

Sustainable animal genetic improvement

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Abstract. Well designed and targeted animal breeding programs allow a sustainable genetic improvement of livestock with increases in animal productivity of 1-2% per annum. Over time, massive improvements have been achieved, e.g. in dairy and pig and poultry production systems, now resulting in higher production that requires much fewer input of resources. Although reproductive and genomic technologies contribute nowadays to increases in rates of genetic improvement, the key to successful breeding programs lies in a strong focus on simple and well-defined breeding objectives, effective investment in trait measurement, a clear understanding of the structure of the breeding program, and efficient systems for genetic evaluation, selection and mating of elite animals. The dissemination of the genetics of selected animals to the wider population also needs consideration, requiring commercial farmers or smallholders to have the means to have access to improved genetics as well as an understanding of the value of using improved bulls. Definition of the breeding objectives as well as evaluation of genetic merit needs to be based on the local environment. Compared with other interventions to improve productivity and stability, genetic improvement is a critical and cost-effective approach as genetic gains are permanent and cumulative.

1 Introduction

The power of long-term genetic improvement has been well documented in various livestock species. For example, in many countries the milk production per cow has more than doubled since the introduction of AI in the 1950ties, with an annual increase of about 2%. In the UK the average milk production per cow per year in the UK was 5151kg in 1990 whereas it was 7899 kg in 2014 (AHDB Dairy), which is a 53% productivity increase in 24 years. In the United States, the production per cow per lactation increased by 72% between 1985 and 2015 (USDA). The genetic trend between 1990 and 2000 was 1092 kg [1] implying that about 70% of the phenotypic increase was due to genetic selection. Likewise, in poultry production, the growth rate of broilers has increased by about 400% between 1957 and 2005 [2], with the majority (~80-90%) of this increase being due to genetic selection. These examples demonstrate that genetic selection implemented in effective breeding programs has the potential to drive large phenotypic changes in livestock resources. In first instance, genetic selection focused on traits that led to productivity improvements. A higher efficiency of

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animal production systems leads to producing more animal product from fewer resources and this is therefore an important contribution to sustainability. However other aspects such a genetic diversity, product quality and the quality of the animals' wellbeing have become additional considerations, leading to adjustments of breeding objectives and breeding strategies. Large phenotypic changes and their consequential effect on productivity are less pronounced in most developing countries. This paper explores briefly the factors that drive the success of breeding programs, and how they might be applied to breeding programs, in particular those in developing countries.

2 Genetic improvement in developing countries

While genetic improvement programs have been very successful in developed countries it has been difficult to establish programs with significant genetic improvement in developing countries. There are several reasons for this. Different socio-economic factors play a main role, as pointed out by Rege *et al.* [3], who both provided an analysis of the role of genetic improvement in African livestock systems. Mostly, individual farmers are smallholders and the aim of the enterprises is focused on food security and overall livelihoods, besides income. Marshall *et al.* [4] described the various roles of livestock holding as well as the many challenges within the production systems and genetic improvement of productivity is not highest on the priority list. Besides, the incentives for increased production are often hindered by the lack of access to markets. Therefore, it is acknowledged that implementing breeding programs in developing countries should be part of a broader approach where infrastructure and market development are important aspects. Nevertheless, with increased population growth, urbanisation and development, the demand for animal products is expected to increase significantly and it is well recognized that genetic improvement of animal resources can play an important role in a development strategy.

3 Between versus within breed selection

One difference between the current situation in developing countries and the state of animal resources in developing countries a few decades ago, is the availability of improved breeds and strain of livestock that exist. A local breeding program is now faced with the choice of improving a local breed versus upgrading by making use of improved breeds elsewhere. In the past an example of the latter has been the upgrading of many local cattle breeds with Holstein Friesian semen importation, initially mainly from the United States. This phenomenon has become known as the 'Hosteinization' of many local cattle breeds. This process has had a large effect of the rate of genetic improvement of many national dairy cattle populations, and at the same time it has greatly decreased the genetic diversity, at least in black and white dairy cattle. There are several reasons why improving a local breed is preferably over importation of exogenous genetics. These include the maintenance of between breed genetic variation globally and local breeds being more adapted to the local environment, both the natural and the socio-economic environment. On the other hand, genetic improvement is about utilizing genetic variation, and this can be utilized both within and between breeds. In other words, it maybe more rational to upgrade a local population, the more so if its production potential falls behind that of alternative breeds. However, a genetic improvement program that uses exogenous breeds would only be successful if it was based on performance data, where progeny of imported bulls are compared with progeny of the local breed, with performance measured in the environment in which we aim to develop improved genetic resources for. Even the creation of new composites based on diverse local breeds, which all are more likely to be more adapted to the local environment, could be a strategy-based on that same principle, especially when indigenous populations are small. In

Australia, the meat sheep industry has made massive genetic gain over the last two decades, with lamb carcass weights improving from 18 to 23 kg. Much of that improvement was based on the introduction of LAMPLAN, a genetic evaluating system that allowed selection of sires across breeds. As a result, breeders are not too worried about ‘pure-breeding’ and more opportunistically use sires that have a mixed breed background. The resulting genetic gain is likely higher than what could have been achieved with within breed selection alone, simply because selection was based on genetic variation across breeds, which is generally higher than within breed variation. Rege *et al.* [3] concluded that breeding strategies for resource poor smallholders should in first instance focus on using appropriate genotypes from the available range of global breed resources. A breeding system should be set up that allows those genotypes to express their potential. My interpretation is that one should be open to what genotypes should be used in local production systems, but that the choice of genotypes should be based on data.

4 Breeding objectives

The definition of the breeding objective is the first and probably most important step to be taken in any activity with the aim of genetic improvement. Defining breeding objective involves simply to define the traits (phenotypes) that need to be improved and the relative weight for each trait, expressing the value of improvement of each trait relative to each other. Defining the value of improvement requires valuation. If this is according to an economic framework, then economic values can be derived from a financial cost-benefit model. However, not all genetic change can be valued in financial terms. Relative weights of traits in a breeding objective can also be derived from an evaluation of the required genetic changes, using a selection index framework [5].

Improving the wrong traits could be equivalent or even worse than no improvement at all. If many breeding animals will be chosen for reasons irrelevant to the breeding objective, then selected parents will be less superior with regard to the breeding objective. It is important in the selection process that the selection criterion is clear, and whether the selection is efficient in relation to the breeding objective. For example, selection based on body measures is less efficient than selection for body weight itself, when the breeding objective is to increase body weight.

Many practical breeding programs suffer from the fact that the objectives are not properly defined. Selection decisions are often influenced by attention for characteristics that are not formally defined in the objective. Furthermore, the outcome for breeding programs is noticed many years after selection decisions are made. Hence objectives have to be designed for future circumstances. These are not always easy to predict in advance.

As pointed out earlier, significant changes in phenotypes have been achieved in many countries by selection on production traits. However, after some time it was noted that these genetic improvements led to negative correlated responses in other traits, often related to fitness and longevity, and this has led to adjustments of breeding objectives, including more traits related to product quality and animal fitness. For example, there is a large body of literature to demonstrate that fertility has decreased in Holstein dairy cattle [6,7]. A more detailed review across species on the effects of one-sided selection for production traits was published by Rauw *et al.* [8]. Adjustment to breeding objectives were often implemented by increasing the selection emphasis on traits that showed undesirable genetic trends as a result of one-sided selection for production traits. The realisation that a more balanced breeding objective is more sustainable in the long term is often the result of observing undesirable correlated responses with selection for production traits only. These correlated responses are not only in fitness traits. Australian research showed selection for lean meat growth in lambs has undesirable effects on the eating quality of lamb meat [9] and breeding programs were

adjusted to address this problem [10]. These adjustments affect the direction of the genetic improvement, but overall it has become clear that sustainable large genetic improvement are possible over time.

Breeding objectives are critical in the development of genetic improvement programs for environmentally sustainable animal industries. These objectives should be related to development goals of such industries. Production efficiency is a main contribution to sustainability, both economically and environmentally. It is important to be able to generate the required outputs, mainly food, while minimizing the resources needed. For example, the selection for growth in broilers has led to an efficiency of growth such that, compared to half a century ago, about one third of the same feed is now required to obtain the same growth. Traits related to animal fitness and health have become more important with the sharp increase in productivity, and improvement of such traits contribute to both productivity as well as animal wellbeing, the latter becoming increasingly important to the social license for animal production. In the last decade, traits directly related to enteric emission of greenhouse gasses from livestock have become a new focus and there is sufficient genetic variation between animals in methane production to allow selection for this trait. Lower methane production is closely related to feed efficiency, making it economically attractive to include these traits in selection indexes [11], and more so when the carbon price becomes a firmer tool in greenhouse gas mitigating policies.

5 Achieving genetic improvement

Breeding goal definition is the first step to be made in designing animal breeding structures. Then, a second step is to implement a structure of gathering information, a recording system, and a genetic evaluation to identify those animals that have the highest breeding value for traits in the breeding goal. After animals are ranked, a mating strategy is required. A third step is therefore to make a well-organised structure for the use of animals with highest genetic merit. In principle, the best males should be mated to the best females in order to obtain the best offspring. Therefore, a tiered structure is usually desirable where the nucleus matings are based on ‘elite matings’ between the males and females with the highest merit in a population (Fig. 1). The resulting progeny from these matings can become selection candidates for the future generation of nucleus animals, and if they are chosen through selection we can expect a genetic improvement with each generation. The nucleus born animals that are not selected as nucleus parents can be used for the dissemination of superior genotypes through the commercial population (the ‘breeding bulls’). Dissemination could be via artificial insemination (AI), in which case a relatively small nucleus could be used to serve a large population of commercial females. However, with natural mating, an additional ‘multiplier’ tier is required. Since the genetic mean of the nucleus increases each generation, the genetic mean of the animals used for dissemination will increase as well, and as a result, the commercial population will be improved. Note that recording of phenotypes to facilitate selection is only required in the nucleus, yet the wider commercial population will benefit. In fact, the rate of genetic gain in each tier will be the same as that in the nucleus, there is simply a genetic lag, typically equal to two generations between tiers if dissemination is only via males.

The breeding nucleus can be an easily identifiable and be physically a separate operation, but it can also be dispersed with multiple breeders using the semen of top sires to service their highest merit cows. The nucleus can also be open to influx of genetic material from other populations or breeds. For the purpose of maintaining sufficient genetic diversity, the size of the nucleus needs to be sufficient as the rate of inbreeding depends on the effective population size. This is largely driven by the number of males that is used each generation, because breeding schemes require usually fewer males than females. A ballpark figure is to

use at least 10 males “unrelated” males each generation [12] but more sophisticated methods are now available to optimally balance the need for genetic gain while constraining the rate of inbreeding. These methods are referred to as ‘optimal contribution selection’, e.g. as implemented in the MateSel software [13].

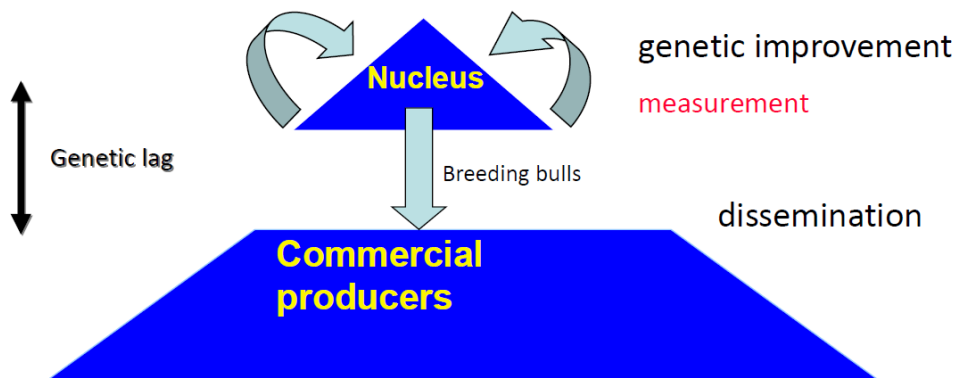


Fig. 1. Diagram of a two-tier breeding structure

6 Success factors in breeding programs

The rate of genetic gain per year (R_{year}) can be summarized by one simple formula from Rendel and Robertson [14].

$$R_{year} = \frac{S_m + S_f}{L_m + L_f} = \frac{i_m r_m + i_f r_f}{L_m + L_f} \sigma_A \quad (1)$$

where the selection differential (S) of parents is determined by the selection intensity (i), the selection accuracy (r) and the genetic standard deviation (σ_A): $S = i.r.\sigma_A$, where the subscripts m and f refer to male and female selection, and the aim is to maximise this selection differential and to minimize the generation interval (L). The formula says in simple words: “mate the very best males with the very best females and do that as soon as possible”. There are a few balances that need to be struck. For example, younger animals have usually lower accuracy of breeding value and it is tempting to progeny test sires in order to have highly accurate estimates of breeding values. However, progeny testing requires several years of waiting time before selected bull can be used, therefore drastically increasing the generation interval. The generation interval can be optimized by balancing the accuracy of selection and the generation interval. Also, selection intensity and generation interval are interdependent, as fewer replacement breeding animals are required every year (i.e. higher selection accuracy) if breeding animals are kept longer. Fortunately, it has been shown that BLUP selection optimises the age structure, and therefore the generation interval, as it allows direct comparison of genetic merit between old and young breeding animals [15].

Although understanding and implementing an efficient breeding structure is important. The key driver of genetic selection is the information that is available for selection. The information that can be used is phenotypic measurement, preferably on breeding animals,

and appropriate data surrounding these measurements, e.g. age and management group, to allow unbiased genetic evaluation. Pedigree information is important to allow the use of information from relatives as well as to link data in different management groups (e.g. through link sires) and data from different generations or age classes. Nowadays, pedigree information can be substituted by genetic information, allowing a more detailed and wider linkage of animals to data. Multiple trait evaluation allows estimation of breeding value based on correlated traits. However, with antagonistic correlations, it is important to measure the key traits in the breeding objective in order to achieve a balanced genetic gain. For example, selecting for higher fertility based on information on body weight only might increase genetic gains infertility, but it will increase the response to body weight even more.

Recognizing the breeding structure in a population is important as well as understanding which decisions are made by which players. Who determines the breeding objective? Who decides on a trait recording scheme? Who makes selection decisions? How does the commercial farmer have access to the improved genetics that flows from the nucleus?

It should be noted that the rate of gain depends on the species, as it is a function of reproductive rates and generation intervals. But within species there is a large variation in genetic gain achieved and this is related to how well the breeding program is run. Breeding programs with a centralised nucleus and clear objectives related to measured traits are relatively easy as there are few decision makers and trait measurement and genetic evaluation can be approached rationally. With a dispersed nucleus, it is more challenging to collect quality data in well-recorded and well-linked management groups. Moreover decisions about breeding animals are made by many individual breeders, it is more challenging to have consensus on selection criteria, especially where more traditional views about animal selection are dominant, i.e. less emphasis on objective measurement of breeding objective traits related to productivity and sustainability and more emphasis on vaguely related criteria related to animal appearance. Successful systems also require an understanding and agreement of selection criteria at multiple tier levels, as buyers of bulls or semen need to have a clear understanding on the differences in merit between the animals on offer.

7 Use of new technologies

Animal breeding has been revolutionized in the last decade by the introduction of genomic technologies. Knowledge of animal genomes and the development of tools such as chips that allow fast and cheap genotyping for thousands of Single Nucleotide Polymorphisms (SNP) have facilitated the introduction of 'genomic selection'. This information is essentially used to link phenotype information from many more animals (compared to pedigree information) to a target animals of which we want to estimate a breeding value. Therefore, we can now estimate breeding values much more accurate at a younger age and for traits that can not be easily measured on breeding animals. Genomic selection mostly affects breeding programs where key objective traits are hard to measure, e.g. in dairy cattle where nearly all traits are sex-limited, and within breeding programs there can be a shift of selection emphasis to harder to measure traits, e.g. more on carcass quality at the expense of just selecting for growth. Moreover, new traits can now be selected for by forming reference populations where traits such as feed intake, fertility or health traits can be efficiently measured in designated cohort of animals. Compared with traditional selection based on pedigree, it is now less important that the animals whose phenotypes is measured are directly related to the selection candidates. Genomic selection has been shown to be able to nearly doubling the rates of genetic gain in dairy cattle programs [16].

Reproductive technologies can also have a substantial impact on the rate of genetic improvement. Artificial Insemination is a key technology for effectively disseminating superior genetic stock from the nucleus, and it can conveniently link data in different

locations, making it easier to import important genetic material from different locations and populations. AI technology has been long used for progeny testing, although that role has become less important in the genomic era. Embryo technology allows making more intensive use of the best females, allowing multiple progeny per year rather than just one, as in ruminants. This can increase selection intensity of females and allows importation of high genetic merit stock from other locations. Sexed semen is now successfully used to determine the sex in targeted matings, e.g. sons of top sires. Sexed semen has great potential in the commercial tier, where more males can be produced for more efficient meat production. The effect of sexed semen on rates of genetic gain in the nucleus however is limited.

8 Conclusion

Animal breeding programs can be extremely powerful in improving the genetic resource in animal production systems, therefore contributing to long term sustainability of the sector. It is challenging to set up effective breeding programs at a national level, with only limited success in many developing countries. The principles and success factors of genetic improvement programs are summarised in this paper. Defining clear breeding objectives relevant to a long-term sustainability goals is a key factor, where improving productivity is still a major component. Breeding goals can be further finetuned, including more emphasis on traits related to animal health and their efficiency and environmental impact. New technologies such as genomics and reproductive technologies can be useful, but only where there is already an existing breeding structure of achieving genetic improvement successfully.

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