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Preserving genetic variance resources in commercial and non-commercial populations

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Abstract

Genetic diversity is the basis for livestock breeding. Diversity within breeds may be reduced by effective breeding methods in commercial breeds; diversity between breeds may be reduced by disappearance of non-commercial breeds. Two means of preserving diversity are discussed: the development of breeding methods that aim at genetic gain yet account for loss of diversity, and the setup of gene banks to preserve current diversity for future use.

Keywords: genetic resources, breeding programmes, gene bank

Introduction

Genetic diversity in plant and animal species is the basis for adaptation and survival as realized by natural selection. In artificial selection, genetic diversity is the starting point for improvement of breeds. In the development of livestock breeds, divergence (i.e. the development of breeds from a population) is the first step. Then due to preference of some breeds over others, reduction of diversity between breeds may occur. This potential reduction depends on the selection goal for each breed. From a practical point of view, breeds consist of populations between which there is only limited or no genetic exchange, and selection is usually performed within populations.

In sustainable animal production, reduction of genetic diversity should be minimized to enable future genetic changes with changing environments and demands. However, current breeding programmes are not optimized for the long term (Dempfle, 1990), and increasingly intensive selection may narrow the genetic base.

This paper investigates the extent to which genetic diversity in animal populations is endangered. The need for measures to conserve genetic diversity and methods to achieve this goal are discussed for both commercial and non-commercial breeds.

Commercial breeds are kept for animal production purposes under selection for increased biological and economic efficiency. Non-commercial breeds are kept for other purposes: as captive zoo-animals or as populations merely serving as a genetic resource ('rare breeds').

Causes and risks of reduction of genetic diversity

The genetic model used in selection is the infinitesimal model (Bulmer, 1980), assuming a large number of genes each having a small effect on a quantitative trait. According to this model, genetic variance of a trait is reduced only during the first generations of selection owing to gametic disequilibrium, and the complete initial genetic variance is restored when selection is stopped. Selection experiments in mice show that after many generations of selection for a trait, a selection plateau is reached. Relaxation of selection or reversed selection lead to reconstitution of the original value for that trait (Buis, 1988), so genetic diversity for many traits may not be much reduced by selection.

However, in the long term there is another cause of reduction of genetic diversity. In populations of limited size, there is a gradual decrease of genetic diversity with time, owing to random genetic drift and increasing genetic relations (unintentional inbreeding) between individuals. The rate of inbreeding is related to the effective population size, N_e. In N_e the numbers of breeding males and females used in each generation are combined in one figure. Genetic drift causes changes in gene frequencies over generations in an arbitrary direction, increasing the chance of fixation of genes and thus decreasing genetic variation. Inbreeding does not change gene frequencies but increases average homozygosity relative to a non-inbred population. The inbreeding coefficient is a measure of increased homozygosity in a population. Increased homozygosity implies the risk of inbreeding depression of characters, i.e. a decrease of their average values relative to a non-inbred population.

Inbreeding depression is usually higher for reproduction and health (fitness) traits than for production traits (e.g. growth, milk yield). The decrease by inbreeding depression is measured as a percentage of the mean value of a trait per % inbreeding in the population. The following figures give an idea of its magnitude. In pigs, Falconer (1989) mentions for litter size a decrease of 0.31% and for body weight at 154 d 0.43% per % inbreeding. For milk production, Hodges et al. (1979) mention a decrease of 23 kg milk and 0.5 kg fat per lactation (only about 0.35%) and Goddard & Smith (1990) about 0.25% per % inbreeding.

Another risk of inbreeding is an increased frequency of recessive homozygous genetic defects. An unintentional advantage of this increase may be the earlier detection of carrier individuals in the population. However, DNA techniques may in future be used as efficient tools to detect carrier animals. The risk of deleterious genes could be successfully minimized, as was proven with the Bovine Leucose Adhesion Deficiency in cattle.

If populations are divided into subpopulations, changes of gene frequencies lead to a redistribution of variance: a reduction within and an increase between lines.

Hence, if breeding organizations select independently - and possibly for different traits - within their closed populations, new variation will be found between populations.

Reduction of genetic diversity in commercial breeds

Current and increasing inbreeding are a measure of the reduction of genetic diversity. Average inbreeding in the US Holstein Friesian (HF) cattle population was 0.36% (Hudson & Van Vleck, 1984); that in the Canadian Holstein population only 0.15% (Miglior et al., 1990). Average inbreeding in Dutch HF test bulls (300 per year) increased from 0.15% in 1984 to 1.55% in 1990 (Huizinga, 1992). Only in this case could an increase be estimated, being 1.40% in 6 yr, i.e. in one generation. An increase of ≤ 1% per generation is usually considered acceptable. Van Dam et al. (1989) analysed the breeding structure of Dutch Landrace (DL) and Dutch Yorkshire (DY) pig breeds. The effective population sizes were estimated as 307 for DL and 469 for DY; average inbreeding was 0.82% in DL and 0.53% in DY. Thus average inbreeding in cattle and pig populations is still relatively low, and inbreeding depression on the mean values of production traits can easily be counteracted by selection. However, this may not be true for traits not under selection as fitness traits often are.

Recent developments in animal breeding may accelerate the reduction of diversity by causing increased inbreeding levels. One development is the use of effective nucleus breeding schemes and intensive selection by best linear unbiased prediction (BLUP) methods (Wray, 1989). Efficient use of family information in BLUP procedures (sire model, animal model) leads to selection of related males and females, thus increasing average inbreeding in nucleus breeding populations. Another result of using relatives' information is the early selection of animals and reduction of the generation interval. Genetic change as well as reduction of diversity are therefore increased per unit of time. Another development is the use of reproduction technology such as multiple ovulation and embryo transfer (MOET) in cattle to increase the number of available oocytes per cow (Ruane, 1989). The consequence is a large reduction of the number of females used in a breeding programme, increasing average inbreeding.

Breeding programmes to minimize reduction of diversity

With respect to sustainable animal breeding, it is important to consider the long-term effects of selection. Current selection programmes are usually directed to short-term gains. Dempfle (1990) studied the difference between short- and long-term selection and simulated the effect of several selection strategies on effective population size and on cumulative genetic gain over 5 to 40 generations. The most precise method, index selection, was superior over 5 generations. The highest gain over 40 generations was obtained by individual selection and restricted (best male and best female) within-family selection, thus favouring unrelated animals.

The selection result can be reduced by inbreeding depression. Based on this balance, Goddard & Smith (1990) suggested a breeding scheme to reach an optimal response in a dairy cattle nucleus population, accounting for both genetic progress and inbreeding depression. They recommended a minimum effective number of 10 to 15 bull sires per generation to obtain maximum net genetic response at a minimum increase of inbreeding. Woolliams & Meuwissen (1993) proposed a scheme in which the additive genetic response is maintained even at decreased inbreeding levels. They selected animals on a combination of BLUP breeding value and expected level of inbreeding in the population, resulting in selection of more unrelated and more accurately evaluated individuals.

Meuwissen & Woolliams (unpublished) optimized breeding programmes for genetic gain under restrictions with respect to the variance of response. They argued that constraining the variation in response simultaneously restricts the accumulation of inbreeding because the variance of response forms a more stringent restriction on effective population size than the rate of inbreeding.

The average degree of inbreeding in a population affects not only measured or selected traits but also other traits. Fitness is expected to decrease, owing to inbreeding depression and a negative correlated response to selection. Meuwissen & Woolliams (unpublished) developed a method to estimate the required effective size of livestock populations to avoid a negative correlation between selection and fitness. They derived a simple formula for such an effective size, leading to a maximum required size of $N_e = 250$.

De Boer & Van Arendonk (unpublished) studied the effect of MOET (see above) in a cattle breeding system by simulation. The use of a smaller number of females was easily compensated by using more males. Because selected females were less related than males, the overall effect was less inbreeding than the other way around at a given genetic gain.

Summarizing these results, we conclude that recently much effort has been put into the development of new selection procedures that aim not only at high genetic gain in the long term, but also at conservation of existing genetic diversity.

Reduction of genetic diversity in non-commercial breeds

Genetic diversity in non-commercial breeds is threatened in two ways: between breeds by the risk of extinction owing to lack of economic interest, and within breeds by their usually low effective population numbers. Owing to emphasis on efficient livestock production, many original, mostly landrace breeds, have disappeared or at least decreased in numbers of animals within the last decades. A classical example of economic use of an almost extinct breed is the use of the Cornish Game chicken as one of the founder breeds (together with Plymouth Rock and New Hampshire) of modern broiler chickens in about 1950 (Crawford, 1990 p. 1003). Until that time the Cornish Game was only used for sport breeding. The economically important trait in this case was a broad-breasted appearance. Another example is the use of the Oxford Down sheep, not long ago threatened with extinction, as a leading sire breed in Britain for the production of heavyweight lambs (Alderson, 1990).

Since 1975, in various countries, organizations have been established to protect these breeds for a variety of reasons - biological, cultural, historical, aesthetical and last but not least as a genetic resource. Many of these breeds possess traits which may be of use in future livestock breeding, e.g. with respect to fertility and resistance. At a global level, FAO is concerned with the conservation of animal genetic resources, including the protection of 'small' breeds. There are two ways of conserving those breeds as a genetic resource for possible future use in livestock production: alive or in gene banks.

Conservation of non-commercial breeds as a genetic resource

Non-commercial and usually 'small' breeds, including captive populations in zoos, are subject to genetic drift. Their numbers of breeding females are often below 1000 and of males below 50. The animals are usually subdivided among small owners or (in case of grazing species) natural reserve preservation organizations. Systematic breeding schemes are therefore hard to perform. With regard to their overall low effective numbers, breeding schemes to minimize a further increase of their average inbreeding should be applied. In zoo animals, Princée (1988) studied the breeding situation of the red panda. Based on a founder population of 142 animals in 1984 in four subpopulations, inbreeding increased at 3-4% per generation with decreasing fertility. Princée strongly recommends migration between subpopulations to ensure survival of the red panda in captivity. The rotational use of rams over herds in a heath sheep population after splitting the population into separate herds, as performed in the Veluwe and Kempen heath sheep in the Netherlands, is another example of this approach. An advisory system to perform most unrelated matings, as in the Friesian horse, is still another possibility to postpone inbreeding. However, results of such procedures are hard to estimate owing to the lack of experimental or even field data.

The costs of live conservation are often a problem in these breeds. They can be compensated partially by a low-economic use in the production of unique products (e.g. sheep or goat milk cheese; traction power of horses in wood culture) or by specific grazing capacities in nature reserve preservation (cattle breeds, heath sheep, goats). Van der Ouderaa (1992) proposed to enlarge the population numbers of 'small' breeds of grazing animals by using them more intensively in nature preservation. He also estimated the costs of subsidiary financing of breeds, based on the difference between their production and that of a comparable commercial breed.

Gene banks

A method to preserve genetic diversity as a genetic resource is the establishment of cryogenic gene banks. The role of a gene bank is that of an insurance system for possible use of present variety in future livestock breeds. For conservation of specific traits, a gene bank has the same function as live preservation of non-commercial breeds. If diversity in future commercial breeds should decrease through increased inbreeding, effective population size may be restored to a certain degree by the use of unrelated material from a gene bank in a breeding system.

There are several organizational (1), technical (2) and breeding-strategical (3) aspects in the setup of gene banks:

1.1 The overall responsibility for conservation: breeding companies (mid-long term), governments and/or EC, FAO (long term)?
1.2 Costs and returns; who pays for a bank (see 1.1) and who is allowed to use the conserved material?
1.3 How is continuity for a period of at least 25 years assured?
2.1 In which form (semen, oocytes, embryos) is conservation to be done? Species-dependent, technical and financial aspects apply here.
2.2 Use of advanced DNA techniques for identification of genes (gene mapping, fingerprinting, microsatellites, PCR-techniques)?
2.3 Is there viability and genetic quality control of input material; safety guarantees (twin banks), registration of sources and traits?
3.1 Which breeds and which genes to conserve: an average of a breed; extremes; special traits; single-trait or major genes?
3.2 How much to conserve and from which (unrelated) animals in relation to effective size?
3.3 The development of special breeding schemes to implement the use of material from the bank in future livestock breeding.

For plants, since 1970 gene banks have been founded in various countries and are organized in the International Board for Plant Genetic Resources. At the National Workshop on Conservation of Animal Germplasm in Ottawa in 1990 it appeared that animal gene banks were still under discussion in Canada, the US and Europe (EC). FAO gives priority to the setup of uniform data banks as a basis for the description of animal diversity. In 1988, FAO and EAAP decided to collect information on livestock breeds and to set up a Global Data Bank for Animal Genetic Diversity in Hannover, Germany (Simon, 1989). This bank serves both for commercial and for non-commercial breeds, and can provide data for the setup of gene banks at national level. In 1991 it contained data on 717 breeds from seven species, originating from 30 countries.

According to the state of reproductive technology of the species, semen, oocytes and/or embryos can be conserved. At present, only freezing and use of cattle semen and embryos are successful. AI organizations have gene banks for short-term use. By conservation of semen of old bulls they can form a simple basis for a genetic resource bank. Cryopreservation of chicken semen is possible since 1978. Levels of fertility of frozen and thawed semen are lower than those of fresh semen, but sufficient for germ plasma conservation (Crawford, 1990 p. 104). For other species and methods of conservation (e.g. tissues, DNA), research is in progress. With regard to the breeding-strategical points mentioned under (3), a bank should be guided by an advisory board of experts.

Conservation of non-commercial breeds in a gene bank is not different from the situation in commercial livestock. Compared with live conservation, the costs will be (much) lower. It is most effective to set up a common bank for both types of breeds or to join an existing system.

In the Netherlands, in 1993 the setup of a genetic bank for cattle has been realized through concerted action of government and AI organizations. The bank has started with cattle of commercial and non-commercial breeds and will be extended to the conservation of other species (e.g. sheep).

Conclusions

In sustainable animal production, the maintenance of genetic diversity is essential for various reasons.

In commercial breeds, it guarantees a future selection potential, favouring the same or possibly other traits than nowadays because breeding goals may change in the long term. A high level of diversity and appropriate breeding systems are important to avoid a decrease of production capacity by inbreeding depression. Efficient breeding systems will only be a danger for genetic diversity when insufficient attention is paid to long term consequences of selection. Recently, breeding methods have been developed to combine high genetic progress with minimal inbreeding.

There is increasing activity in the preservation of non-commercial breeds as a genetic resource to conserve traits that may be important in future livestock breeding; for these, often small, populations, breeding programmes are being developed to reduce loss of diversity.

For both commercial and non-commercial breeds, (combined) cryogenic gene banks are being set up as genetic resources for future use in sustainable livestock breeding systems.

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