
Livestock straight-breeding system structures for the sustainable intensification of extensive grazing systems

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Animal breeding aims for genetic improvement of livestock by utilising the genetic variation available, both within breeds and between breeds. The animal genetic variation can be used to accommodate interests and farmers' wishes to make livestock more efficient in using available resources to produce human food and other agricultural products. In general, improved performance leads to more animal products for the same amount of input resources. As selection and breeding of animals is a gradual process, it is more likely that the main stakeholders in the production system are able to adapt to the intended changes. Moreover, genetic change is permanent and the improved production system does not necessarily require a continuous use of more expensive or more sophisticated input factors. Gradual genetic improvement is the most sustainable form of improvement of the efficiency of a production system.

Breeding goal definition is the first step to be made in designing animal breeding structures. The breeding goal identifies those animal traits that farmers would like to be improved. Then, a second step is to implement a structure of gathering information, a recording system to identify those animals that have the highest breeding value for traits in the breeding goal. This step of identifying high genetic merit animals is called 'breeding value prediction'.

A third step is to make a well-organized structure for the use of animals with highest genetic breeding value. This structure should facilitate the dissemination of superior genotypes through the population, a quick and widespread use of selected animals. These second and third steps could involve considerable investments, especially the second step of recording. Investments will have to be recovered by the increased efficiency of production in later generations. Development of breeding structures that will be effective is of great importance.

Section 1 Animal breeding and breeding structures

1.1 Animal breeding-directional improvement

Animal breeding helps to achieve the development objective

- Defines what is the 'best' animal - Breeding goal
- Identifies the best animals by recording - Breeding value
- Uses the best animals - Breeding structure

Why does selection lead to improved productivity?

Part of the observed differences between animals is due to genetic effects. Since parents pass their genes on to progeny, we are able to obtain 'better progeny' if we use the best animals to become a parent.

A breeding programme works according to the following principles:

- order animals according to performance. The better performing animals are expected to have above average genotypes;
- selected animals will pass on their better genes to their offspring, therefore, average genetic value of offspring will be higher than the previous generation.

Selection and dissemination

Improvement of animal performance through genetic selection can be achieved through decision-making towards selection of the right breeding animals and making the right matings. The genetic value and phenotypic performance of future offspring can be improved if the better breeding animals are used as parents for the next generation. We refer to this process as genetic improvement.

An important second issue is which animals are actually improved? The value of superior individuals is limited if they do not efficiently contribute to the improvement of the gene pool of a whole population of animals in a village or a region. Genetic improvement should not be isolated and limited to just the animals in a single herd (or a few herds). The industry-wide impact of genetic improvement depends on the process of dissemination of breeding animals.

Genetic improvement and dissemination of genetic improvement are the two main factors of a regional breeding programme.

If parents are selected based on observed performance, we can increase the average genetic value of offspring and therefore achieve a sustained improvement of performance over generations.

- **Genetic improvement** can be obtained by selecting and mating the best animals as parents.
- **Dissemination** of selected genes through a whole population achieves increased productivity of a production system in a region.

Running a breeding programme involves more than simply ‘selecting the best animals and mating them’. To select animals and to be able to allow the right matings requires a provision of a certain infrastructure. Selection decisions need to be based on information. Some kind of visual appraisal or a more formal performance measurement of animals is needed as well as an animal identification system. Matings can be carried out by physically joining the mating pairs that were planned or alternatively, genetic material (e.g. semen) of the selected breeding animals could be provided otherwise, e.g. in the form of straws of fresh or frozen semen.

The **structure of a breeding programme** provides:

- a system for gathering information about the assessment of animals in the production system;
- the ability to compare animals for genetic merit and select the best;
- the conditions that the selected males and the selected females are mated in a desired way.

There are several levels of sophistication here.

Data recording can be by:

- 1) visual appraisal (cheap, maybe not easy and possibly subjective);
- 2) objective recording of performance traits related to profitability (more accurate); and
- 3) additional pedigree recording and animal identification (allowing the use of information on related animals and accurate estimation of breeding value).

The mating provision can be a matter of :

- 1) not allowing the inferior males to mate with females in the herd (e.g. by castration, separation);
- 2) using separate paddocks for different males, allowing the matings of the right males with the right females; and
- 3) using artificial insemination, allowing more specific matings, intensive use of sires and dissemination of its genes over a larger area.

Breeding structures can be defined even under the most basic conditions, they do not necessarily require sophisticated systems of data recording and genetic evaluation, nor do they require use of reproductive technology. Those technologies can have a large impact on rates of genetic improvement, as well as on the design of the most optimal structure. The optimal breeding structure is very much determined by ‘what is possible’ and ‘what is optimal’. Environmental or infrastructural restrictions, tradition and socio-economic conditions have to be considered when planning a breeding programme.

Socio-economic importance of breeding structures

Structures are important, not only because they have an effect on the efficiency of genetic improvement, but also because they have an impact on the structure of the whole animal production system. For example, the introduction of artificial insemination in dairy production systems has a whole range of consequences. Not only can bulls now be used widespread and selected based on an accurate progeny test, but also the selection decisions are now made by the AI organization rather than by small farmers or stud breeders. It requires a cultural acceptance of the technology, it introduces a dependence of farmers on the AI organization and it requires the AI organization to deliver semen when needed and a communication system between farmers and AI-provider. This has obvious socio-economic implications and may be a key to the success or failure of a breeding programme. Therefore, besides considering discussing the technical elements of genetic improvement and alternative structures that may be considered, socio-economic as well as genetic implications of such structures will both be discussed.

With the introduction of breeding methods, the right balance has to be found between:

- what is possible from a technical point of view? and
- what is optimal and accepted by the decision-makers and users within the socio-economic context of a production system.

Communication and logistics in breeding structures

A breeding programme is focussed on the improvement of a population. Usually this implies that activities related to the breeding programme have to take place at different locations, but in a coordinated fashion. A breeding programme requires a structure where information and animals or genetic material are exchanged between locations. This requires a lot of interaction and communication between many stakeholders. It is ultimately the (small) commercial farmer who will have to profit from genetic improvement in the context of his production system. For genetic improvement he has to select animals within his herd, but more likely he will need to import breeding animals from elsewhere. Stud breeders could provide these breeding animals or breeding organizations, or they could be obtained from a centralised nucleus, which is run by a cooperative where the farmer is one of the members. The farmer has to understand the added value of improved breeding animals, otherwise he is unlikely to cooperate or willing to make a contribution to any investment in genetic improvement. Also, the farmer may have a role in providing performance information about his animals and such information should be collected according to a defined protocol. Some people will be involved in the recording and analysis of information and this information has to stream back to the persons that have to make selection and culling decisions. Other people are involved in the actual animal selection and are responsible to ensure that the selected animals are mated in an optimal way. Therefore, a very important aspect

A breeding programme description requires a blueprint for roles and responsibilities of key players

in starting up a breeding programme is in **defining roles of key players and how they interact.**

These Guidelines help policy-makers, field technicians and farmers to define their breeding structures, they account for a broad range in country capacity and are applicable to all important animal species and production environments. Designing a breeding programme means taking a range of decisions in a logical order. This paper deals with each of these decisions in further detail and tries to achieve such an order. To provide a helpful tool the decision-making process is broken down in sequential steps and users will be guided step-by-step. For each step or decision, examples are used to illustrate the step, background information is given as to why this step is important, how to find data to make a sound decision and possible pitfalls that may occur in some areas. Some examples of breeding structures for different species will be presented and discussed.

1.2 Guidelines on breeding structures

The purpose of the Guidelines is to assist nations to develop National Farm Animal Genetic Resource Management Plans which will become both a component of the National Diversity Plan and a basis for developing livestock breeding policies. In these Guidelines, management of AnGR includes identification, description and characterisation of AnGR, the active utilisation of AnGR to increase food production (including animal productivity and product quality) and other agricultural production, the conservation of endangered livestock breeds for future use, access to AnGR and the monitoring and reporting elements.

1.3 Links to other guidelines for development of farm animal genetic resource management plans

For domestic species, issues of utilisation and conservation cannot be separated; both are critical components of management of AnGR. Most AnGR reside in developing countries where the need to increase food production and to reduce poverty are greatest. The breeds that farmers use today are different from the breeds that they used in the past and from the breeds that they will use in the future.

Management of livestock AnGR seeks to ensure that appropriate genetic material is used and developed and will be available to meet future challenges of changing environments and human preferences. The most important use of these Guidelines is to set priorities for the design and implementation of national AnGR management activities thereby better targeting needs. In addition, the Guidelines will assist in describing the nations' AnGR to the global community.

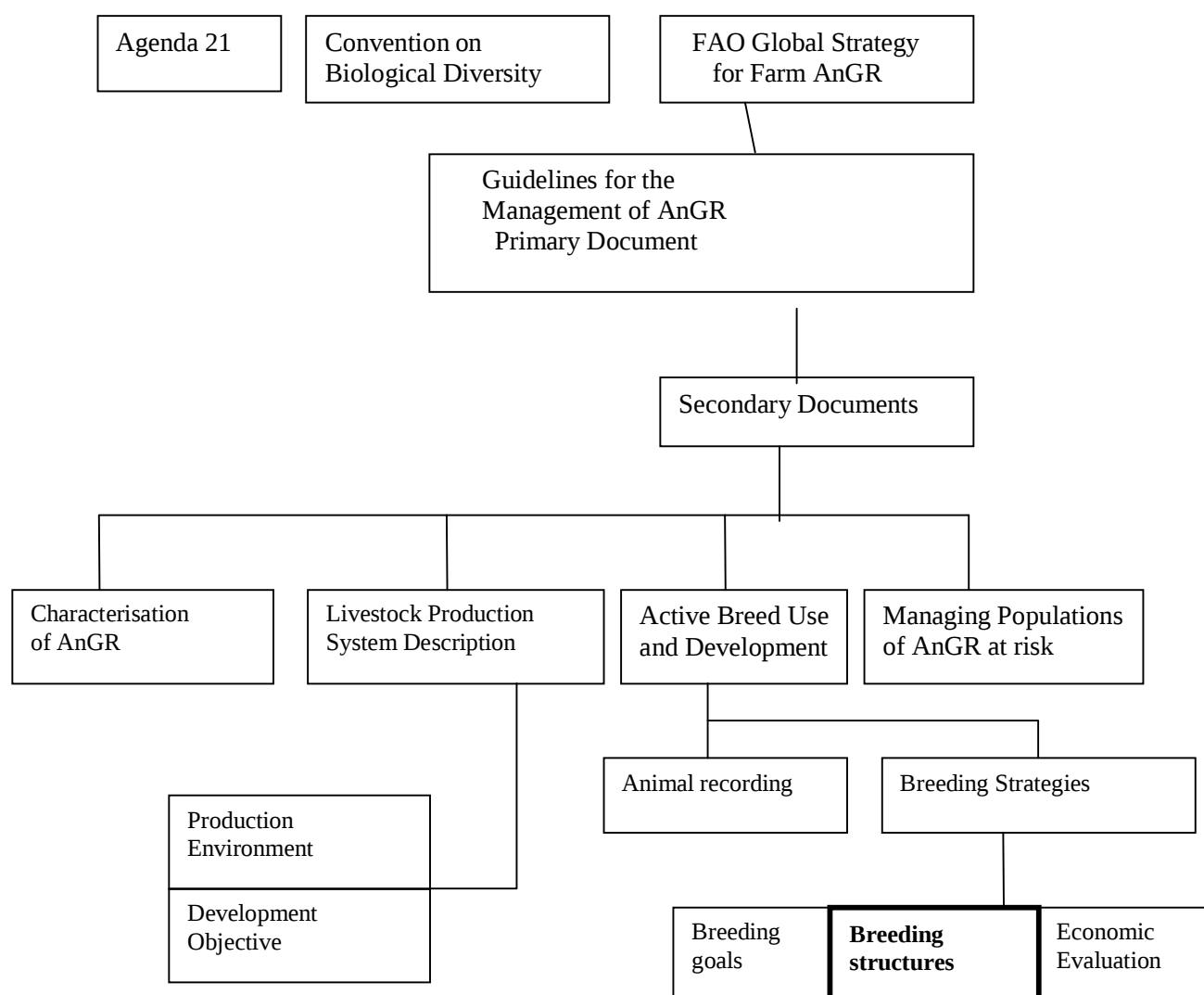


Figure 1.1. Breeding structure guidelines in the context of National Farm Animal Genetic Resources Management Plans.

Structure of these guidelines:

- definition of terms and issues in breeding structures:
 - terminology;
 - key issues and stakeholders;
- definition of the main factors determining genetic improvement;
- analysis of current situation, breeding structures in production systems;
- a step-by-step approach for design of breeding structures;
- creating of alternatives and making decisions in a breeding programme;
- discussion on socio-economic implications, risk factors, success factors.

The word ‘structure’ is an abstract term and particularly in the context of a breeding programme, it is somewhat hard to identify or define. These Guidelines will help you to determine your current breeding structure and define possible alternatives. Before doing that, we will introduce some of the terminology.

The **structure of a breeding programme** provides:

- a system for gathering information about the assessment of animals in the production system;
- the conditions that allow selection of males and females as parents for future progeny and the matings of these animals in a desired way.

It is relevant for two aspects of an improvement scheme:

- the genetic improvement aspect: how do we determine the genetically superior animals and how can we mate them?
- the dissemination aspect: how do we ensure that those superior animals disseminate their genes quickly throughout the whole population.

Every owner of domesticated animals has to consider how he wants to breed his female stock. He can use males that were born from his own stock but only to a very limited extent, as inbreeding has to be avoided. Consequently, the germplasm has to come from elsewhere. One model is that a group of farmers work together and exchange their male livestock. Another option is that germplasm is obtained from a local farm (known as a ‘good breeder’) as a one way delivery route, without having to return another male. Breeding males could also be obtained from another village or another region.

A farmer is interested in obtaining ‘good breeding stock’. If obtained from elsewhere, someone has to produce such stock and the definition on ‘what is good’ has to be agreed upon. The seedstock breeder could invest in continuously improving his animals genetically and this improvement has to be recognised by the local producer. In defining the breeding structure, the roles of the different players in a breeding structure have to be made clear. For this purpose, identification of the roles is required. This can be based on two questions:

- where does a farmer obtain his germplasm?
- is a farmer involved in producing improved germplasm?

Knowledge of such roles is important, as with one group of farmers (“the producer”) it is relevant to discuss how and where to obtain replacement stock (males) whereas with another farmer (“the breeder”) it is relevant to discuss performance and pedigree recording and selection strategies. It

Section 2. Structure of breeding programmes (definitions)

2.1 What are breeding structures?

may be that these roles are combined in one person, depending on whether the breeding programme has a one tier structure or a multi-tier structure, with breeders, multipliers and commercial producers (see Section 2.3).

A distinction needs to be made between cross-breeding structures and straight-breeding structures. In a cross-breeding system, the males and females originate from different populations. In a straight-breeding structure, males and females originate from the same population. This also creates another important breeding issue, which is avoidance of inbreeding by avoiding the mating of animals that come from the same or related parents. Avoidance of inbreeding should be an explicit objective of a breeding programme, in addition to the other main objective of making genetic improvement with respect to a number of traits defined in the breeding objective.

2..2 What is the breeding population?

In general, a breeding population is basically a group of animals that share a common gene pool. The animals have common parents and in principle mate with each other to sustain the population size. A small farmer with only a few sheep cannot consider his flock as a breeding population because he will have to introduce a new male almost every breeding season. Otherwise he would have to mate his ram to his own offspring. The farmer may buy a ram from the neighbour and in turn sells his own young ram to another neighbour and so on. The whole set of flocks in the area would then be considered as a breeding population, as the genetic makeup is determined by the genetic constitution of rams that were swapped across herds. Even if only one of the farmers in the region is actually selecting and manages to breed genetically superior rams, the whole region will ultimately profit from this, as the genes are flowing through all flocks. Of course, the first farmer who uses this good ram will profit first, but offspring of the ram will be sold to others later on. This process can possibly take many generations. A more efficient way of quickly spreading the genes of the very good ram is to use him across flocks but this may not always be physically possible.

Larger herds or flocks could consider themselves as one breeding population if they import relatively few new animals as breeding parents. However, to avoid inbreeding, importation of animals from outside is necessary on a regular basis. The rate of inbreeding is closely correlated with population size (see also the Guidelines on Management of Small Populations at Risk). Local breeding populations of larger groups of farmers are mostly the kind of population that the FAO AnGR programme is targeting. A local population is usually adapted to a local environment and improved productivity can be achieved with a genetic improvement programme. Moreover, a population consisting of a larger group of farmers is usually more viable, as it has more potential for genetic improvement. The reason is that in larger populations there is more opportunity to exploit the existing variation among animals (there is a greater chance of finding

very good animals). Furthermore, a selection programme in a larger population would be less restrained by inbreeding problems.

A breeding population consists of a group of animals that share a common gene pool and that can sustain themselves by intermating. Ideally, a breeding population is large and there is sufficient movement of animals (or genetic material) across herds or flocks and across different areas covered by the population.

A regional or national population. From a breeding point of view, the larger the population, the better, for reasons described in the previous paragraph. However, there are two potential dangers of considering breeding populations on too large a scale. The main issue is that organizing a breeding programme on a larger scale requires a high standard of infrastructure and communication across the working area. If these standards cannot be met, there is a high risk of failure. The other issue is that the natural or social environment may be quite different across the region considered. Climatological and social factors are an integrated part in the definition of breeding objectives. If breeding objectives are different, it is more difficult to improve the animals in such a way that it pleases the producers across all regions (environments). However, breeding objectives should be quite different before the advantages of working in a large breeding population is offset by targeting more specific breeding objectives in a split population. For example, production environments in temperate climates for dairy production may vary to some extent but there is worldwide exchange and use of bulls across these environments.

From a breeding perspective, a breeding population is preferably large, to utilise more variation and to avoid inbreeding. Breeding objectives may slightly differ across sections within the population, but exchange of suitable animals across areas can be extremely fruitful.

From an organizational perspective, the main restriction for the population size is the degree of infrastructure that is available. Sufficient communication across the different locations of the breeding programme area is needed to successfully run and coordinate a breeding programme.

2.3 Examples of breeding structures

The tier system

Different breeding structures can be distinguished by identifying different tiers. The simplest structure is a one tier breeding programme. The herd of mature animals consists of males and females. As in most species the male fecundity is much higher than the female fecundity, many less males are needed to produce the next generation of offspring. As males and females are born in equal proportions, we can select the best males for the breeding herd, but we may need all females that are born to replace the breeding female from the current generation.

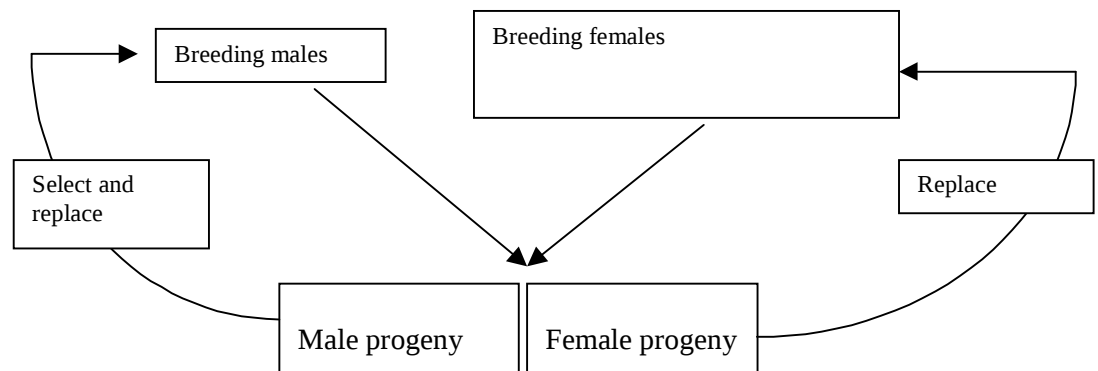


Fig. 2.1 Example of a simple one tier breeding structure.

Features of the one tier breeding structure are:

- males and females in the population are replaced by their own progeny;
- less males than females are needed for reproduction, therefore, males can be selected more intensely and females cannot be selected, or with less intensity.

Notice the provisions by the structure that condition a breeding programme:

- information needs to be available on the animals to know which of the males are best;
- the mating condition has to be fulfilled. The unselected males should NOT mate with the females. We may want to keep them for fattening, but unselected males either have to be castrated or kept apart from the female herd.

Two tier breeding structure

If a large group of farmers does not obtain their replacement breeding animals from their own progeny, they have to go out and buy them. More often than not, it is the males that are brought into the herd. In a multiple tier structure, selection and genetic improvement take place in one group of herds, where replacements are generated and selected in herds with the highest genetic level, indicated as breeding nucleus. The farmers at

the commercial level just obtain (buy) these selected animals for use in their herd, i.e. they obtain their replacements from the nucleus herds. Usually, only male replacements are obtained from the nucleus, female replacements are often generated on farm. Commercial farmers can genetically improve their herd without having to performance record or select themselves.

The two-tier model is used in many animal production systems. The nucleus is formed by 'stud breeders', farmers who are actively selecting and try to improve their seedstock. They sell seedstock to commercial farmers, a group of producers mostly focussing on animal production itself. Producers are (and need to be) less worried about breeding and selection. Their way of genetic improvement is to buy seedstock from a higher tier. In breeding terms, they continuously receive new and improved genes from the nucleus tier. The genetic mean of production tier is somewhat lower than that of the nucleus, but the rate of improvement is, in principle, equal. The difference is indicated as genetic lag. The reason for this difference is that stud breeders (in the nucleus) will use their very best animals for further improving their own stock, whereas the other animals are sold to the lower tier.

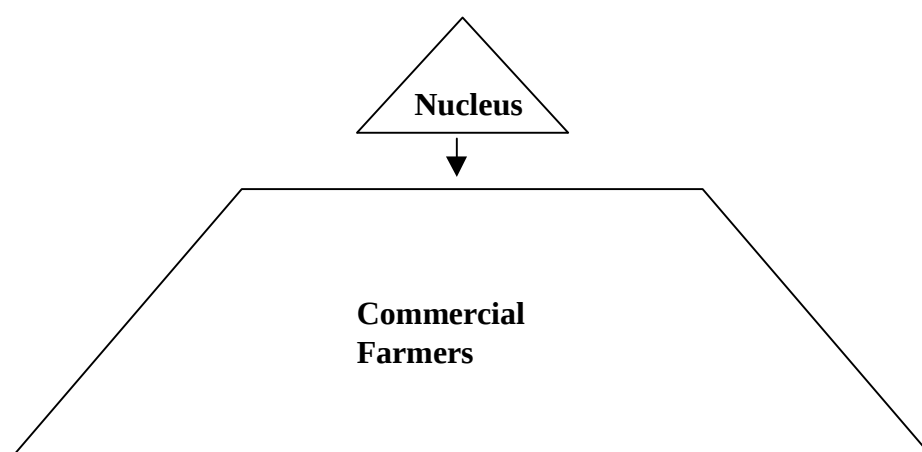


Figure 2.2. The two tier breeding structure

Obviously, a farmer would buy a 'good' male, i.e. he needs a male that he considers having good 'breeding value'. Breeding values are determined within the breeding programme, as will be discussed later. They could be of high accuracy (e.g. the bulls could already have progeny and these can be evaluated) or have lower accuracy (the bull is bought based on visual appraisal, without formal recording of performance). In a two (or multi-) tier breeding structure, there has to be a flow of germplasm and information from nucleus to commercial. The only flow back would be a (financial) reward for obtaining the breeding animal (or service). A two tier breeding

structure only works if the commercial farmers have the capacity to acquire breeding stock from the nucleus.

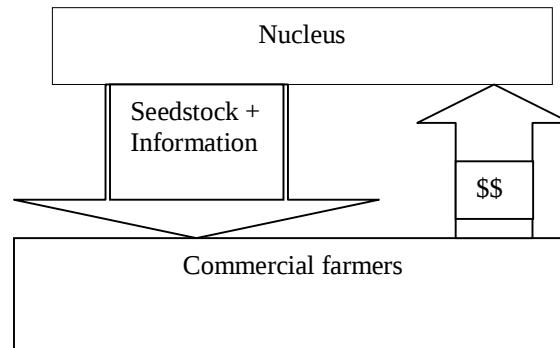


Figure 2.3. The nucleus delivers seedstock to commercial farmers and needs to include information on animal pedigree and estimated breeding value.

Three (multiple) tier system

A multiple tier system, i.e. a structure with more than two layers, is in fact not different from a two-tier structure. Selection and genetic improvement takes place in the nucleus and breeding animals are sold from the nucleus to have progeny in lower tiers. A reason why more than two tiers are needed is that the number of nucleus animals are usually not enough to breed all animals that are in the commercial tier.

Example

Imagine a nucleus with 500 breeding females, producing 250 male offspring every year. Some males are needed within the nucleus and a few others may die, hence, there will be about 200 males available to breed to commercial females. However, if the commercial population encompasses 100 000 animals, each of the nucleus males would have to serve 5 000 females. In natural mating conditions, this is not physically possible. Suppose a male can be mated to 50 females. A multiplier layer can be established of 10 000 breeding females. These will all be mated to the 200 males from the nucleus, bringing 5 000 male offspring. It is easy enough to sire the whole commercial population as only 2 000 males ($=100\,000/50$) are needed.

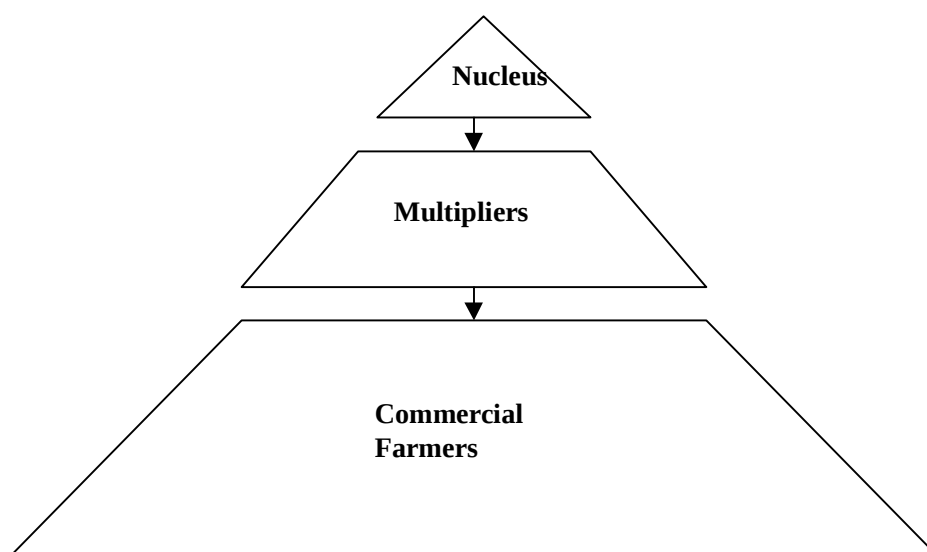


Figure 2.4. The three tier breeding structure.

The recording of performance and/or pedigree takes place within the nucleus tier, being either one or a group of herds. In existing breeding programmes, such a group is commonly known as the ‘stud breeders’. The extent of recording will have an effect on the rate of genetic improvement in the nucleus (see later). Also, the exchange of genetic material between different nucleus herds affects genetic improvement. This will be discussed in Section 3.

2.4 Exchange and communication between tiers

Between the nucleus and a lower tier (either multiplier or commercial) there is simply a flow of germplasm. This could refer to animals, semen, eggs or embryos. The point is that the improved genes are transported from one tier to contribute to the next generation in the lower tier.

It is not strictly necessary that the flow of animals (or semen) be accompanied by any other information. In the simplest case, the commercial farmer is happy about obtaining a bull and does not worry about its breeding value. However, a commercial farmer could also be given the opportunity to pick a bull from a list of bulls, each of them having a breeding value and ranked accordingly. Such information requires that commercial farmers would understand the concept of ‘breeding value’ and also that there is a reliable genetic evaluation system in place that unbiasedly ranks all bulls produced in the nucleus.

There are a few advantages if commercial farmers can pick bulls based on information on breeding values:

- 1) it ensures that commercial farmers are more sure to get 'value for money';
- 2) they could better use bulls that they think are particularly good for their situation. For example, a farmer that has some problems with fertility would pick a bull that is particularly good in fertility. In a way this allows for some individual variation in breeding objectives within a more generic objective that is targeted within the whole population;
- 3) there is some psychological advantage of presenting breeding values as it may stimulate commercial farmers to pay attention to using 'good bulls' thereby stimulating their participation in genetic improvement.

Even in many developing countries it has been a formidable task to teach commercial producers the ideas behind breeding values. The first extension task is to convince them that bulls produced from the nucleus can be expected to produce better offspring than any local unknown bull. Identifying variation in breeding value in the group of bulls coming from the nucleus does not essentially increase the rate of improvement, but it may stimulate participation in and uptake of genetic improvement.

Roles of different tiers in a breeding structure

- Nucleus:
 - Performance and pedigree recording, selection and genetic improvement. Needs to be at least a part of the population.
 - Replacements for nucleus parents are recruited from selected progeny born from nucleus parents.
- Commercial:
 - The part of the population of animals in the production system that does not actively take part in recording and selection can be improved genetically by obtaining breeding stock from the nucleus.
 - Replacements for commercial parents are recruited from progeny born from nucleus animals (usually the males at least).
 - Most male progeny will not have offspring themselves, young females are usually needed for replacements in the existing herd.

Roles of different tiers in a breeding structure (cont'd)

Multiplier:

- If the nucleus is too small to serve the commercial population with breeding stock, nucleus males are mated to a group of females to form a multiple tier. Progeny born from multiplier dams are used to breed commercial animals.
- Males usually pass on genetic improvement from the nucleus to lower tiers.
- Commercial farmers simply buy (obtain) bulls that were born from the tier above them, i.e. from the nucleus or from the multiplier.
- All genetic improvement is made in the nucleus. The other layers will be improved at the same rate, but their genetic value lags some generations behind.

The nucleus population needs to have an adequate size of a breeding population, such that the inbreeding rate is limited. The effective size should be large enough (roughly at least a few hundred animals (preferably more)). The size of the nucleus population is not determined by the number of animals born, but by the number of male and female parents used. It is important to realise that the effective population is mainly determined by the lesser represented sex (usually males). Enough males should be used in each generation to keep sufficient population size and therefore to prevent high rates of inbreeding. (See also Section 3, Annex 2 and Guidelines on Small Populations).

The size of the nucleus is mainly determined by the minimum number of males and females that should be kept for a sufficient effective population size. Roughly, this implies that at least ten to 15 males should be used in each generation for a viable population size.

The best nucleus animals are selected as parents of the next generation of nucleus animals. Animals born from elite mating (i.e. nucleus-born animals) that are not selected as parents for the nucleus will be used as parents for the lower tier. Hence, the expected mean of the nucleus should be higher than that of the lower tier.

2.5 Further comments on multiple tier structures

Size of nucleus population

Selection in a multiple tier structure

If genetic improvement only takes place in the breeding nucleus, this group of individuals will have the highest genetic mean. The multiple tier will have a lower genetic mean, equal to two generations of genetic improvement if only males are transferred from nucleus to multiplier and one generation if both males and females are transferred. The difference is referred to as genetic lag. The same lag will appear for the difference between multiplier and commercial. In a three-tier structure with only males contributing to lower tiers, the genetic mean of nucleus and commercial tiers is expected to be equal to four generations of genetic improvement. When some selection takes place in a lower tier, this will decrease the genetic lag (with a higher tier), but the lower tier will not have a higher rate of response than a higher tier (for more detail, see Bichard, 1971).

Some of the very best animals of lower tiers contribute to the nucleus as well, given that their breeding value could be estimated and compared with breeding values in the nucleus. Such individuals would migrate upwards to the nucleus. A nucleus that is open to imports from lower tiers or from sister tiers is indicated as 'open nucleus'.

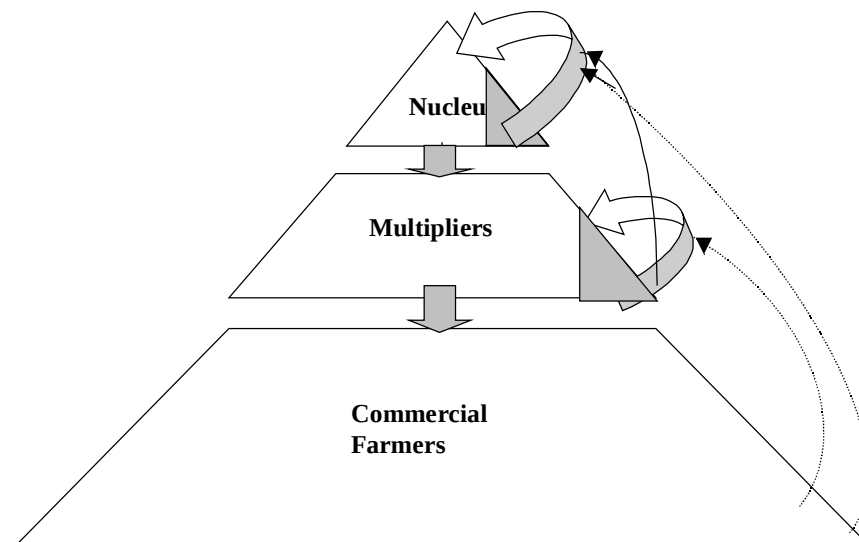


Figure 2-5. A multi tier breeding structure with selection in nucleus and possibly in lower tiers and downward and possibly upward migration of genetic material.

Import from lower tiers

The structure presented here shows a one way stream of genetic material from the nucleus down to the commercial population. In practice, it is possible that animals from lower tiers become parents in the nucleus. For example, an animal with superior performance could be born in multiplier and could be very interesting to use as a parent in the nucleus. Of course, this is only possible if some kind of performance recording in lower breeding tiers (other than nucleus) is used.

Open nucleus systems

Open nucleus systems provide about ten percent more genetic gain than a closed nucleus system, as the breeding programme will profit from the additional chances from more animals potentially being candidates for selection. When performance recording is carried out beyond the nucleus, a nucleus breeding structure should be open to the influx of the best animals from lower tiers.

Note that the inbreeding level does not substantially decrease by opening the nucleus to lower tiers. The reason is that animals in a lower tier are somehow already related to nucleus animals.

Import from other nuclei

A breeding nucleus should in principle always be open to other nuclei. The main advantage here is that this will introduce new families ('fresh blood'), therefore rejuvenating the nucleus gene pool and decreasing inbreeding. Another reason for introducing genetic material (or animals) from other (genetically better) nuclei is that it is a quick way to improve the genetic mean of the existing nucleus. For example, most European dairy breeding programmes have upgraded with Holstein-Friesian genes during the eighties. Basically, many of the sires that were used to obtain young bulls were imported (by way of semen) from the USA, leading a rapid change in genetic mean. The population that is imported has to be genetically interesting with a high genetic mean for the breeding goal traits. As different breeding populations are often not genetically connected and jointly evaluated, breeding values of animals from different populations are usually not so easy to compare.

The breeding nucleus could be open to good animals from lower tiers, giving some more genetic improvement. However, trait measurement below nucleus level would be required.

The nucleus should be open to other populations with comparable or higher genetic means. This can bring fresh blood (lower inbreeding) and potential rapid genetic importation of valuable genes into the breeding population. Exchange of genetic material between nuclei is needed to be able to compare their relative genetic level.

**Genotype by
environment
interaction**

When ranking of genotype based on merit differs between environments, we speak of genotype by environment (GE) interaction. This phenomena is quite likely to happen between environments that are distinctly different, e.g. pure-bred Friesian perform better than tropical breeds in temperate environments, but they are not competitive in most tropical conditions. GE also exists within breed, as some bulls are better for one environment (or market) and other bulls are better for another environment. GE interaction is relevant in breeding programme design, as there is a danger that animals are selected in the nucleus in much better conditions than in which the commercial population produces. Typically, a nucleus is held at central research facilities with abundance of feed whereas the commercial population produces in much harsher conditions. Selecting breeding animals based on performance in nucleus conditions will be less efficient for improving commercial performance if there is a significant GE interaction. The efficiency is proportional to the genetic correlation between the nucleus and the commercial environment. For correlation between nucleus environment and commercial environment of 0.5, only 50 percent of the selection differential in nucleus animals will be expressed at the commercial level. The best advice here is to create a nucleus environment that is as close as possible to the commercial environment. There is some advantage to having better controlled environmental conditions in the nucleus environment, as it increases heritability and selection accuracy.

If the nucleus environment is very different from the commercial environment, then the efficiency of selection at the nucleus level is reduced proportionally to the genetic correlation between performances in the nucleus and the commercial environments. The environmental conditions for performance testing in the nucleus should mimic the commercial conditions.

**2.6 Who are the
key players in a
breeding
programme?**

**Identifying nucleus
and commercial herds**

Although it may be easy to draw a structure of a breeding programme, as in Figures 2.1 to 2.4, in practice it is not at all easy to identify such a structure. However, identifying the existing breeding structure is an important condition for being able to run the breeding programme. In particular, the roles of the different participants in a breeding programme have to be clear and each key player should be aware of his or her role.

The nucleus is identified as the group of 'elite breeders'. Formally, it is the group of animals with the best (estimated) genetic merit. With a genetic evaluation system and genetic links across herds / flocks, the best animals can easily be identified. Without such a system, it is more difficult to identify the best animals across herds or flocks. In that case, the part of the population that actively records performance and pedigree and selects animals based on some estimate of breeding value, is going to be the

nucleus, as those animals are more likely to show superiority due to selection.

Farmers that do not actively record and select animals are part of the commercial. On average, the animals born in these herds are not as good as nucleus animals, as their parents are less highly selected. Commercial farmers should seek genetic improvement by obtaining stock from the nucleus. In practice, these will be males (or just semen).

It is quite possible that commercial farmers occasionally have a superior animal. This would be unnoticed if performance were not recorded. If a commercial animal's performance is obviously outstanding, she should be part of the nucleus, meaning that she should be mated to a top male. In practice, such an animal can be bought by nucleus farmers or by a central nucleus cooperative. The farmer may also keep this promising animal, inseminate it with semen from a top-bull and sell a male calf to the nucleus (cooperative). This would be an example of upward migration: the best animals in a lower tier can be promoted to a higher tier in the breeding structure. An open nucleus scheme would allow such migration.

- The nucleus consists of the group of animals with the highest genetic mean. Usually, those are owned by 'elite breeders' or by a central cooperative, where an active recording and selection policy is in operation;
- ideally, an across herd/flock system of genetic evaluation confirms these roles (if selection takes place in a group of animals performing at several locations);
- producers that do not record or select should obtain replacements from the nucleus. In practice, they buy males (or semen);
- occasionally, outstanding performers at the commercial level (if detected) could become part of a nucleus.

Every farmer should be free to buy or to replace from his own stock. The point is that given his role, one strategy is better than another. A commercial farmer with no recording cannot select his animals. The genetic mean of his herd can be expected to be lower than that of nucleus herds. He is better off by buying his males from the nucleus.

How does a farmer define his role?

A breeder with a high genetic mean and with a recording system in place is generally better off by replacing his stock from within the herd, with an occasional importation of breeding stock from another herd.

Emergence of nucleus herds

In a village-breeding programme, with many small farmers, there may not be such a distinction initially between breeders and producers. When animal recording is set in place in some herds, these will emerge as the nucleus herds because of the initial genetic lift possible due to selection. Also, those farmers who import germplasm from other areas could be lifted genetically and a genetic lag created. If all village herds are recorded, each animal could potentially be selected as breeding animal for the next generation. The nucleus animals are the best animals based on estimated genetic merit and their offspring will be genetically better than those of lower tiers. All progeny born in the next generation would profit from this selection immediately. When farmers are somehow privatised, some distinction will gradually evolve between farmers who are better able to select and utilise best breeding stock and others who are not. The first group will typically become the 'elite breeders' who will be favoured by local buyers and effectively a nucleus structure will emerge.

Other roles

The requisites in the breeding structure, namely:

- gathering information;
- making selection decisions;
- carrying the desired matings;

require coordination. As a breeding programme involves communication between nucleus breeders and producers or among breeders themselves, important roles have to be defined for coordination purposes. The social economic infrastructure is very important here. Exchange of breeding animals maybe feasible, but buying breeding stock may not be feasible for smallholders. Two socio-economic models can be distinguished:

Cooperative village structure with smallholder farmers

If farmers have smallholdings and little buying power, a cooperative structure may be the best working model. Each participant could measure a number of animals (e.g. his own) and a coordinator would need to be appointed to keep track of records and to analyse the information that was collected. There needs to be a consensus about measuring standards and recording practices need to be checked regularly. For example, animals need to be measured for weight at similar ages and muscularity would have to be scored in a predefined way. Selection decisions have to be made, preferably based on the recorded traits and turned into an index of estimated breeding value. Some additional inspection of candidate breeding animals usually takes place here, to ensure physical and reproductive fitness of the breeding animals. The mating scheme could be simple if all animals of the cooperative were in the same central herd. Males that are not selected for breeding should be castrated or kept separate from the breeding females otherwise, there would be a need for a facility where selected breeding males are kept and participants could come to breed their female livestock. The largest challenge here is that sufficient consensus and participation be achieved regarding the decisions made. The coordinating role therefore involves:

- designing and facilitating a performance recording system, ensuring cooperation of participants;
- making selection and mating decisions, designing a system of mating and exchange of breeding animals between locations, again ensuring participation and cooperation through extension and education.

Privatised small farmer structure

Where farmers have some economic independence and sufficient economic power to buy (and sell) livestock, coordination of the breeding programme could be modelled based on private initiative. For example, measuring efforts could be left to the farmers' own initiative, as they may or may not want to acquire the role of breeding nucleus animals. Selection and mating decisions would be driven by competition, where quality and price of breeding stock would be the driving forces. Such a system may seem self-sustainable and self-regulating. However, it is far from guaranteed that it will succeed. It is required that producers understand the concept of genetic improvement, breeding value and that they have to be willing to pay for breeding animals with higher genetic merit. Furthermore, there has to be an agreement on the information that is provided with breeding animals, i.e. agreement on the selection index. The producer needs access to information about breeding animals available and the logistics have to be in place to acquire the improved genetics (through bull or semen). The coordinating role here involves:

- extension and education about genetic improvement, breeding objectives, breeding values and selection index;
- standardising performance-recording procedures, agreement on breeding objectives;
- provisions for livestock or semen trading.

Summarising

Critically important coordinating tasks are needed to facilitate the performance and pedigree recording scheme, the selection decisions and the mating provisions;

the coordinating role is coloured in depending on socio-economic infrastructure. The role varies from managing and decision-making to educating and facilitating. In either case, the degree of participation of producers is the measure of success;

farmers take a role either as breeders or producers and sometimes these are combined. Breeders need to be aware of methods to improve animals. Producers need to be aware of the availability of genetically improved seedstock.

Section 3. Making genetic improvement

In essence, the two key questions in animal breeding are: *Where to go?* and *How to get there?* Running an animal breeding programme, either on a single farm or in a larger context, involves answers to these questions. These can be worked out in more detail as follows:

- What is the breeding objective: which traits need to be improved and how important are different traits in relation to each other?
- What and who do we measure? Which traits, which animals?
- Do we need to use any reproductive technology (Artificial Insemination, Embryo Transfer) if possible?
- How many and which animals do we need to select as parents for the next generation?
- How to mate the selected males and females.

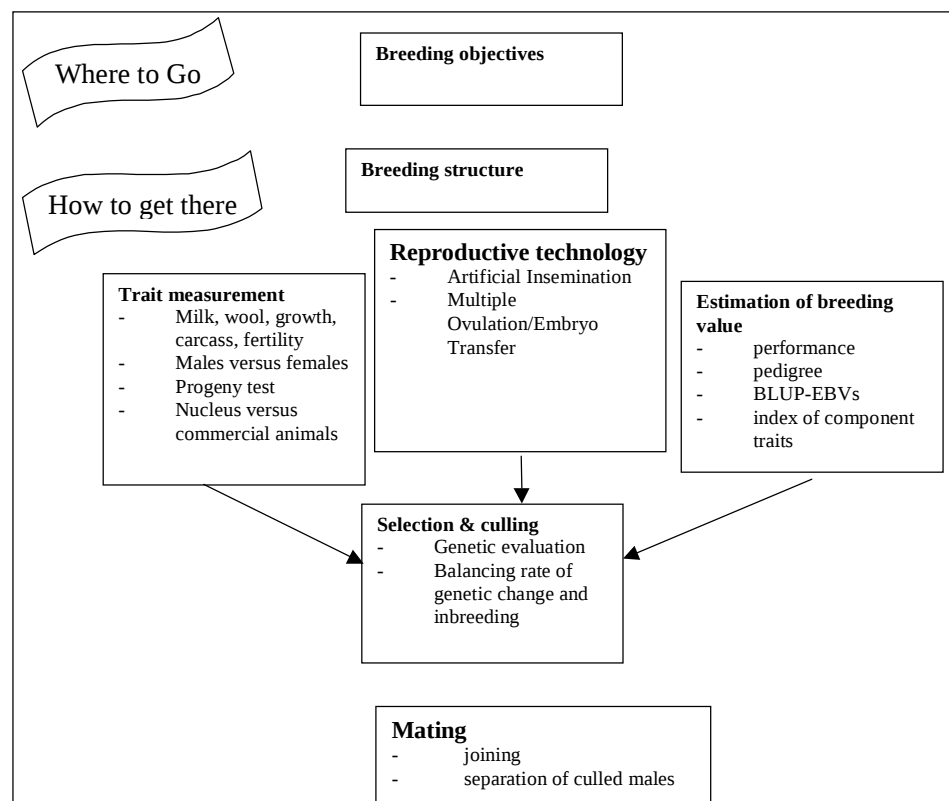


Figure 3.1. Decision issues in animal breeding.

3.1 Breeding objective

The definition of the *breeding objective* is the first and probably most important step to be taken (see also The Guidelines on Breeding Objectives). Improving the wrong traits could be equivalent or even worse than no improvement at all! If many breeding animal males are considered for reasons *irrelevant* to the breeding objective, then the selected group will not be as good with regard to the breeding objective as was expected. It is important in the selection process that the selection criterion is clear and that the selection is efficient in relation to the breeding objective.

Many practical breeding programmes 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 programmes is noticed many years after selection decisions are made. Hence, objectives have to be designed for future circumstances. It is quite difficult to predict such circumstances and it is even harder to define objectives that are reasonably stable over time. Taylor (1997) has given examples of the beef industry where breed objectives have either been fluctuating or consistent over the last decades, resulting in either little change or significant progress, respectively.

The amount of genetic improvement that can be made depends on four key factors:

- | | |
|-------------------------|-------------------------------|
| • Selection Intensity | Should be as high as possible |
| • Genetic Variation | Is more or less a given fact |
| • Accuracy of selection | Should be as high as possible |
| • Generation interval | Should be short |

These key components together form the complete picture of genetic improvement and they interact with each other. A more detailed explanation on the prediction of genetic improvement rates for a given design is presented in Annex 1.

Before any selection decisions can be made, there is a need for selection criteria. This implies a definition of a breeding objective and assessment or recording of performance related to this objective.

In this Section, we will follow through the steps that affect genetic improvement and consider how each of them can be influenced in various circumstances.

Besides the four main components that determine rate of genetic improvement, extra consideration has to be kept in mind continuously, that is that the number of animals selected should be high enough to avoid inbreeding.

Genetic improvement can only be made if there is performance recording and preferable pedigree recording. In extensive livestock systems, measurement effort is mainly concentrated in the nucleus, i.e. a centralised nucleus herd and a group of progressive farmers working together in recording and selection. Sometimes, selection decisions can be made by individual farmers, but it is more efficient if the breeding strategies are coordinated between them. This depends also on the size of each of the herds.

3.2 Breeding Strategies

3.2.1 Basic elements of genetic improvement

3.2.2. Who is involved in steps to achieve genetic improvement?

When there is no breeding structure in operation, the breeding strategies need to apply to a population that has started to record performance. This could either be a whole village herd or flock, or only a part thereof.

In this Section, we will refer to such specific circumstances, if it is relevant.

3.2.3 Steps in selection of animals

A: Create Selection criteria

For each animal, we transform phenotypic information into Estimated Breeding Values (EBVs). This process is called genetic evaluation:

- the simplest form considers individual performance only. Selection is then on phenotype;
- a correction of performance for environmental effects (herd, season, age) is needed;
- more sophisticated methods such as Best Linear Unbiased Prediction (BLUP) use information in locations and throughout the years, using links through the pedigree. Moreover, information from relatives can be used;
- when more traits are measured, each of them needs to be weighed by its relative economic value, which can be done in a selection index framework (see Annex 1 of Breeding Objectives);
- multiple trait selection combined EBV of different traits, again by weighing them with the relative economic value (see Annex 3).

It is important that selection criteria represent, as closely as possible, the pre-defined breeding objective!

Pitfalls

There are numerous examples where at the moment of selection many other traits and criteria are considered that are NOT part of the breeding objective. This can seriously decrease the actual selection intensity (and therefore limits genetic improvement).

Other criteria that are acceptable:

- traits like infertility, sperm quality, etc. naturally need to be considered;
- some type traits like scores for legs, udder, etc. These are often indicated as 'functional type traits' and have some relation to a sustainable animal productivity (e.g. related to longevity). Ideally they should then be part of the selection index and their value should be considered in relation to the breeding objective. Considering them separately, besides a formal index, gives a large risk that such traits might get more attention than they deserve. It may be hard to realise a sound objective scoring system for functional type traits, but it is

quite essential if they are perceived to be of economic value (see further Guidelines on Breeding Objectives);

- a genetic defect is a valid reason for excluding animals from selection.

Other criteria that are doubtful:

- some traits may be related to productivity, but they are indirect measures. An example is the size of a dairy cow. Many dairy farmers believe that a cow needs to have 'body volume' in order to be a good producer. However, a much wiser option is to directly assess the productivity itself. Direct selection for the objective traits is in most cases much more efficient than selection on traits that may be distantly related. Selection on a correlated trait is only advisable if the objective trait itself is hard to measure or has low heritability;
- colour characteristic (spotted skin, black wool, red-cattle). This may be a selection criterion for cultural or commercial reasons, as in some markets such deviations are not accepted or attract lower prices. However, if such arguments are not valid, selection for 'beauty' should be avoided, otherwise breeding can become a costly hobby!

Other criteria that are not recommendable:

- other type traits such as scores for frame size, 'dairyness', etc. One problem with such traits is that they are often scored or assessed quite subjectively. A bigger problem is that such traits are often not related to production efficiency. If they are, they should be measured and/or given an economic value in the breeding objective;
- inclusion of production of (distantly) related individuals. There are examples where highly productive cows were not selected because dams or grandam did not produce terribly well. If relatives' information is used in EBV estimation, such criteria are completely redundant and they would be counted twice. If such information was not used in the formal EBV, it is likely to be overvalued, as distantly related phenotypes say little about an individual's genotype.

B: Compile a list with selection candidates

From each sex, all animals at reproductive age are selection candidates. Selection should predominantly be based on the selection criterion.

C: Selection of breeding animals

- *How many to select from each sex?*

In principle, select as few animals as possible from each sex.

The restriction here is mostly reproductive rate. The number of males and females that are needed as breeding animals need to be sufficient to maintain the herd size. Breeding animals need to leave enough mature

progeny from their own sex during their lifetime to replace them and their contemporaries.

Example

Ewes drop on average 0.8 lamb per year and they have on average five lambings. Each ewe produces four offspring in her lifetime. Half of those lambs will be females, so from every two female lambs born, one is needed for replacement.

Rams are joined with 25 ewes and they are used for two breeding seasons. In total a ram produces 40 offspring and one out of 20 new-born male lambs needs to be selected for replacement of old / culled rams.

Note that only those progeny that survive to maturity and are able to reproduce themselves need to be considered. Therefore, a breeding animal needs to produce at least two progenies that survive to maturity. If more progeny can be produced, we can select among the new-born progeny since we do not need to keep all of them.

As reproductive rates of males are generally much higher than that of females, we generally need a lot less breeding males than females. In other words, males can be selected more intensely and can generally be replaced at a younger age. Also, if breeding males can have a large impact due to their high reproductive rate, we wish to make sure that their breeding values are accurately known. If AI is used, males can be selected based on an accurate progeny test. Note that waiting for progeny test results may take a while and introduces a longer generation interval. This has to be offset by higher accuracy of selection. In an optimal situation, BLUP-EBVs can be used to optimise the proportion of very best young bulls with no progeny test and the very best progeny tested bulls (see next paragraph).

– *Comparing animals with unequal amounts of information.*

If selection index or BLUP is used to estimate EBVs, animals can be easily and fairly compared when they have unequal information. The selection criteria should be in equal units (e.g. dollar value index). Animals with less information will have less accurate EBVs and their EBVs are likely to be closer to the mean (remember an animal with no information has an EBV value of zero). Animals with more information have more chance to be in the top, only the very best animals with less information could make it to the top. Therefore, selection is optimal, taking more animals with accurate EBVs and only the very best animals with less accurate EBVs.

Note that unequal information is often caused by unequal age. For example, older males may have a progeny test, whereas younger animals have only their own performance or information on dam or sibs.

Although BLUP-EBVs optimise the use of young animals with inaccurate EBVs and older animals with more accurate EBVs, it does not take risk into account. If bulls are going to be very widely used in the commercial population (using AI), there is an argument for minimising the risk that the bull is less glorious than expected (in terms of true breeding value as well as in terms of possible carrying of some significant genetic defects). To avoid risk, a decision could be made that only progeny tested bulls be used in the commercial population. In this case, some possible genetic gains (from optimising generation interval) are sacrificed for limiting risk.

– *Comparing animals from different age classes*

By keeping breeding animals longer, more offspring can be produced on each of them and we can therefore select more intensely among those progeny. More intense selection means greater selection differential among the selected parents, thus increasing the rate of improvement. However, using breeding animals for a long time leads to long generation intervals, which decreases the rate of response. The optimum generation interval for a static situation can be found as in the example (Annex 1). It turns out that if selection is based on BLUP-EBVs, which are comparable over age classes, we simply select the best animals from all the candidates *irrespective of age class*. The reason is that BLUP-EBVs are fairly comparable over age class. The larger the rate of genetic improvement, the more we would select the younger animals, since they have an advantage due to genetic trend. The optimum generation interval can therefore easily be found by simply ranking animals of BLUP-EBV and ranking them.

– *Limiting the rate of inbreeding*

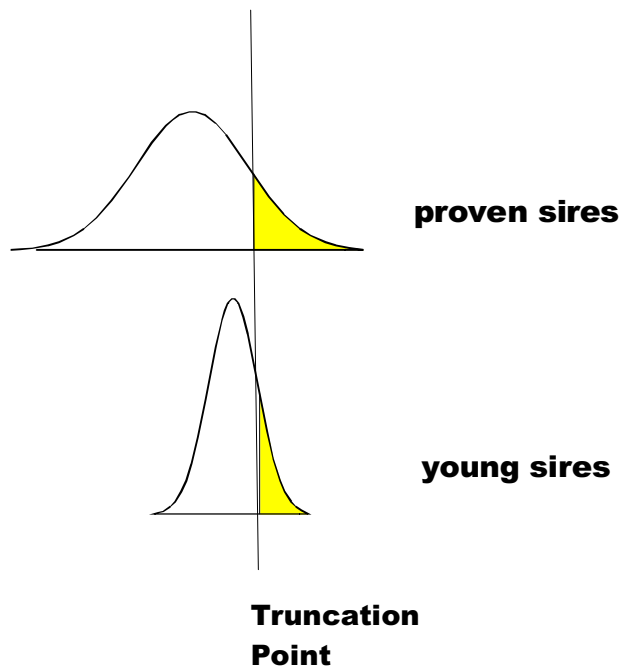
The rate of inbreeding in a population depends on effective population size (see Annex 2). In practice, a sufficient number of males should be used for each generation. In the Guidelines on Management of Small Populations, the target is to have a minimum effective population size of 50, corresponding to a rate of inbreeding of one percent. This means that at least 13 males should be used in each generation in a closed population. A village herd could use fewer males if they regularly import new males from neighbouring villages.

Note that if the candidate males are related to each other, the population size is effectively smaller. Either more males would need to be selected or selection should be such that the selected males are not too closely related.

However, if an outstanding male exists, selection of some more of his sons should not be avoided. Software exists to optimise the number of males selected, given the genetic relationships of the selection candidates and their breeding value (see next section).

Optimising generation interval by using BLUP-EBVs

When optimising a breeding programme, a dilemma often arises whether young or older animals should be selected. Selecting young animals is good for achieving a short generation interval, leading to more genetic gain. However, younger animals usually have less accurate EBVs and less accurate selection leads to less genetic gain. Older animals generally have more accurate EBVs but selecting them would lead to longer generation



intervals. Another (but essentially similar) argument against selecting older animals is that they are expected to have lower EBVs. If there is a genetic gain per year, animals born x years apart are expected to differ x times the annual genetic gain.

It is not easy to optimise selection over different age classes. However, the solution appears to be remarkably simple. The optimum strategy is a compromise, i.e. select the best of each of the age classes. The proportion that should be optimally selected from each age class is automatically achieved if simply the best animals are selected based on their BLUP-EBVs. James (1986) has given a formal proof of this result. Selecting animals on BLUP-EBVs irrespective of their age automatically optimises the generation interval. The condition is that EBVs need to be 'corrected for age' or, in other words, they need be comparable over age classes. The figure illustrates this point. Younger animals have on average better EBVs, but also generally less variation in EBVs. The optimum proportion of younger animals depends on the difference in the variance of the EBVs within age classes (i.e. on the accuracy) and on the genetic lag between age classes (i.e. on the genetic gain per year and the number of years).

Selecting on BLUP-EBVs across age classes is an example of such a dynamic rule, to determine the genetically best animals at a given moment.

D: Creating mating lists.

To create an optimal mating list from a given set of selection candidates, each with their estimated breeding values, is not an easy task, given that the selected animals should be both sufficiently good and not too closely related to each other. Particularly BLUP-EBVs could be quite similar for related animals as the BLUP method uses relative's information, making EBVs of related individuals more alike.

Ad hoc advice to be given here is:

Be sure to use at least ten to 15 males every generation and more if many of the males used are related to each other. Do not overuse breeding animals within the nucleus.

Import regularly from populations with similar genetic mean. It is important to have exchange programmes with other groups that have similar breeding objectives and similar breeding strategies, such that it can be expected that their population is improved at the same rate.

In the nucleus, the most important aim of a particular mating structure should be to make connections between animals used in different locations, seasons or years, meaning that progeny from as many parents as possible are compared with a location at a given time.

Generally, mating strategies can be formulated, such as:

- avoiding direct mating of closely related individuals;
- mating the very best of the selected males to the very best of the selected females (known as assortative mating). On average, the group of progeny born in the next generation is not affected, but there will be more variance among the progeny. This has some advantage in terms of genetic gain (typically about five percent);
- “nicking”: for breeders it is often important to be able to make specific combinations of bull B mated to cow C (and daughter of famous grandsire G). Such dedication is extremely important for the enthusiasm and interest in the breeding programme (as long as the breeding objective traits are targeted). In scientific language, nicking is indicated as ‘utilising dominance’. Utilising dominance variation is often not of primary importance for improvement of pure-breds. It can have more impact if breeding animals are selected from different breeds or lines, as heterotic effects between breeds can be utilised. When multiple traits are involved in the breeding objective, assortative mating could be useful, matching qualities in different parents for different traits. Formally, this is only useful if the traits show optimum values. Otherwise, improvement of traits is linear and a certain disadvantage for trait A could be offset by increased advantage for trait B.

Making such specific matings to match different traits is generally more useful at the commercial level, where most of the production is realised.

In a nucleus, such matings are less useful, because the specific interactions between sires and dams cannot be passed on to progeny and the main objective of a nucleus is to produce genetically improved progeny to be disseminated to the commercial level.

Software

Computer programmes exist to optimise selection decisions for a given list of candidates with pedigree information and EBVs on each of them. Such programmes can be very valuable tools, especially when EBVs are estimated with the BLUP procedure. Brian Kinghorn at the University of New England (Armidale, Australia) has developed software to create mating lists that allow finding the right balance between genetic progress and genetic diversity within the population. From a list of selection candidates, their EBV-values, pedigree and optimal mating lists are produced. The method allows for very practical considerations like 1) logistical constraint like mates being on different locations; 2) possibility and cost of using AI or MOET mating group size, etc. (e.g. paddock system); 3) cost and ease of importation within the herd or flock. This software is particularly useful for low input extensive breeding systems. For further information see <http://metz.une.edu.au/~bkinghor/matesel.htm>

Summarising:

Select as few breeding animals as possible from each sex, as a small proportion selected leads to high selection intensity and parents with higher merit.

The lower limit is determined by reproductive rate and inbreeding:

- the selected proportion needs to be $2/p$ at least, where p is the number of mature progeny produced by a breeding animal in her/his lifetime;
- the number of males used in each generation should be at least 15.

Animals with unequal information content and from different age class can be fairly compared and generation intervals are optimised when using BLUP-EBVs for selection criteria.

When breeding animals are going to be intensely used in the commercial population, a progeny test could be a requirement for AI bulls to avoid risk.

Generation intervals should be short

Only the very best breeding animals should be kept for another breeding season, others can be replaced by new and young breeding stock.

It is important that each decision taken in an animal improvement programme should be taken in the context of the central dogma that determines rate of gain:

Genetic gain = (selection intensity * selection accuracy * genetic SD)/ generation interval

3.2.4. Give balanced attention to each of the factors that determine genetic improvement

To be cost effective, judge which of the factors is easiest to improve!

For example, accuracy of selection as well as intensity of selection are directly related to genetic improvement and increasing either of those by five percent will give a five percent improvement of the rate of genetic gain. Increased accuracy could be achieved for example by a more accurate measurement of correlated traits. However, this may be costly and in the same breeding programme it may be much easier to increase the selection intensity by five percent (e.g. by simply using less parents for breeding).

It is important to know in a breeding programme where the big gains are

Those are changes that are easy to implement and most cost effective. A good breeding programme is not characterised by sophisticated reproductive technology and genetic evaluation software, but rather by cost effective decisions, giving the biggest part of the possible genetic gains for the limited resources available.

These are discussed in more detail, giving examples and typical pitfalls for each component. Subsequently, how the different components are related to each other is discussed.

In the starting up phase of a genetic improvement programme, not achieving sufficient selection intensity is one of the most common failures. This is very unfortunate since improving selection intensity is usually among the cheapest and most cost-effective measures that can be taken in breeding programmes for extensive production systems.

Some common pitfalls are:

- *The number of animals used for breeding is much higher than necessary.* There are examples of village flocks running together with as many male as female stock. However, the number of males needed for

Pitfalls in obtaining sufficient selection intensity

breeding purposes should be much lower: the male to female ratio should be around 1:10 to 1:50, depending on the species. A simple first step in the breeding programme is therefore to select among males and only to keep the better part and *ensure that other males do not contribute to reproduction!*

- *The actual number of candidates considered for selection is much lower than necessary.*

The actual selected proportion is usually lower than it seems because animals are usually assessed for a number of reasons. The effective selection intensity depends on the number of animals selected as taken from a group *assessed for the breeding objective considered.*

Example

Milk production in the Sahiwal herd mean 1 500 kg /lactation, phenotypic SD=300 kg.

One hundred young cows are available for selection and to improve milk production the best 40 are kept for breeding and making another lactation. We should only consider taking the best based on the criteria 'milk production'. Suppose 20 percent is not eligible for another lactation due to disease or other health problems. The selected proportion could be 50 percent, giving selection intensity of 0.8, hence the average production of the selected cows could be $1\,500 + 0.8 \times 300 = 1\,740$ kg.

In practice, other selection criteria are often considered as well, e.g. the size of the cow, their temperament or their colour. In that case, effectively, there are fewer animals available for selection for milk production. Suppose 25 percent of the 80 eligible cows are considered inappropriate for such 'other reasons', then the selected proportion for milk production would be $40/60 = 67$ percent, giving a selection intensity of 0.5. The average production of the cows would only be $1\,500 + 0.5 \times 300 = 1\,650$ kg.

The loss in dam superiority would be 37.5 percent and loss in genetic improvement in progeny would be nearly 20 percent.

In most breeding programmes, the main reason for obtaining a smaller response than possible is due to sub-optimal selection intensities because animals are not rigorously selected using the criteria defined as breeding objectives.

In practice, this point therefore needs to be of primary concern. It is indeed not always easy to define selection criteria as a 'trait' and attach a dollar value to it, as is needed for inclusion in the breeding objective. The Guidelines on Breeding Objectives discuss this point in more detail.

- *Biased estimation of breeding value*

The basis of estimation of breeding value is phenotypic performance. However, phenotypic performance is to a large extent determined by environmental factors. The performance of animals should be evaluated as relative to a contemporary group, i.e. a group of animals kept in the same conditions, measured at (more or less) the same age, etc. Comparison of different animals across herds, ages, etc., is only possible when genetic evaluation methods have been corrected for such influences.

Pitfalls in selection accuracy

It is not the green grass that an animal eats that makes him a valuable breeding animal, but its performance relative to other animals kept in the same conditions!

- *Confounding environment and genetic effects*

Problems arise if environmental factors are confounded with genetic factors. The most common are that different sires are kept in different paddocks. If the paddock effect is large, an apparently good performance of a bull's offspring could be not the results of his genes, but of the good paddock. Notice that even sophisticated genetic evaluation systems like BLUP cannot correct for such complete confounding. If the performance of animals or their sires is going to be compared, it is important to create genetic links between such fixed effects. Hence, bulls should not be repeatedly bred to the same group of dams, bulls should be used throughout the years and across herds (if possible). See Annex 3 for an example.

Genetic links, i.e. usage of animals across herds and throughout the years, is critical for the ability to compare breeding value of individuals across herds and throughout the years.

- *Inaccurate recording and measurement errors*

The reliability of a recording system is obviously an important factor in the reliability of estimated breeding values. If pedigree information is used, reliability of the animal identification system and correct knowledge of parentage is very important. See Guidelines on Animal Recording.

Pitfalls in obtaining a short generation interval

The value of a quick turnover of generations is often underestimated in animal improvement programmes. The longevity of good breeding animals is often respected.

A good breeding animal is very valuable. However, some of the offspring will soon be better.

In each breeding season, a good system replaces part of the breeding animals with young replacements. If replacements were selected based on breeding value, they are likely to be better than many of the older breeding animals. On average, the progeny drop is equal to their parents, but the selected progeny should be better. The best breeding animals from previous breeding seasons could remain in the herd. Once a breeding programme gets going, each new progeny drop is (on average) genetically superior compared to the previous because of continuous genetic improvement.

Replacement rates should be particularly high for males, as few are needed and they can be selected with high intensity.

3.2.5 Different factors in genetic improvement are interdependent

Alternative options for breeding programmes need to be assessed, which can be done based on an analysis of the most important factors that determine rate of genetic gain:

- selection intensity
- selection accuracy
- generation interval.

However, it should be pointed out that the different factors interact and a balance has to be found.

The most important interactions are:

- *Generation interval versus selection accuracy*
Selection of young animals will not only lead to short generation intervals, but may also imply lower selection accuracy because young animals have generally less information available (no repeated records, maybe no own performance, no progeny test).

Solution: Selection based on BLUP breeding values optimises generation interval. If risk is to be avoided, some more weight could be given to more accurate EBVs, for example, breeding bulls for the commercial population need a progeny test as a minimum requirement.

- *Generation interval versus selection intensity*
If more young animals are retained as breeders and a high replacement rate is applied, the generation interval may be shorter, but selection

intensity will also be lower since more animals of the new-born generation are needed for replacements.

Solution: First determine the number of breeding animals needed, then select based on BLUP-EBV. The number of young animals to replace older breeding animals will be optimised. Without BLUP, a good feel for the optimum replacement rate can be obtained using calculations as in Annex 1. Very useful software to assist in such calculations exists: GENUP, module AGES, see <http://metz.une.edu.au/~bkinghor/genup.htm>

- *Selection accuracy versus selection intensity*

In many cases limited resources are available for trait measurement. Decisions have to be made like:

1. Measure fewer traits (giving lower selection accuracy) or measuring fewer animals (giving lower selection intensity).

Solution: A balance has to be found here. The loss in accuracy from measuring less traits can be evaluated using selection index theory. The loss in selection intensity can be easily determined by comparing different proportions selected and the associated selection intensities.

2. Testing fewer bulls in progeny testing, with more progeny per bull, or testing more bulls with fewer progeny each.

Solution: Suppose five bulls need to be selected and 200 progeny can be tested. Testing ten bulls with 20 progeny each gives a selection intensity of 0.8 and selection accuracy of 0.76 (heritability 25 percent), whereas testing 20 bulls with ten progeny each gives a selection intensity of 1.27 and a selection accuracy of 0.63. As 0.8×0.76 is smaller than 1.27×0.63 , it is better to test more bulls with fewer progeny.

To make selection decisions, we need to consider:

- The number of males and females selected:
 - select as few breeding animals as possible to increase selection intensity;
 - select enough breeding animals in order to drop enough progeny for replacements;
 - select enough breeding animals in order to limit the rate of inbreeding.
- Which animals are selected?
 - select the animals with the highest estimated breeding values (EBV);

3.2.6 Balancing rates of genetic change and inbreeding

- select enough animals from different families to minimise co-ancestry of future parents (i.e. to minimise the genetic relationships among selected animals in order to minimise inbreeding).
- How intensively is each of the selected breeding animals used?
- how many matings per male, are some used for AI? The very best breeding animals could be used more intensely, but too much use of them would lead to more inbreeding.

**Select as few animals as possible and only the very best.
Select enough breeding animals with enough genetic diversity
(different families) and do not overuse breeding animals.**

For high rates of genetic improvement, as few as possible breeding animals should be selected, but a minimum number of about 15 males per generation is needed to restrict inbreeding. If selected breeding animals are related to each other, a higher number is needed or other unrelated animals should be selected. Breeding animals should not be used excessively.

Intensive use of the best breeding animals outside the nucleus is acceptable. If an exceptional bull is available and AI can be used, there is no problem to let it have many progeny in the commercial population. It is the inbreeding in the nucleus that is relevant for the sustainability of the breeding programme. However, using AI-bulls from the same family very intensively will ultimately also lead to repeated inbreeding in the commercial population.

Remember that controlling inbreeding is equivalent to controlling genetic variation and controlling risk of a breeding programme. The risk of a breeding programme can be described as the probability that due to chance, the result is much worse than expected. The factor chance is greatly increased when only a few breeding animals are used or when they have animals with many genes in common. **One should never bet too much on one horse** (or bull or ram, in this case)! Therefore, rules to limit inbreeding will also limit risk in the breeding programme and ensure sufficient variation in the population.

Limits in making genetic improvement through selection are set by:

- the reproductive rate of breeding animals;

One could invest in boosting reproductive rates (e.g. artificial insemination);

- uncertainty about true genetic merit of animals;

One could invest in better or more trait measurement, pedigree recording and in improved genetic evaluation methods and in creating a linkage between information obtained from different locations and periods, genetic markers.

3.3 Decisions about investments in a breeding programme

- Reproductive rates determine the minimum requirement of animals needed for reproduction of the population. If animals could have more offspring, less would need to be selected and selection intensity would be higher.
- Uncertainty about genetic merit forces us to measure performance of animals and its relatives. Genetic evaluation is used to obtain the best estimate of genetic merit for a given amount of information (data and data-structure). More information gives more selection accuracy but often with diminishing returns.

As pointed out earlier, investment decisions in animal breeding programmes can be assessed in the context of the three components contributing to the rate of genetic change: selection intensity, selection accuracy and generation interval. It is important to know in a breeding programme where the big gains are. Those are changes that are easy to implement and most cost effective. In this section, some ‘easy’ and ‘costly’ measures in breeding programmes will be evaluated.

The benefit of abundant and good measurement is that we are better able to identify the genetically superior animals. Using more information leads to more accurate selection and more genetic improvement.

3.3.1 Measurement Effort

If resources are limited, trait measurement may be confined to a small group of animals, e.g. only nucleus animals are measured. A next option could be to perform a progeny test. This would increase male selection accuracy, particularly for low heritable and /or sex-limited traits but the expense is a longer generation interval and the actual costs of organizing a progeny test.

There are two main questions:

- Which traits should be measured?

This depends on:

- the breeding objective: preferably traits in the breeding objective should be measured;
- ease and cost of measurement;
- how important is the trait compared to other traits?

Some breeding objective traits are not easy or very costly to measure and there could be correlated traits that are easier/cheaper to measure. When measuring correlated traits, the genetic correlation between the measured trait and the breeding objective should be high.

The marginal value of measuring an additional trait can be determined by using selection index methods (see Annex 1 in Breeding Objective Guidelines).

- Which animals should be measured?

At least the nucleus animals should be measured for performance and pedigree.

When starting from scratch, a part of the population could be measured, usually consisting of a group of 'progressive farmers'. Such a group will automatically form the nucleus.

Whether more animals in the population will be recorded depends on the social and technical infrastructure and on costs. Furthermore, animal recording serves more purposes than for genetic improvement (see the Guidelines on Animal Recording). Recording more animals has some advantages with regard to genetic improvement:

- effectively, a larger nucleus could be established, with a larger possible selection intensity and less inbreeding;
- an open nucleus system could be applied with the possibility for the best animals in lower tiers to become nucleus parents.

When recording is an investment for genetic improvement, a cost-benefit analysis could help in deciding whether more animals should be measured. The benefit can be determined from the increase in rate of genetic improvement, using principles of basic theory and considering the change in each of the main factors determining rate of genetic gain. The increased selection intensity and increased selection accuracy will be the main factors to change. The rate of improvement can be given a dollar value and be multiplied by the number of animals in the breeding population. Such an assessment is at sector or national economic level, which is appropriate if government funds are invested into the breeding project. In a privatised

breeding structure, individual breeders can gain from more measurement by increasing their chances of obtaining the best breeding animals, therefore selling more breeding stock. The economic value from such a perspective is more difficult to estimate.

There is clearly a cost component involved in animal recording. However, animal recording is not only useful for the purpose of genetic improvement. It also is a very important tool in herd management and it allows the comparison of alternative production systems. (For a detailed discussion on this topic, see the Secondary Guidelines in the AnGR-FAO Programme on Data Recording). If done for the purpose of genetic improvement only, it is usually not necessary to measure all animals in the commercial population. Typically, a pig breeding company would not record the whole commercial pig population but rather concentrate their efforts on measurement of nucleus animals only.

3.3.2 Optimising testing efforts

In general, there are two reasons why it is usually not cost effective to record a whole population for the purpose of genetic improvement.

Firstly, the purpose of recording many animals is to obtain high selection intensity but there is not a linear relationship between proportion selected and selection intensity. Suppose we need to select 100 breeding animals. For a selected proportion of ten, one and 0.1 percent we would need measurements on 1 000, 10 000 and 100 000 animals, respectively. The selection intensities would be 1.755, 2.665 and 3.367, respectively. Hence, for a tenfold of measurements each time, the increase in selection intensity would be only 52 and 26 percent, respectively.

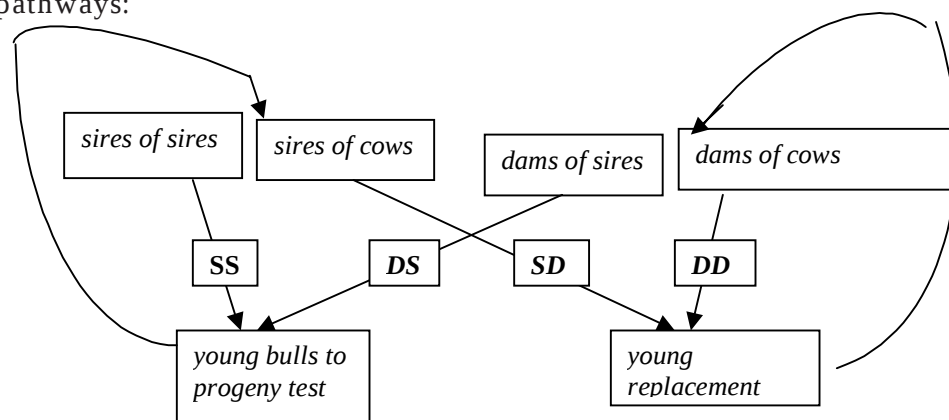
Secondly, some animals have a lot more chance to be good future breeding animals, even before they are measured. Those are the offspring of the best animals. Hence, if a limited number of animals is to be recorded, then recording an elite group of offspring from the best parents is most cost-beneficial. Animals from average parents have a smaller chance to be selected and measuring these is therefore less useful. Hence, nucleus animals have highest priority when it comes to investing measurement effort.

A special case of investment in measurement is a progeny test. Typically, not all males are progeny tested but only the males born from 'elite matings', i.e. the matings of the very best males with the very best females.

Progeny testing and the 4-pathway breeding structure

Progeny testing is only a practical option if AI is used. AI facilitates testing of progeny across herds and the investment in progeny testing is only paid off if the bulls selected based on progeny tests can be widely used. Progeny testing is expensive and obviously not all males born in the population are progeny tested. Only the best young males are progeny tested, i.e. the offspring of the very best dams and sires.

A typical design of a breeding programme arises in the case of progeny testing: the 4-pathway breeding structure. It consists of the following pathways:



More detail and an example of a 4-pathway breeding structure is given in Annex 4.

The example shows some different parameters that need to be evaluated in deciding on a progeny-testing programme. Those are 1) the number of males progeny tested; and 2) the number of offspring generated per progeny tested male.

An important feature when designing a progeny test is to distribute the progeny over different herds or locations. In genetic evaluation, the phenotype from the progeny is compared with the phenotypes of progeny from other sires. If the animals in a particular management group are all descending from one sire, there is no basis for comparing them with offspring from other sires. For examples on distribution of progeny over different herds see Appendix 4.

The effective number of progeny is maximised when each progeny of a bull is compared with progeny from a maximum number of other bulls.

Phenotypic measurements are turned into *Estimated Breeding Values (EBVs)*. In principle, animals can be selected based on own performance when performance is recorded. For sex-limited traits (recorded on females only), selection of males could be based on performance of the dam. Adjustment for important environmental effects increases the selection accuracy. Effects that need to be adjusted for are like season, year and herd of performance and age of the animal.

3.3.3 Genetic evaluation effort

Pedigree recording adds significant value to genetic evaluation. Firstly, it allows the use of information on relatives, leading to increase selection accuracy (five to 20 percent, depending on heritability). Secondly, it allows across herd comparisons, as different herds have generally offspring from common ancestors (sire or sire of bulls used). Across herd evaluation has the advantages of allowing fair comparisons of EBVs across herds, leading to selection of more animals from the genetically superior herds.

Nowadays, sophisticated statistical methods are readily available, leading to *Best Linear Unbiased Prediction (BLUP)* of breeding values. See Annex 3 for properties of BLUP. A genetic evaluation system using BLUP relies on good data measurement, a good structure of data (breeding animals across herds) and proper pedigree recording. If these prerequisites are in place, investment in BLUP methodology is usually highly cost-effective. However, putting a genetic evaluation system in place has two sides to it:

- the technical side of organizing performance and pedigree recording to a central unit, the actual genetic evaluation (data analyses) and return of EBVs and other data summaries (genetic trends, culling advice, etc.) to the breeders;
- the extension side: breeders have to understand and accept the EBVs that are produced and they have to know how to use them. There is no sense in running a genetic evaluation if the results are left untouched by the end-users.

Use of reproductive technology can be another *investment option*. Most of the main factors that determine genetic gain are directly influenced by the reproductive rate of the breeding animals. A higher reproductive rate leads to the need for a decreased number of breeding animals, therefore increasing the intensity of selection of these animals. If reproductive technology is technically possible, for example AI, the benefit can be expressed in terms of increased genetic rate of improvement, which in turn has a dollar component attached to it. More offspring per breeding animal also allows more accurate estimation of breeding value.

3.3.4 Investment in reproductive technology

Reproductive technology allows the intensive use of superior breeding stock. An obvious consequence is possibly that the most popular breeding animals are overused and the population could encounter inbreeding problems. Typically, as new technologies in animal breeding allow faster

genetic change, long-term issues such as inbreeding and maintenance of genetic variation become more important.

Besides a direct effect on rate of genetic improvement, mostly due to a higher selection intensity and increased selection accuracy, another important consequence from increasing reproductive rates is to disseminate superior genetic stock more quickly. The influence of a superior beef bull would be much higher if thousands of offspring could be born, rather than if the superiority is passed on through the production of sons via natural mating. As reproductive rates are basically multiplying factors in a breeding structure, any improvement in reproduction will justify higher investment in improvement of the nucleus breeding stock.

Any introduction of reproductive technology has to be cost effective and accepted by the farming society.

Artificial Insemination

Technically, there is a need for:

- resources and expertise in AI services (semen collection, freezing and / or storing and insemination);
- a certain infrastructure. Once an AI service is running, the distribution centre has to be contacted by individuals who need the service and the service needs to be delivered within 12 hours. Communication lines (telephone) are therefore essential.

Advantages of AI appear at two levels:

- Distribute semen across a number of nucleus herds. This is useful for establishing genetic links between the different nucleus herds (essential for genetic evaluation in the whole nucleus). Furthermore, particular mating may be better targeted, e.g. the best bulls mated to the very best cows. AI use in a dispersed nucleus may be feasible, as the nucleus farms maybe expected to have higher management skills, being able to detect heats, separate females from other bulls and communicate their request for insemination services to the distribution centres. With nucleus farms of reasonable size, semen might be stored on site, but it requires the presence of AI technicians on the site.
- Distribution of AI-semen from proven bulls to commercial farmers for the purpose of dissemination of genetic improvement may be more problematic. In many countries, producers are smallholder farmers and the skills and infrastructure may be insufficient to allow AI services. Again, when inseminating by AI, the farmer has to be able to detect heat and contact the semen distribution centre, which has to be able to serve within 12 hours. Furthermore, he needs to be able to muster and tie up the cows that need to be served. For most extensive production systems, this will be very labour intensive. For dairy production systems it may be feasible, but for meat production under extensive grazing systems, it is likely to be impractical. To facilitate communication with

local farmers, local distribution centres at village level are advisable. More importantly, local centres can familiarise farmers with the concept of AI and with information about the breeding animals that they will be using.

Multiple Ovulation and Embryo Transfer

The use of multiple ovulation and embryo transfer (MOET) is costly and requires highly developed technical skills. Application of the technique is feasible in large centralised nucleus herds. The main advantage is a higher selection in the females and more accurate breeding value estimation. The latter is due to the fact that animals will have more siblings and if performance recorded, more information from relatives (provided that BLUP is used for genetic evaluation). The result is that animals have a reasonably reliable breeding value at a younger age, particularly when the main traits are only recorded for one sex (females). Practically, this could mean that with the selection of males, there is no need to wait for a progeny test. Males could be selected based on half sib sisters. The gain in generation interval is large and overcomes the loss of selection accuracy from replacing a progeny test by a sib test. MOET breeding programmes are therefore characterised by:

- increased reproductive rates of females;
- selection at younger age (especially of males in case of sex limited traits);
- more potential for high rates of inbreeding.

The cost and skills involved in MOET breeding programmes are likely to be high and in most cases it may be better to invest these resources in more basic pre-requisites of a successful breeding programme: performance and trait recording, extension and dissemination.

Effect on breeding structures and socio-economic implications

Use of reproductive technology and reproductive rates by themselves has a large impact on socio-economic structures of a livestock industry. In breeding structures where AI is used, the ownership of the breeding animals is usually transferred to larger breeding organizations, such as AI cooperatives or private breeding companies. If the large part of genetic improvement is removed from the farm or village level, the dedication to genetic improvement may disappear. Moreover, the farmers have to be willing to accept AI as a tool for reproduction and breeding.

The first and most important mating decision is to make sure that the selected males and females are mated with each other. Culled males should be kept separate or castrated. Culled females should not be bred and should be removed from the herds at an appropriate time.

Any mating strategy will require provisions. With natural mating, animals to be mated have to be joined in the same paddock but separate from

3.3.5 Investment in mating structures

AI has great potential in breeding programmes to exchange semen between different nucleus herds and to disseminate genetic improvement to the production tier.

AI requires technical skills at the AI centre as well as on the farm end, with most important communication lines between the two. It is not likely to be used at the commercial level in extensive grazing systems for beef production.

Use of AI will take genetic improvement activities away from the farm, resulting in an increased need for extension and communication to farmers about their need to participate in genetic improvement.

other animals at reproductive age. AI can be used to target specific matings but AI again requires other provisions, as described in Section 3.3.3.

Section 4. Identifying structures and key decisions

4.1 Is there any performance and/or pedigree recording?

This Section gives a step-wise guidance towards identification of current breeding structures. Case studies describing very basic structures moving to more advanced structures exemplify the issue.

Recording here is used in the broadest meaning of the term. Even the simplest form of recording (e.g. 'in the farmer's memory') and selection (the farmer picking his 'best animal') could lead to small amounts of genetic improvement. However, recording and selection should be preferably formal, objective and documented, as it is more likely to be accurate and unbiased.

4.2 Is there any selection based on performance traits?

Without recording and selection, there can be no genetic improvement. Production systems without recording can only be improved genetically by bringing animals that were selected elsewhere based on merit, into the population.

4.3 What is the current breeding structure?

Breeding structures should always exist, even without recording, selection or importation. They would not contribute or enhance genetic improvement but they are simply designed for the purpose of reproduction and avoidance of inbreeding. Genetic improvement can be built into such existing structures.

Case 1: No recording, exchange of breeding males between different village flocks

A village consists of a hundred small farmers, each with ten chickens and a rooster. Farmers exchange roosters each year to avoid breeding their chickens to their own male progeny. From all new-born progeny, all females are kept as replacements and one male is randomly chosen for further breeding (to exchange with a young male from another farmer). There is no further pedigree or performance recording. The production system is such that chickens are kept for egg production and produce one offspring annually.

In this case, the breeding structure is flat, there is only a commercial population and the nucleus is basically absent. There is no selection and therefore no genetic improvement. There is some organized breeding (exchange of roosters) to keep inbreeding at sufficiently low levels. Hence, the only breeding objective is control of inbreeding, but there is no breeding objective in terms of definition of performance traits that are defined and need to be improved.

1. Selection is possible if not all progeny born in a population are needed for reproductive purposes.

Females

In species with low reproductive capacity (cattle, sheep) most females born are needed to replace older animals in the breeding herd or flock. With higher reproductive rates (some prolific sheep breeds, goats, pigs, chicken), each female leaves sufficient progeny such that not all new-born females are needed for breeding purposes. Also, when breeding females are kept longer in the herd, replacement rates are lower and less females are needed for replacement.

The last strategy is not always advisable. In an on-going breeding programme, new-born individuals are (on average) better genetically than animals from older age classes and turnover of breeding females should be reasonably high to keep generation intervals short (see discussion in Section 3.2.2).

Males

Males generally have a high reproductive rate as each male can be mated to several females. Selection in males is always possible, the more so with higher reproductive rates (higher females to male ratios).

4.4 Identify selection possibilities

2. Identify who is eligible for selection

Selection should take place before reproductive age. Selection should be based on some information about breeding value. Animals not selected should be culled if they do not contribute to the production system.

There are several situations possible:

- no performance recording. Animals are selected based on visual appraisal or a 'subjective' score of performance. This can be the phenotype of the individual or the phenotype of the parents. For example, in dairy production systems, males are selected at birth and non-selected males are culled (or sold to other production systems). Also, females from bad performing cows are culled after birth, as there is no sense in raising them until first calving;
- performance recording, measurable on females only after reaching the reproductive age (dairy situation).

Males cannot be selected based on own performance. Breeding sires are selected based on dam performance. If AI is used, they can be selected based on progeny tests but only a small group of males will be progeny tested. The selection of males to be progeny tested (first stage of selection) will be based on dam performance, or on sire and dam EBVs if a genetic evaluation system is up and running. The best strategy is to mate the best dams to the best sires (elite matings) and progeny test the males coming out of such matings, as described in the 4-pathway breeding structure. The males with the best progeny test will be selected as breeding bulls for the larger population (second stage of selection of males).

Females are generally all needed for herd replacement. There can be some culling by not keeping the female calves from the worst-producing cows;

- traits are measurable before reproductive age (beef and wool).
Animals can be selected based on own performance or on an estimated breeding value based on all available information (BLUP-EBV). Animals not selected for breeding still contribute to the production system, so there is no loss in keeping them until after trait measurement.

The best parents that were selected can be called 'parents of nucleus'. These animals are elite animals either because they are selected themselves or because they descend from the best animals in the previous generation, from a small group of animals that were selected based on performance recording. Their offspring will automatically be more valuable than offspring from average animals. The best of the offspring from nucleus animals become nucleus animals themselves. Investment in performance recording should first be targeted to such nucleus born animals. Investment in progeny testing is an example of limiting recording to 'nucleus born' animals.

A typical role of commercial animals is that they generate animal products but never will create progeny for the next generation. This is the fate of most males, as only a few of them are needed for breeding. Generally, females have low reproductive rates and it is necessary that most females leave progeny to keep up the size of the population of production animals.

Case 2. Additional to Case 1 there is subjective assessment of performance

In addition to Case 1, farmers now assess their chicken. Suppose they have a fair idea of ranking their hens based on egg production. Even for this simple assessment of performance, it may be already necessary for each hen to have her own nest or cage. If all farmers in the village would subjectively assess their animals, the whole population is 'performance recorded' (although not very accurately). For example, each farmer can nominate his very best hen. As there is no official and objective recording, we assume it is not possible to compare animals from different farmers. The rooster that will be picked now will descend from the best female (with a male offspring). Here it is necessary to identify which males descend from which hen.

The breeding structure is a flat structure: a single tier structure. The reason is that all animals are performance recorded (assessed) and the breeding animals that are used (one male and all females from each flock) are equally contributing to the next generation of chickens. We cannot identify some breeding animals that are from an 'elite group', i.e. that we expect beforehand to be better than others because of some special selection of parents.

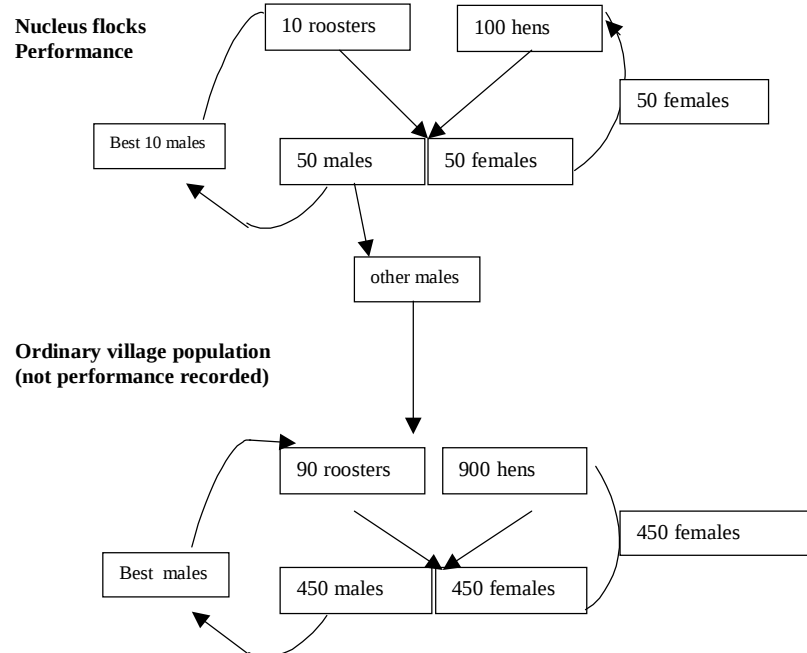
Hence: Single tier breeding structure.
 Some genetic improvement, as the selected
 roosters can be expected to be better than
 average.

Case 3. Formal performance recording in part of the population.

Suppose now that ten farmers (ten percent) start to officially record egg production. They count and record the eggs laid over a certain time period. They also register the pedigree for each new-born (pedigree recording). Other farmers in the village do not record (or only subjectively record as in Case 2). Within the group, the ten farmers only exchange their best roosters.

Initially, nothing changes to the chicken population in the village. However, after one year it may be expected that the chickens of the group of ten farmers are better than average, as the farmers have more accurately selected their best males. The difference may not be extremely large if they used only dam performance as a selection criterion for males. However, the group might even apply BLUP, allowing them to use information on relatives (more accurate EBVs) allowing comparison of animals across flocks. The best ten males can now be selected from the best ten hens across flocks, allowing a higher selection intensity (best ten out of 100 rather than best out of ten giving $i = 1.78$ rather than $i=1.52$). More animals will be selected from the flocks that happen to have better animals. As the elite group will have higher genetic means after some time, it makes sense that all progeny born in the elite group become the source for other farmers in the village for roosters. Animals born in elite flocks are likely to have a higher genetic mean than ordinary village flocks. A two tier breeding structure emerges.

When a nucleus emerges, the elite group provides males to other “commercial” farmers. These producers do not use males born in their own flocks; rather they recruit them from the elite flocks, with a higher genetic level.



In Case 3, it is easy to identify the nucleus, as it consists of the group of elite farmers, who performance record and work together in selection and use of males. Genetically, there is initially not much distinction between males in ordinary and nucleus flocks, as they both will be used as a rooster in a village flock and their genetic mean does not differ very much. In the longer term, the nucleus animals will have a higher genetic mean, as they descend from the best animals. The males in other flocks are average animals in their own generation but from the best nucleus parents in the previous generation. There will be a genetic lag of two generations between the nucleus animals and commercial animals, meaning that the genetic mean in the nucleus today will be achieved by the commercial in two generations.

Case 4. All farmers record performance and pedigree on their animals.

The males born in ordinary flocks can now be selected, making the genetic lag between nucleus and commercial tier a bit smaller than two generations. As breeding values can be determined for all village animals, the selected males used as nucleus sires do not all have to be born in the nucleus themselves. The best village males might be just as good as some nucleus born males (although the village average is lower). The smaller the genetic lag between nucleus and commercial, the less difficult it will be for a male born in ordinary flocks to compete with males born in the elite flocks.

If performance recording commenced for all village animals at the same time and the selected males were randomly distributed over the different village flocks, then there would be no reason to distinguish a nucleus from the commercial population. However, it makes sense to mate the best males to the best females, as this increases the chance of genetically good offspring. Under such circumstances, the nucleus consists of the best male and female parents, who are possibly dispersed over several herds.

The logistics of natural mating may prevent to exactly mate the best males and females, as the good hens are probably scattered over many flocks. A practical solution is to gather the best hens and keep them together in one, or a few nucleus flocks, each joined with a selected male. The actual nucleus is then physically centralised (central nucleus). If AI was used, it would not be necessary to physically bring together the best animals and the nucleus could be dispersed over many herds (dispersed nucleus). However, in most low input production systems, natural mating is used and a centralised nucleus would have to be formed. A central nucleus is also a good, more intensive trait measurement or measurements that are hard to standardise in field conditions.

4.5 Create mating provisions

Mate best males to best females. This is straightforward in a centralised nucleus. In a dispersed nucleus, AI is needed to target specific matings. Some practical reasons for specific matings are:

- 1) targeting heterosis (between breeds) or dominance (within breeds);
- 2) target optimum values in non-linear traits (e.g. birth weight).

Summarising:

A nucleus is formed when a group of animals can be expected to have a higher genetic mean because they are more effectively selected (due to performance and/or pedigree recording and cooperation in exchange and joint use of males.)

The genetic mean of the nucleus will be lagging behind the next tier. The genetic lag is equal to two generations if only males are used at a lower tier. This lag is reduced to one generation if both females and females born in the nucleus are used as parents in the next tier.

In a breeding programme, the best males should be mated to the best females. In a low input production system with natural mating, this can be realised when the best females are physically brought together in a centralised nucleus.

An individual animal qualifies to be a nucleus parent if it is among the best of its contemporaries. If all animals are recorded and artificial breeding can be used, animals do not need to be physically part of a central nucleus. However, performance recording would be confined to a smaller group of herds and natural mating requires the best females to be physically together with the best males, making a central nucleus an easy and workable option.

Section 5. Decision-making

Breeding Objective

Description of a clear breeding objective, definition of the relevant traits involved and determination of their relative economic value in the production system which is targeted by the genetic improvement efforts. Decisions are made by the breeding cooperative or by private breeding organizations, in both cases to optimise genetic improvement and to maximise use of breeding animals at the commercial level and ultimately, to increase animal productivity of commercial production systems.

Which animals?

Determine trait and pedigree recording. If insufficient recording is taking place, a recording system needs to be set up. This area requires a conscious decision about investment of resources in a recording project (see Guidelines on Trait Recording).

With limited resources, recording of males should have first priority (if traits are measurable on males), higher selection intensities can be achieved in males.

Next, measurement could be restricted to a nucleus or to a small group of herds to become a nucleus. The number of animals that are performance recorded should be at least equal to the size of a potential breeding nucleus, i.e. several hundred breeding females. Recording a larger part of the population has some advantages like:

- 1) making producers more aware of productivity and therefore more interested in genetic improvement;
- 2) monitoring the actual progress in the commercial population;
- 3) some additional (about ten percent) possibility for genetic improvement by making use of superior commercial animals as nucleus breeding animals.

Progeny testing should be considered if AI is relatively easy to apply. Only the use of AI can guarantee sufficient use of a breeding bull in the commercial population to justify the investment in a progeny test. AI also helps to create progeny of one sire at a number of locations.

Which traits?

The traits to be measured are determined by the breeding objective. Preferably, breeding objective traits should be measured. Other traits could be measured additionally when it is difficult to obtain high accuracy for breeding objective traits. This is the case when BO traits have low heritability or when they are measured later in life. Measuring additional traits to include as selection criteria is only useful when they are highly heritable and have a high correlation with the breeding objective. Other traits could also be measured instead on BO traits when they are much easier (and cheaper) to measure. Decisions on whether a trait should be measured or not can be made in the selection index context. The evaluation criteria are increased accuracy (of estimating total genetic merit) and expected response per generation. For some examples and further information, we refer here to the Guidelines on Breeding Objectives and Trait Measurement.

Breeding cooperatives should design and plan a measurement strategy. A coordinating office to design and manage performance and pedigree recording systems needs to be established. Private breeding organizations could set up such recording systems themselves. They either record within

their own nucleus or they need to seek cooperation with farmers to organize their trait recording. In a cooperative system, it might be easier to gain farmers' cooperation in recording and later in distribution of breeding stock. However, decisions in the selection need to be to the point and rigorous, which is often easier achieved in private breeding organizations.

**Use of
reproductive
techniques**

Artificial insemination mainly creates faster dissemination of genetic superiority to the commercial population. The effect on the rate of genetic improvement is mainly:

- more selection intensity on the male side;
- more accurate estimation of breeding value across herds;
- more accurate selection of males, based on progeny tests.

Use of reproductive techniques on the female side are generally more expensive and logistically more difficult to achieve. Increasing reproductive rate, e.g. by multiple ovulation and embryo transfer, is useful for species with low reproductive rates, such as cattle and sheep. Using MOET, the number of calves of breeding cows could increase from one to around ten per year. The benefits are:

- more selection intensity on the female side;
- more accurate estimation of breeding value, as family sizes are larger and animals will have more information on sibs. A possible result is that animals can have an estimated breeding value with a reasonable accuracy earlier, therefore making it easier to select young animals as a nucleus parent. This could typically decrease generation interval, with relatively less decrease in selection accuracy. A potential danger is an increased rate of inbreeding. With high reproductive capacity in males and females, it is advisable to apply selection rules that not only increase merit, but also restrict average co-ancestry of selected individuals.

The logistic challenge with MOET is that at the time of embryo transfer, a group of recipient cows needs to be available and synchronised. In a centralised nucleus, the application of MOET is well feasible under many circumstances, as all activities can take place at one location.

If technically and logistically, reproductive techniques as AI and MOET are achievable, then their application is generally cost-effective as increased genetic improvement can be passed on to many individuals in the population.

Genetic evaluation

Performance records jointly with pedigree records form the basic input for a BLUP breeding value estimation procedure. BLUP breeding values ensure a fair comparison of potential breeding animals across herds and age classes. BLUP requires pedigree recording and genetic links between herds and years. If the conditions for such genetic evaluations cannot be

met, phenotypic selection within herds is an alternative. This is considerably less efficient than BLUP selection but for high heritable traits it may be a good and cheap alternative to BLUP.

The investment in genetic evaluation consists of a central office where all recorded information is stored in a central database. Genetic evaluation software is relatively easily available but for specific applications, some customisation might be needed (see further Guidelines on Genetic Evaluation). The quality of the EBVs can be partly evaluated based on computed accuracies. However, accuracies do not reflect biases and lack of links between different herds, years or locations.

Regular ‘quality control checks’ can evaluate the quality of the genetic evaluation system. An important quality control is a check on changes of sequential EBVs on the same animal over time. The change of an animal’s EBV in subsequent evaluations (years) depends on its accuracy and the additional information used. The largest concern should be a consistent change in EBV over time, when more data appear. Consistent and directional changes may indicate bias in genetic evaluation. For example, animals that are preferentially treated will have high EBVs initially, but as information on progeny emerges the EBV will decrease.

The process of selection of breeding animals based on their estimated breeding value and determining their matings, is indicated as mate selection. The selection part refers to the creation of selection differential (difference between selected animals and their contemporary group). Basically, as few animals as possible should be selected for breeding purposes, with the only restriction being the number of animals required for a minimum population size and the number needed for reproductive purposes. Minimising co-ancestry among selected individuals can more formally optimise the minimum population size and restrict inbreeding. Mate allocation can also prevent short-term inbreeding and to some extent, long-term inbreeding. Mate allocation can be particularly useful at the commercial level, by matching AI sires to individual cows for the purpose of avoiding birth problems. In general, traits that have an optimum value are candidates to apply corrective mating to. Also, combinations of traits can lead to ‘profit heterosis’ (see example).

Mate Selection

Example of 'profit heterosis' in mate selection

An example here is protein yield per lactation viewed as the product of yield and percentage of protein. In the example below, the latter two traits are assumed to have fully additive inheritance, but corrective mating would slightly increase total yield.

Example: Population mean 3 000 3%

Bull A, Cow A +300, -.2%

Bull B, Cow B -200, +.3%

AxA gives +92.4 AxB gives +93.0

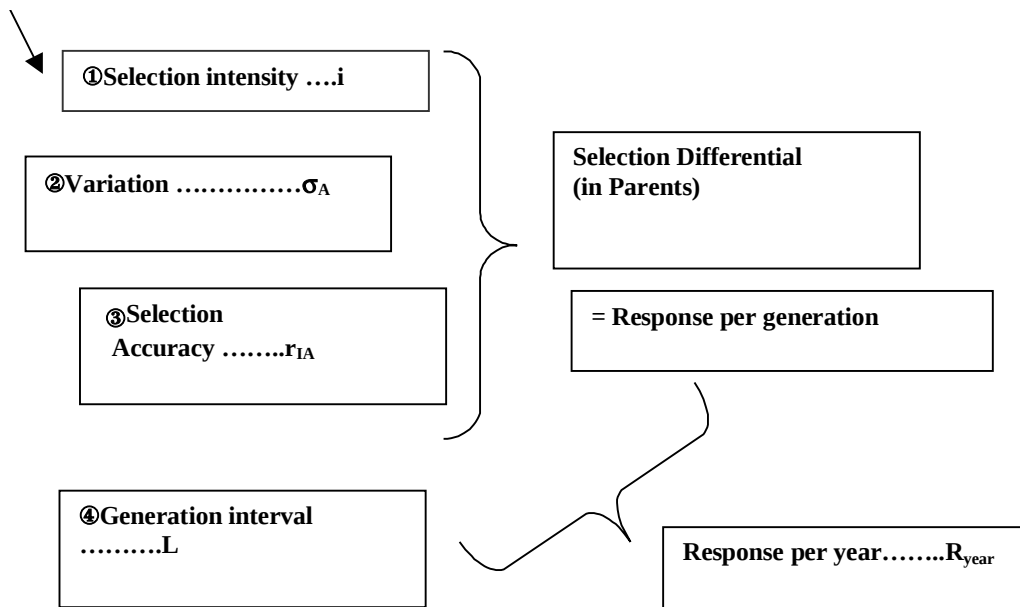
BxB gives +92.4

The amount of genetic improvement that can be made depends on four key factors:

- Variation
The best animals will stand out more if there is more variation in the trait measured, i.e. they will be relatively more above the mean.
- Selection Intensity
The selection intensity is the superiority of a selected group (in standard normal units). The larger the proportion selected the larger selection intensity. We may expect that the average of the very best animals (say top five percent) to be higher (on average) than the average of, for example, the best 50 percent.
- Accuracy of selection
The better we are able to assess true genetic merit of animals, the more of what we see as 'good' in the selected parents will be passed on to the next generation.
- Generation interval
The longer it takes for good animals to drop their progeny, the less progress can be made on an annual basis.

Annex 1. Basic elements of genetic improvement

Proportion selected



1.1. Selection accuracy

All of the differences between animals at the phenotypic level will not be passed on to their progeny, as it is not all due to their genes.

The estimated breeding value (EBV) gives the part of observed differences that we believe is due to additive genetic effects.

Half of the EBV of each animal will be passed on to progeny as an animal gives only 50 percent of its genes.

In the process of genetic evaluation, genetic parameters are needed such as heritability for each of the traits and genetic and phenotypic correlations between the traits. Genetic parameters together with the amount of information on an animal determine accuracy of EBV and therefore accuracy of selection.

The accuracy of selection tells us how sure we know that a particular good animal has also a good breeding value. With no information, the accuracy of an EBV is zero and with full information it is one. As most traits have heritability considerably lower than one, there is always error in estimating a breeding value from phenotypic observations. Only a progeny test based on a large number of progeny can give an almost perfect accurate EBV.

The accuracy of selection depends on the heritability of the trait selected. It is equal to h ($=\sqrt{h^2}$) if selection is based on individual phenotypic performance only.

Furthermore, if information from parents, sibs or progeny is used, the accuracy will increase, the more so for traits with low heritability. Therefore, if family information is used, it becomes less important whether a trait has low heritability or not.

Using family information is more effective when heritabilities are low. Data from tropical countries tend to show low to moderate heritabilities, suggesting that using information from relatives would be more useful. The expected increase in accuracy may be up to 50 percent for low heritable traits.

The accuracy of an EBV based on relatives' information can be calculated from the selection index theory. In routine genetic evaluations with BLUP, it is calculated (or approximated) from the mixed model equations. For a progeny test there is a simple formula to approximate accuracy:

$$\text{The accuracy of the progeny test is } = \sqrt{\frac{n}{n + a}}$$

This simple formula allows the quick determination of the accuracy, for a given progeny test based on n progeny, for a trait with heritability h^2 (where

$a = (4-h^2)/h^2$). Notice that n refers to the *effective number of progeny*. In a badly designed progeny test where progeny of the same sire are often compared with each other in the same management group, the effective number of progeny is lower than the actual number of progeny.

For an individual record: $n_{\text{effective}} = 1-(1/N)$ where N is the number of individuals in the contemporary group.

For n progeny of a sire : $n_{\text{effective}} = n_{\text{sire}}-(n_{\text{sire}}/N)$ where N is the total in a contemporary group.

The formula for the effective number of records shows that the information content of a record reduces to zero if there are no other animals (or progeny from other sires) to be compared to the same contemporary group.

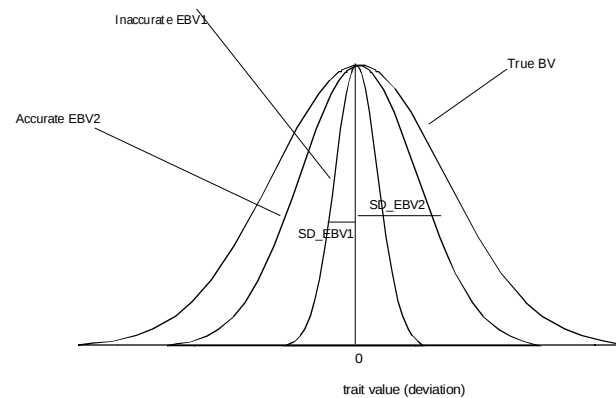
Selection based on repeated records on the same animal increases accuracy, because the ‘heritability’ of a mean of repeated records is higher than that of single records, the more so if repeatability is low.

Some examples of accuracy		
<u>Information used</u>	<u>$h^2 = 0.10$</u>	<u>$h^2 = 0.30$</u>
1) Own information only	0.32	0.55
2) Mean of 5 full sibs	0.32	0.48
3) Mean of 10 half sibs	0.23	0.33
4) 1 + 2 + 3	0.43	0.65
5) Mean of 1 000 half sibs	0.49	0.50
6) Mean of 1 000 full sibs	0.70	0.71
7) Mean of 5 progeny	0.34	0.54
8) Mean of 10 progeny	0.45	0.67
9) Mean of 100 progeny	0.85	0.94
10) Mean of 2 repeated measurements		
Repeatability = 50%	0.37	0.63
Repeatability = 80%	0.33	0.58
11) Mean of 3 repeated measurements		
Repeatability = 50%	0.39	0.67
Repeatability = 80%	0.34	0.59

Estimated breeding value will be more spread out if they are more accurate.

The spread in EBVs (more formally: the standard deviation of EBVs) is determined by genetic variation and accuracy of breeding estimation. The more information used for estimating breeding values, the higher accuracy of EBVs, the more they are spread out.

In the extreme case where there is no information on animals, there will be no distinction: all EBVs would be at the value zero (i.e. no spread). With more information or higher heritability, the spread in EBVs will be closer to the spread in true breeding value. Therefore,



The standard deviation of Estimated Breeding Values is equal to the accuracy (of EBV) times the genetic standard deviation (SD(A)).

$$SD(EBV) = r_{IA} \cdot SD(A)$$

1.2 Selection intensity

The animals that we select as breeding animals have to be above average. This superiority of selected parents is often indicated by the term *selection differential*.

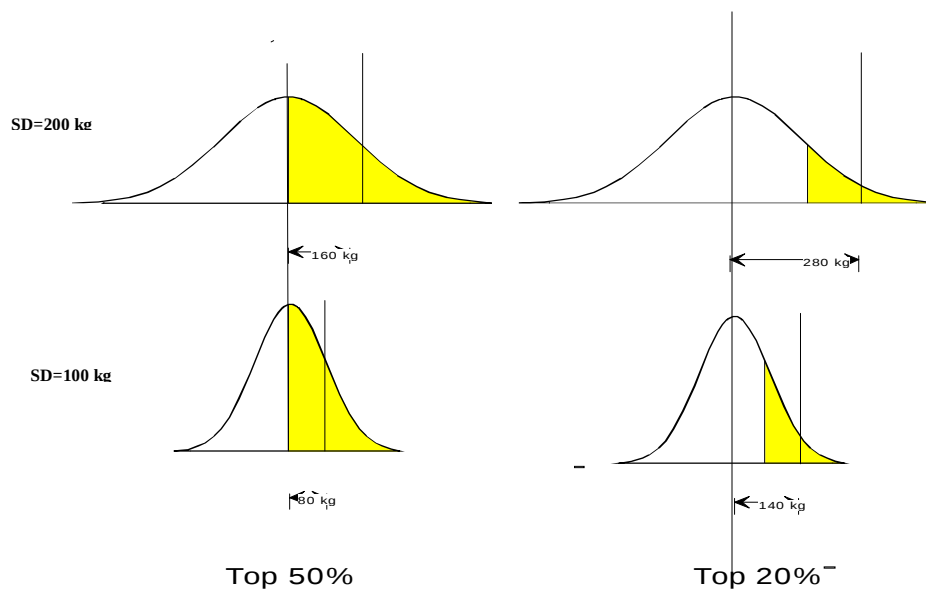
Selection differential is easy to measure for a given group of animals: it is the difference between average of the selected group and the average of the group they were selected from. Even if animals have not yet been measured, the superiority of selected parents can be predicted from the intensity of selection and variation of the selection criterion. The following illustrates this. The normal curve indicates how a population of animals is distributed for a certain trait-value. Selection differentials are indicated as the difference between the average of the selected animals (shaded area) and the average of all. The smaller the fraction of animals selected, the

larger the selection intensity. Also, the more variation in the selection criterion (e.g. EBV!), the larger the superiority of the selected group.

Selection intensity is inversely related to the proportion selected.

The proportion selected is

- The number of animals selected as parents
- The number of animals considered for selection



Selection Intensity i is the number of standard deviation units that selected parents are superior to the mean. It allows us to predict the performance of a selected group of parents.

The relationship between proportion selected and selection intensity is

- Note the trend, fewer selected -----> more intensity
- Use Tables or sub-routines to find i given p (Falconer and MacKay, 1996)
- Selection intensities for males are mostly different from those of females. Due to their higher reproductive rate, less males are needed in breeding and males therefore usually have higher selection intensity.
- When the population selected from is small, selection intensities are slightly reduced. For example, the best out of ten will not be as good, on average, as the best ten percent of 1 000. The selection intensities are 1.75 and 1.52, respectively. There are special Tables (in Falconer & MacKay, 1996) or sub-routines used for small populations. Corrections become reasonably substantial if the population to select from is smaller than about 25.

Proportion Selected p	Selection Intensity i
0.001	3.4
0.005	2.9
0.01	2.7
0.05	2.1
0.10	1.8
0.25	1.3
0.50	0.8
0.75	0.4
0.95	0.1

The superiority of selected parents is often indicated by the term *selection differential*.

Selection differential = selection intensity * SD (selection criterion)

If selection is on phenotype, we can use the phenotypic SD and predict the phenotypic superiority of the selected group.

If selection is on estimated breeding value we can predict the superiority of the selected group in genetic value. Half of this will be passed on to offspring.

Selection differential = selection intensity * SD (EBV)

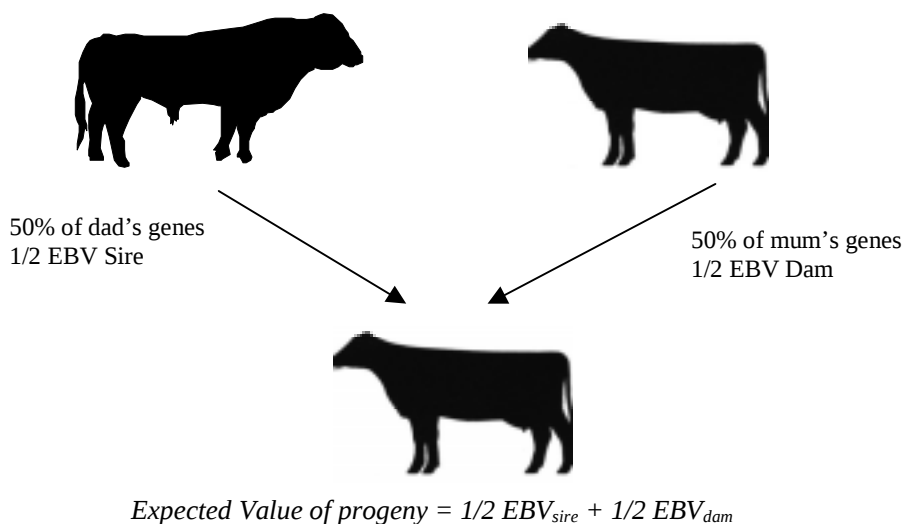
= selection intensity * selection accuracy * SD(true breeding values)

Wool production in sheep. Population mean 2 Kg ,
SD = 0.5 Kg

In a closed flock of 100 ewes, 100 lambs may be born annually and 60 percent can make it to reproductive age. Therefore, we have 30 young males and 30 young females that could be maintained in the flock as breeding animals. The 30 young females may be all needed for replacement of ewes. This makes the proportion of females selected equal to 100 percent and selection intensity for females equal to zero.

We may want to select four out of the young males as breeding rams. The proportion selected would be $4/30 = 13$ percent and the selection intensity for males is 1.63. If the males could be selected based on their wool yield at one year of age, we expect the average of the selected males to be $2 + 1.63 \times 0.5 = 2.8$ kg

The expected genetic value of the next generation is equal to the average EBV of selected parents. More accurate EBV as well as higher selection intensity will have a direct effect on genetic improvement.



1.3 Generation interval

- Generation intervals should be short.

For an efficient genetic improvement programme, the rate of genetic change *per year* is important. Hence, we are more interested in the genetic improvement we can make on an annual basis. In planning a selection programme, account has to be made for how quickly we can ‘turn over’ a generation. We use the concept of *generation interval*. This is the average age of the parents at the birth of their progeny. The longer it takes before the selected parents drop their progeny, the slower the response per year. The response per year is simply the response per generation, divided by the generation interval.

The generation interval is determined by the age of the parents. As we keep breeding animals longer in the herd, the longer the generation interval, the less genetic improvement per year.

Generation intervals usually differ between males and females. Since less males are needed as females, males can be replaced earlier, so there is more potential to have short generation intervals on the male side. Most young females usually need to be retained as replacements, as female reproductive rates are usually low (at least for sheep and cattle). This leads not only to low selection intensity on the female side, but also to long generation intervals, as females are kept for the length of their productive life.

Notice in the following that generation intervals of both males and females are important. Even if females are not selected, their generation interval contributes to the annual rate of genetic improvement.

1.4 Prediction of the annual rate of genetic improvement (R_{yr})

$$R_{yr} = \frac{i_m * r_{TI-m} + i_f * r_{TI-f}}{L_m + L_f} * \sigma_A$$

with: Intensity of selection = i

Accuracy of selection (accuracy of EBV) = r_{TI}

Genetic Standard Deviation = σ_A

The generation interval = L

Note that males and females (can) have different selection intensity, a different accuracy of breeding value and a different generation interval.

Example. Selection for fleece weight in sheep: prediction of rate of genetic change.

Herd and age structure:

Consider a 100 ewe flock. There is one breeding cycle per year and the weaning rate for females is 80 percent. Each year, 24 new replacement females are added to the flock. The ewes remain a maximum of six breeding seasons around (until the age of seven years). Due to some culling and mortality (about 15 percent per year), the number of ewes per age class decreases with increase in age.

The number of ewes joined per ram is 25. Rams are kept for one breeding season.

- Age structure

<u>Age at drop of progeny:</u>	2	3	4	5	6	7	<u>TOTAL</u>
No. of Rams:	4	-	-	-	-	-	4
No. of Ewes:	24	21	17	15	13	10	100

- Generation intervals

Males: L_m = two years = average age of rams 'dropping' progeny.

Females: $L_f = \frac{24 * 2 + 21 * 3 + 17 * 4 + 15 * 5 + 13 * 6 + 10 * 7}{100} = 4.2 \text{ years}$

- Selection intensities

100 ewes give $0.8 \times 100 = 80$ progeny, 40 male and 40 female.

Males: Proportion selected: four young rams selected out of 40 available = $4/40 = 0.10$

giving $i_m = 1.786$ = male selection intensity

Females: Proportion selected = $24/40 = 0.60$ giving

$i_f = 0.644$ = female selection intensity

- Selection accuracy

Assume selection is based on own performance

Heritability (h^2) = 0.30

Phenotypic standard deviation = 0.4 kg

Genetic standard deviation (σ_A) = $\sqrt{(0.30) * 0.4} = 0.22 \text{ kg}$

Accuracy of selection (r_{TI}) based on own performance = $\sqrt{(h^2)} = \sqrt{(0.30)} = 0.547$

- Response

$$R_{yr} = \frac{i_m * r_{TI-m} + i_f * r_{TI-f}}{L_m + L_f} * \sigma_A = \frac{1.786 * 0.547 + 0.644 * 0.547}{2 + 4.2} * 0.22 = 0.047 \text{ kg}$$

$R_{year} = 0.047 \text{ kg}$ increase in fleece weight predicted per year.

Alternative: Keep one ram for two matings: This decreases selected proportion to $3/40$; i_m is increased to 1.887 and generation interval in males (L_m) is increased to 2.25. Response = 0.050 kg

**1.5 Genetic merit
in the 4-pathways
structure**

A numerical example will give some more idea of a 4-pathway breeding structure, with dairy as an example. Notice that reproductive rates of males and females are important variables in designing such a structure.

Selection Intensities

Assume a commercial dairy cow population of one million animals. Assuming an average herd life of a dairy cow of four lactations implies that 25 percent of the cows needs to be replaced annually. With a female reproductive rate of one calf per year, this implies that at least 50 percent of all new-born females need to be kept as herd replacements. Allowing some loss in the rearing period (including birth), this number may be taken a bit higher, e.g. 70 percent. Hence, for the DD selection path, we need at least 70 percent of the commercial cows to breed their replacements and selection intensity cannot be very high.

To inseminate one million cows, we need about 50 breeding bulls (a rough figure, also given that there is usually quite a large variation in number of inseminations per breeding bull. In order to produce so many breeding bulls, we might want to test about 500 young bulls. This gives a selected proportion in the SD path of ten percent. This number is somewhat arbitrary. It can be optimised depending on expected gain (more selection intensity if more tested) and cost of testing.

The 500 young bulls have to be generated by test matings. We need at least 1 000 births, but allowing for some deaths and early culling of young males, we plan 2 000 elite matings. Hence we need to select 2 000 elite cows. This gives extremely high selection intensity in the DS path, as there is a very large cow population available. Suppose that 30 percent of the cows is found suitable as elite dam based on reasons other than milk productivity (e.g. type traits, legs, udder, mastitis history, etc), then effectively 2 000 out of 300 000 could be selected based on milk production criteria (=0.7 percent). We could all do 2 000 elite matings with one top breeding bull. However, this would quickly give too much inbreeding. A number of five sires selected for elite matings may be suitable. The selected proportion for the SS path then becomes $5/500 =$ one percent.

Selection accuracies

Selection of males is based on a progeny test. The number of progeny tested per young bull depends on the total number of bulls tested and the number of cows made available for test matings. Let 20 percent of the population be used for test matings, i.e. 200 000 cows. This gives 400 progeny born per sire but with some loss, only 100 of those will be cows completing a first lactation. We obtain therefore selection accuracies of males of 0.87 (based on tests of 100 progeny with heritability equal to 0.25) and females of 0.50 (based on own performance). The last figure is an average, as some cows have more known lactation records at the time of selection than others.

Generation intervals

The average generation interval for cows to breed cows is assumed to be 4.5 years. We assume the same is true for elite cows. Bulls are selected after a progeny test and their average age will be 6.5 years when their progeny have produced the first milk lactation record.

The following Table can be constructed:

Table 1.2. Genetic contribution and its components for each of the four selection paths in a dairy cattle breeding programme.

Selection path	Selected proportion	Selection intensity	Generation Interval	Selection accuracy	% contribution to genetic gain
SS	5 / 500	2.65	6.5	0.87	45
DS	2 000 / 300 000	2.79	4.5	0.50	24
SD	50 / 500	1.76	6.5	0.87	27
DD	70%	0.47	4.5	0.50	5

The formula for genetic gain in a 4-pathway breeding structure is an extension of the earlier version for 2-pathways (with sBO being the SD of the breeding objective, i.e. genetic standard deviation). This formula is known as the formula of Rendel and Robertson (1950).

$$\begin{aligned}
 \delta G_{\text{year}} &= \frac{\sum_{i=1}^{\text{nr_of_paths}} \text{intensity} * \text{accuracy} * \sigma_{\text{BO}}}{\sum_{i=1}^{\text{nr_of_paths}} \text{generation_interval}} \\
 &= \frac{(i_{\text{SS}} \cdot r_{\text{SS}} + i_{\text{DS}} \cdot r_{\text{DS}} + i_{\text{SD}} \cdot r_{\text{SD}} + i_{\text{DD}} \cdot r_{\text{DD}}) * \sigma_{\text{BO}}}{L_{\text{SS}} + L_{\text{DS}} + L_{\text{SD}} + L_{\text{DD}}} \\
 &= \frac{(2.65 * 0.87 + 2.79 * 0.5 + 1.76 * 0.87 + 0.47 * 0.5) * \sigma_{\text{BO}}}{6.5 + 4.5 + 6.5 + 4.5} = 0.235 \sigma_{\text{BO}}
 \end{aligned}$$

Hence, we may expect an annual genetic improvement equal to about one quarter of a genetic standard deviation (σ_{BO}). This is equal to about 1.24 percent of the mean (given that $\sigma_{\text{BO}} = h * \sigma_p$, $h^2 = 0.25$ and σ_p (phenotypic standard deviation) is ten percent of the mean).

Notice that each part contributes to the sum of generation intervals over paths. Hence, even if we would not select cows for producing within herd replacements, they would still contribute to the sum of the generation intervals. The reason is that genes have to pass through this pathway in order to end up in commercial cows. If we would only keep calves from

older cows, it would take longer before improved genetics flow on to future generations, whether we select these cows or not. The contribution of each pathway to the total genetic gain can be calculated by multiplying selection intensity and selection accuracy in each pathway (Table 1.2).

The numerical example used here contains many simplifications. For example, in order to test 500 young bulls and aiming at about 100 progeny records for each of them, we need to inseminate at least 200 000 cows with semen from unselected test bulls. This is 20 percent of the cow population being inseminated by untested young bulls rather than selected proven bulls. Calling test inseminations a fifth ‘selection path’ (YB for young bulls) we can adapt the formula (assuming tested young bulls are unselected males from elite matings and having a generation interval of 3.5 years

$$= \frac{(i_{SS} \cdot r_{SS} + i_{DS} \cdot r_{DS} + 0.80(i_{SD} \cdot r_{SD}) + 0.20(i_{YB} \cdot r_{YB}) + i_{DD} \cdot r_{DD}) \cdot \sigma_{BO}}{L_{SS} + L_{DS} + 0.80L_{SD} + 0.20L_{YB} + L_{DD}}$$

$$= \frac{(2.65 \cdot 0.87 + 2.79 \cdot 0.5 + 0.80 \cdot (1.76 \cdot 0.87) + 0.20 \cdot (0) + 0.47 \cdot 0.5) \cdot \sigma_{BO}}{6.5 + 4.5 + 0.80 \cdot 6.5 + 0.20 \cdot 3.5 + 4.5} = 0.241\sigma_{BO}$$

hence, the correction for the use of some unselected test bulls has only a small effect on the annual gain. In fact, the gain is somewhat increased. Apparently, the loss from using some unselected young bulls on part of the population selection is partly recovered by the reduction of the generation interval. It should be noted that although they are not progeny tested and therefore unselected, young bulls are on average better than the generation from which the proven bulls are selected from as they descend from a younger generation of elite parents. Young bulls could therefore be quite competitive to proven bulls. However, there is some more risk involved in using them, as the EBVs are not known very accurately.

1.6 Realised and expected response

The example in this Chapter has shown that even for a more complicated breeding programme, such as the 4-pathway-structure in dairy, the response can be predicted relatively simply. The predicted response as worked out in the example is a reasonable prediction of the genetic improvement that could be achieved in a breeding programme. The realised response, however, is generally lower. Realised response predicted for dairy breeding programmes such as in this example were around 0.7 percent to one percent of the mean, about 30 percent lower than predicted here. The main reasons why realised responses are lower than expected are:

- there is some variation in the outcome of the breeding programme as it is the result of many random processes;
- the model to predict response is a bit simplified and contains some errors;
- the actual selection policies are sub-optimal.

Variation in response

At the level of an individual and considering inheritance at one locus, we know that the inheritance process is stochastic: one could inherit either the good allele or the bad allele from a heterozygous parent. Similarly, for quantitative traits, there is genetic variation within families as full sibs have not all the same genotype. On top of genotype, the environment and other random effects create additional unpredictable variation in the observed phenotype. Hence, we may expect a certain outcome of a breeding process, but there will be some variation around this outcome. Breeders or breeding organizations all do their best in generating good bulls, but breeding the number one bull is partly a matter of chance. Obviously, the occurrence of occasional topper in a breeding programme will have an impact on overall genetic improvement. The dairy bull ‘Sunny Boy’, bred in The Netherlands in the late eighties, managed to have over one million offspring worldwide!

The outcome of the whole breeding programme varies less if the breeding population is larger, since the effect on individuals will become smaller. Hence, the population size is a relevant parameter to determine variation in response. Population size depends on the number of males and females effectively used in the population, which is also used to predict inbreeding. In the example described here, it is mostly the number of sires that determines effective population size. A breeding programme using sufficient sires will have higher effective population size, leading to less inbreeding, but, also less variation in response. Hence, a breeding programme design that avoids inbreeding will also be less prone to risk. Note that it is not only the number of sires and dams used, but also the extent to which they are used that is important. In most dairy breeding programmes similar to the example, a number of 50 breeding bulls is not unrealistic, leading to about 20 000 inseminations from each bull. However, the very best bulls which are used may have close to a 100 000 progeny, while the worst may have not more than a few thousand.

Simplifications and errors in the prediction formula

Predicting genetic response in a breeding programme is based on a whole lot of assumptions concerning biological and genetic models. Biological parameters are related to mortality and culling due to disease or infertility, average productive life, etc. The genetic model is based on a very large (‘infinite’) number of loci. Although it is unlikely that this genetic model is realistic, it most probably produces reasonably accurate prediction of selection, even if there are some loci with larger effect. Possible interactions between environment and genotype could be important for certain specific cases, but are less likely for bulls that are both tested and used over a larger range of environments (herds) and regions.

The number of offspring of each breeding animal is assumed equal, but in reality, the best bulls will have more offspring and they will also have more offspring tested. Furthermore, the prediction formula does not

account for some loss of variation due to selection nor does it take into account effects of inbreeding. Selection candidates are also assumed to be unrelated, but in reality, they may be half or full sibs, therefore decreasing somewhat the selection intensity. On the other hand, selection of bulls can be optimised over age classes, as an occasional good bull may be used for elite matings for a number of years and this somewhat increases the realised gains.

Errors may be the result of using incorrect heritability or genetic correlations in breeding value estimation and there may be registration errors in recording of performance or pedigree. An estimate for the degree of pedigree errors has been as high as ten percent in some countries. Furthermore, EBVs could be biased due to preferential treatments or due to unequal variances in different herds. A common problem in dairy cattle breeding is that progeny tests from young bulls turn out to be lower than expected based on the parental average. It is mostly the dam's EBV that is expected to be biased and over-predicted. This is partly due to the fact that dams EBVs are less accurate, as they have no progeny test and partly due to preferential treatment, as farmers may want to pamper their best cows in order to get a lucrative bull dam contract. Another possible explanation could be that the genetic evaluation system might be somewhat sub-optimal in the extremities. As only a very small fraction of cows is selected as bull dam, those animals can deviate several standard deviations from the mean. It is not unreasonable to assume that in the extremes, somewhat more of the differences may be due to extreme environment, giving over-predicted EBVs. Dairy breeders tend not to fully rely on EBVs of commercially tested bull dams. This is also one of the reasons why some dairy breeding organizations have moved to central test herds for elite cows, with the idea of obtaining less biased bull dam EBVs.

Some of the simplifications used in the prediction of rate of genetic change could be avoided with more complicated modelling, as has been done in a number of studies. Overall, simplifications and errors may over-estimate the realised genetic response up to 20 percent and is therefore not the only reason for the discrepancy between realised and predicted response. Furthermore, the simple formula gives a reasonable approximation for ranking of alternative breeding programmes. For example, the change of response with a smaller number of young bulls tested, or smaller number of test progeny per young bull can be easily assessed. The prediction of genetic change may be optimistic, but the ranking of a different breeding programme is likely to be more robust toward the assumptions made.

The rate of inbreeding in a population depends on effective population size. In practice, a sufficient number of males should be used in each generation.

Inbreeding occurs more frequently in small populations. The reason is that in a small population there is a large chance for an individual to mate with a related individual. Inbreeding therefore depends on population size. If males have a lot more offspring than females, we only need a few males to breed the next generation. So, even if the actual population is reasonably large, there can be a high chance of mating a relative if only a very few males were sires of a current generation. Therefore, population size is measured by how many parents are used *in each of the sexes*. Inbreeding depends on *effective population size* rather than actual population size.

Effective population size is equal to true population size if an equal number of males and females are used for reproduction in equal amounts. However, the number of males used is much smaller and in that case, the effective population size is mainly determined by the number of males used.

$$\text{Effective population size: } N_e = \frac{4N_m N_f}{N_m + N_f}$$

where N_f and N_m are the number of males and females used as parents in each generation.

This formula gives much more weight to the lesser represented sex. Note that if $N_m = N_f$ then $N_e = N_m + N_f$ as you might expect.

Example:				
nr males per generation	2	2	5	20
nr females per generation	2	200	200	200
Effective Population Size (N_e)	4	7.9	19.5	72.7

The average inbreeding co-efficient at **generation t**:

$$F_t = 1 - \left[1 - \frac{1}{2N_e}\right]^t$$

and the relative increase of inbreeding in each generation, is *the Rate of Inbreeding*:

$$\Delta F = \frac{1}{2N_e}$$

Annex 2. Limiting the rate of inbreeding

Note that it is assumed here that all males are unrelated to each other. If the males used in a nucleus population (or village herd) are related to each other, effectively the population size is smaller. Software exists to optimise the number of males selected, given the genetic relationships of the selection candidates.

Annex 3. Best linear unbiased prediction

BLUP is used to give EBVs for commercially important traits. It has the same capabilities as the selection index, plus a lot more. Whereas the selection index uses information from defined sources (e.g. fleece weight on self, fibre diameter on self, fleece weight on sibs), BLUP uses all available information.

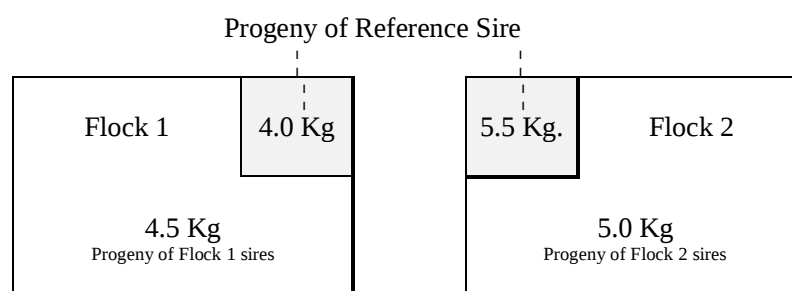
1. BLUP makes full use of information from all relatives.

BLUP does not have to give separate attention to sib testing, progeny testing, own performance, etc. Use of information from all relatives (even those long dead) is simultaneously handled. This gives more accurate EBVs and more selection response.

2. BLUP accounts for fixed environmental effects (management group, herd, season, year, etc).

This means that animals can be compared across groups, giving wider scope for selection. For example, comparing across age groups means that older animals have to prove their competitiveness at every round of selection.

As a different example, consider two flocks with mean fleece weights of 4.5 and 5.0 Kg. Is the second flock 0.5 Kg better **genetically**? This depends on the flock environmental conditions. Using a reference sire with random mate allocation helps:



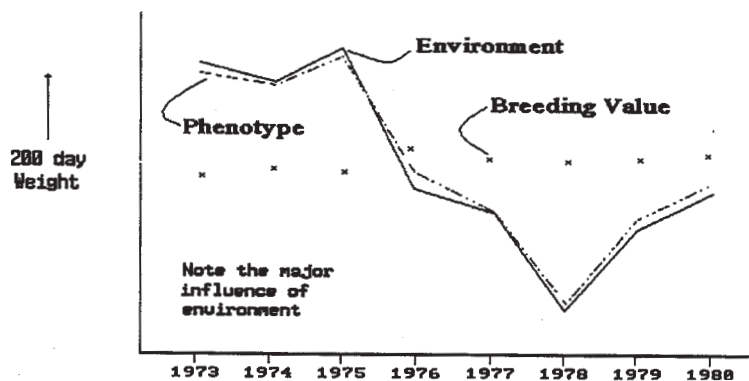
The reference sire is inferior in the 4.5 kg flock and superior in the 5.0 kg flock, so the 4.5 kg flock must be better genetically.

By How much? In Flock 1, the reference sire progeny is worse than Flock 1 sire progeny by 0.5 Kg. Assuming many progeny, the reference sire breeding value inferiority must be twice this, because of the diluting effect of ewe mates of equal merit. So the reference sire is 1 Kg genetically inferior to Flock 1 sires and by a similar argument, he must be 1 Kg genetically superior to Flock 2 sires. Thus, if the flock sires are representative of their flocks (or if they are equally selected) then Flock 1 is 2 Kg genetically superior to Flock 2. Given the observed average merit of the flocks, the Flock 1 environmental effect must be 2.5 Kg below that of Flock 2.

BLUP can both calculate and use this information automatically whenever there are such genetic linkages available, i.e. whenever relatives are spread across different groups.

3. BLUP gives genetic trends.

The approach used in the last example could be used to test the genetic differences between animals born in different years, instead of different flocks. This ability to compare the EBVs of animals born and measured in different years means that year mean EBVs can be calculated and genetic trends reported.



4. BLUP can handle unbalanced designs easily:

a selection index using sib information faces the problem that each candidate does not have the same number of sibs (n):

One solution is to construct an index for each number of sibs involved but if progeny information is available the same problem exists. BLUP handles this imbalance automatically by constructing a custom selection index for each animal. However, it only needs to report the EBVs and not the index weights.

5. BLUP can cater for non-random mating:

such that males can be compared via their progeny even if some had been allocated better mates. This can only be done where the mates were allocated on the basis of their recorded performance,

such that BLUP can account for their EBVs when evaluating the males concerned.

6. BLUP can account for selection bias:

e.g. consider ranking bulls on the first two lactations of their daughters. The worse bulls, who had worse daughters, will have benefited more from culling of daughters on first lactation performance.

7. BLUP relies on good genetic parameters:

as with the selection index, BLUP assumes that the estimates of genetic parameters it uses are valid (i.e. reasonably close to the truth) and that the genetic model we use is valid (e.g. that the variance due to sires is $\frac{1}{4}V_A$).

8. USING BLUP.

BLUP gives estimates of breeding value (EBVs or s) for the traits of interest. The breeder only needs to weigh these by economic weights to provide an index which s/he can select on:

$$\text{Index} = a_{11} + a_{22} + a_{33} + \dots$$

Annex 4. Optimising progeny testing across herds

Assume progeny testing of ten sires, each with ten progeny and the test capacity is in ten herds.

Comparing the efficiency of progeny testing (measured by accuracy of the EBV of the sire) of different strategies:

- one sire per herd;
- pairs of herds, each with two sires, with a sire five progeny in each of two herds;
- sires are used in two herds (five progeny/herd), but each time compared with another sire: sire one in one and two, sire two in two/three, etc.
- each sire one progeny in each herd.

In the following the 'design' matrix represents the number of progeny of each sire (rows) in each herd (columns)

10	0	0	0	0	0	0	0	0	0
0	10	0	0	0	0	0	0	0	0
0	0	10	0	0	0	0	0	0	0
0	0	0	10	0	0	0	0	0	0
0	0	0	0	10	0	0	0	0	0
0	0	0	0	0	10	0	0	0	0
0	0	0	0	0	0	10	0	0	0
0	0	0	0	0	0	0	10	0	0
0	0	0	0	0	0	0	0	10	0
0	0	0	0	0	0	0	0	0	10

Sires are used in one herd only and in none of the herds can we compare progeny of two sires.

Accuracy of each bull = 0.00

5	5	0	0	0	0	0	0	0	0
5	5	0	0	0	0	0	0	0	0
0	0	5	5	0	0	0	0	0	0
0	0	5	5	0	0	0	0	0	0
0	0	0	0	5	5	0	0	0	0
0	0	0	0	5	5	0	0	0	0
0	0	0	0	0	0	5	5	0	0
0	0	0	0	0	0	5	5	0	0
0	0	0	0	0	0	0	0	5	5
0	0	0	0	0	0	0	0	5	5

Sires are compared pairwise, each pair in two herds only. There is some accuracy, but a lot less than possible.

Accuracy of each bull = 0.447

Note that bulls from different pairs cannot be compared. The average EBV of each pair will be zero. A bull has bad luck if he happens to be in a pair with a very good bull.

5	5	0	0	0	0	0	0	0	0
0	5	5	0	0	0	0	0	0	0
0	0	5	5	0	0	0	0	0	0
0	0	0	5	5	0	0	0	0	0
0	0	0	0	5	5	0	0	0	0
0	0	0	0	0	5	5	0	0	0
0	0	0	0	0	0	5	5	0	0
0	0	0	0	0	0	0	5	5	0
0	0	0	0	0	0	0	0	5	5
5	0	0	0	0	0	0	0	0	5

Bulls pairwise connected within a herd, but different pairs in each herd such that they are all connected. EBVs of bulls are now comparable across herds. However, still a loss in accuracy, as within a herd, each progeny of a bull is compared to progeny of only one other bull (and to other progeny of the same bull, which is not providing information about the bulls' EBV)

Accuracy of each bull = 0.475

1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1

Perfect distribution

Accuracy of each bull = 0.60

Note that the accuracy is smaller than $\text{SQRT}[n/(n+15)] = 0.63$ with 15 = alpha for $h^2 = 0.25$. This 'theoretical' accuracy would hold if bulls were compared to a very large number of other bulls.