulmer-effects.
5. The only practical way to break long time inbreeding is to immigrate genes from other breeding population. Such refreshing of blood to local breeds has been done in many breeds during the history. The question of where to find a breed that can be accepted to be used, may become a question of life or death for some populations.

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Figure 1. Plot of average sire posterior mean (SPM) in the probability scale (threshold model) and mean predicted transmitting ability (BLUP-PTA) of sires by birth-year of daughters for mastitis.

(Heringstad, B., R. Rekaya, D. Gianola, G. Klemetsdal, and K. A. Weigel. *J. Dairy Sci.* 86:369–375).

