Preface

The first version of the notes were written by John Gibson for a Nordic graduate course in Denmark in 1992. When Johan was asked to give a similar course in Denmark four years later, it was decided to combine the material into a joint set of lecture notes. From that point onwards, the (parts of the) notes have been used in several other courses. In recent years, Jack Dekkers has made a considerable contribution to the notes. Over time, the notes have changed which reflects the developments in the fields as well as feedback we have had in teaching animal breeding and genetics.

For the Chapter on Inbreeding, we have made use of material prepared by John Woolliams and Theo Meuwissen for an international course in 2000 in The Netherlands. We greatly acknowledge their contribution.

We would like to thank the students attending courses in which these or an earlier version of the notes were used for making teaching an enjoyable experience and for all their comments and suggestions towards improving these notes.

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Chapter 1

Introduction

(Based on Bijma and van Arendonk, 2004)

There are two fundamental questions faced by animal breeders. The first asks: “What is the best animal?” Is the best Labrador the one with show-winning conformation or the one with exceptional retrieving instinct? Is the best dairy cow the one that gives the most milk; the one with the best feet, legs and udder support; or the one that combines performance in these traits in some optimal way? These are matters of intense debate among breeders, and, in truth, no one has all the answers. The question is an important one, however, because the answers determine the desired direction of genetic change for breeding organisations and people keeping farm or companion animals. The second question asks, “How do you breed animals so that their descendants will be, if not “best”, at least better than today’s animals?” In other words, how can we genetically improve animal populations? This question involves genetic principles and animal breeding technology, and is the subject of this course.

1. What is the best animal

“Best” is a relative term. There is no best animal for all situations. The kind of animal that works best in one environment may be quite different from the best animal under another set of circumstances.

When we describe animals, we usually characterise them either in terms of appearance or performance or some combination of both. In any case, we talk about traits. A trait is any observable or measurable characteristic of an animal.

Some examples of observable traits –traits we would normally mention in describing the appearance of an animal- are coat colour, size, muscling, leg set, udder conformation, and so on. Some examples of measurable traits –traits we would likely refer to in describing how an animal has performed- are body weight, daily milk production, time to run a mile, etc. There are hundreds of traits of interest in domesticated animals. Note that in none of the examples of traits mentioned above is the appearance or performance of a particular animal described. An animal may be red and weigh 343 kilograms at 1 years of age, but red coat colour and 343 kg yearling weight are not the traits- the traits are simply coat colour and weaning weight. Red and 343 kg are the observed categories or measured levels of performance for the traits of coat colour and yearling weight. They are the phenotypes for these traits.

In animal breeding, we are mainly concerned with changing animal populations genetically. From a genetic point of view, therefore, we want to know not only the most desirable phenotypes, but the most desirable genotypes as well. That is because an animal’s genotype provides the genetic background for its phenotypes and it is the genetic material that is passed on from parents to its offspring. Summarised in an equation:

\[ P = G + E \]
where P represents an individual’s phenotype, G represents its genotype, and E represents the environmental effects - the effects that external (nongenetic) factors have on an animal’s performance\(^1\). In other words, its genotype and the environment it experiences determine an animal’s phenotype.

The word genotype is used in several ways. We can speak of an animal’s genotype in general, referring to all the genes and gene combinations that affect the array of traits of interest to us. An example used later on in this section involves a “tropically adapted” genotype. In this case, the genotype includes all the genes and gene combinations affecting heat resistance, parasite resistance, and other traits that make up tropical adaptation. This sense of the word genotype is generally implied in this chapter. We can also speak of an animal’s genotype for a particular trait, referring to just those genes and gene combinations that affect that trait (e.g., heat resistance). Or, as we will see later in this course, we can limit the definition of genotype even further in which case it refers to a particular gene only (e.g., an animal has genotype AA for the kappa-casein gene). In any case, the genotypes of our animals’ descendants are what we can change with breeding methods. Favourable changes in genotypes result in improved phenotypes.

To answer the question “What is the best animal?” we need to determine what traits are of primary importance and what genotypes are most desirable for those traits. Most breeders, if they have some experience, have an opinion about the key traits and better genotypes. A Thoroughbred breeder, for example, might describe the perfect animal as “…. fast, but with enough endurance and heart for the longer distances, and easily rated”. A pig breeder version might be “…. a healthy pig with a good growth and good carcass quality.” There are probably as many opinions of this sort as there are breeders and for the most part they are quite subjective. In order to develop a sense of the important traits and best genotypes in a more objective way it is important to understand the role of the genotype in the system of the farm. This means that the importance of traits will depend on the physical environment under which animals are kept, the management system as well as economic factors. If you think about it, it will become clear that a number of the components of the system will interact with each other. For example, the best preventive health program (management) depends on the kinds of pathogens in the area (physical environment) and the costs of vaccines, dewormers, etc. (economics). To determine which health program is the most cost-effective, you must have knowledge of alternative programs, local pathogens, and treatment costs and understand how treatment programs interact with these other factors to affect profitability. Similarly, the best genotype depends on the local environment, the management practises in use, and the costs of inputs and prices of animal products. To determine the best genotype, you must have knowledge of environmental, management, and economic components and understand how they interact with the genotype to affect profitability.

Knowledge of the function of the animal and the interactions between the genotype and other components of the system is necessary if we want to develop sensible goals for breeding programs, in other words, if we want to develop appropriate breeding objectives. Knowing, for

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\(^1\) This mathematical expression is oversimplified but it will do fine for the purposes of this discussion. Later on we will see that there might also be an interaction between the G and E.
example, that parasite resistance is critically important in tropical climates, breeding objectives in the Tropics emphasise traits such as tick count (a measure of tick resistance). In temperate regions, on the other hand, less emphasis is placed on parasite resistance and more emphasis is placed on other traits.

2. Population structure and breeding objective

In the process of determining the best animal, you might ask, “Best for whom?”. The answer to this question depends on the function of the animal, the structure of the population and the role of the “breeder” within that structure. Most populations can be thought of as having a pyramidal structure: a relatively small number of breeders at the top selling breeding stock to a larger number of multipliers who in turn sell animals to a great number of end users.

The pyramid suggests a flow of germ plasm – genetic material in the form of live animals, semen, or embryos – from the top down, the elite breeders producing the most advanced animals, breeders at the multiplier level replicating those animals, and end users benefiting from the genetic improvement occurring at the higher levels. Ideally, breeders at each level try to produce animals that will be in the greatest demand by their customers at the next level down, with the ultimate result that the best animal is the animal that is the most useful or profitable for the end user. End users can thus be defined as the individuals whose particular needs should form the basis for determining breeding objectives.

In food and fibre producing species (sheep, cattle, swine, and poultry), the end users are commercial producers. These are the persons whose primary products are commodities for public consumption. Commercial dairy farmers produce milk; commercial swine producers produce pork; commercial poultry farmers produce eggs, chicken and turkey. Commercial producers are in most cases not the end of the production chain; beyond them are the processors (dairy plant, slaughterhouses), the retailers and consumers. But the commercial producers are end users because their particular needs reflect the requirements of the entire production chain. They need animals that are physically and reproductively sound, healthy and perform efficiently in their environment. They also need animals that possess the product and performance characteristics required by the retailers and consumers. The importance of these latter characteristics should be reflected – when the market system functions well - in the prices paid to the commercial producers for their products. In the Western world, the interest of consumers in the system of production has increased over time. This increased awareness of consumers has resulted in an increased emphasis on health and welfare traits in the breeding objective of farm animals and reduced emphasis on primary production traits (e.g. amount of milk, growth rate and litter size).

The breeding industries for recreational and companion animal species (horses, dogs, cats, etc.) differ somewhat in structure from the livestock industries. The pyramid arrangement is still present, and markets for specialised types of animals exist, but seedstock/commercial divisions are usually less clear and the end users may not be breeders at all. Consider, for example, Labrador retrievers. The end users of Labs are hunters and pet owners. These persons may or may not choose to breed their animals, and the qualities that are important to them are those that contribute to retrieving ability, companionship, health, aesthetics, or some combination of these.

2 Person answering the question
traits. Among Labrador breeders there are elite breeders and multipliers, but the term commercial producers does not really fit here because no consumable commodity like meat, eggs or milk is being produced. The various horse industries provide similar examples. End users of horses range from owners of the most valuable racing animals to causal riders to those that keep miniature horses as pets.

3. How are animal populations improved?

The purpose of animal breeding is not to genetically improve individual animals- once an individual is conceived, it is too late to change the genotype of that animal- but to improve animal populations, to improve future generations of animals. To this task breeders bring two basic tools: selection and mating. Both involve decision-making. In selection, it is decided which individuals become parents, how many offspring they may produce, and how long they remain in the breeding population. In mating, it is decided which of the males we have selected will be bred to which of the females we have selected.

Selection

Selection is used to make long-term genetic change in animals. It is the process that determines which individuals become parents, how many offspring they may produce, and how long they remain in the breeding population. Most of us are familiar with the term natural selection. Natural selection is the great evolutionary force that fuels genetic change in all living organisms. We commonly think of natural selection as affecting wild animals and plants, but in fact it affects both the wild and domestic species. All animals with lethal genetic defects, for example, are naturally selected against- they never live to become parents. Natural selection cannot be ignored but the kind of selection of primary interest in animal breeding is artificial selection. The idea behind selection is simply this: to let individuals with the best sets of genes reproduce so that the next generation has, on average, more desirable genes than the current generation of animals. The animals with the best sets of genes are said to have the best breeding values. They are – from a genetic point of view- the individuals with the greatest value as parents. In selection, we try to choose those animals with the best breeding values: the animals that will contribute the best genes to the next generation. The result of successful selection is then to genetically improve future generations of a population by increasing over time the proportion of desirable genes.

To see how selection works, consider the simplest form of selection: phenotypic selection or mass selection. In this type of selection, the performance of the individual is the only information used in making selection decisions. No attention is paid to the pedigree of the animal or the performance of its sibs (brothers and sisters) or of any progeny it may have produced. For example, if you were using phenotypic selection for weaning weight to determine whether a particular ewe lamb was to be kept for breeding, you would base your decision strictly on her own weaning weight. In practise (meaning outside of scientific laboratories), phenotypic selection in its pure form is increasingly rare, but it makes a good example, as we will also see later on during this course.

Figure 1.1 depicts phenotypic selection for increased body size in mice. The largest mice in each generation are chosen to become parents of the next generation, and the result over time is an increase over time in average body size. The idea of using the phenotype for body size as the
selection criteria is based on the expectation that phenotype for size is a reasonable indicator of the genes affecting body size. It is the genes, after all, which are transmitted from parent to offspring. In other words, it is assumed that phenotype for body size in mice is somehow related to breeding value for body size. If that were not the case, phenotypic selection for this trait would be a waste of time. The relationship between phenotype and breeding value is therefore a very important one, and this relationship is reflected by the heritability. When heritability of a trait is high, phenotypes are generally good indicators of underlying breeding values, and phenotypic selection will be effective in changing the level of the trait. When heritability is low, phenotypes reveal little about breeding values, and phenotypic selection will be ineffective. Judging by the rapid increase in body size of the mice in Figure 1.1, body size must be quite heritable. Not all traits are as heritable. The heritability of fertility in mammals, for example, is generally quite low. Estimating the heritability of a trait involves statistical techniques to estimate the extent to which relatives resemble each other for the trait of interest, compared with unrelated animals. The actual methodology involved and a description of the methods is beyond the scope of this course.

Most animal breeders are unlikely to limit themselves to individual performance information alone in making selection decisions. They will use information on relatives as well. For example, when a dog breeder purchases an eight-week old puppy from another breeder, she probably does not base here choice on just the conformation and personality characteristics evident in such a young puppy. She wants to evaluate those same traits in the littermates, the dam and the sire. She might want to see a copy of the puppy’s extended pedigree to learn more about its ancestors. Similarly, when beef cattle breeders evaluate a sire to use via artificial insemination (A.I.) they look further than the sire’s own performance for growth rate. They want to know something about the growth performance of his progeny.

![Figure 1.1. Illustration of phenotypic selection for increased body size in mice](image)

The above examples illustrate that selection decisions are based on a combination of information. In this course we will outline how the different sources of information can be combined into a single prediction of the breeding value of the animal. The strength of the relationship between the true breeding value and its prediction is measured by the accuracy. When accuracy is high, predictions of breeding values will normally be good ones – they will closely reflect the
The traits mentioned so far in this chapter – such as weaning weight in sheep, body size in mice, fertility, conformation and personality in dogs, milk production in dairy cattle- have all been polygenic traits. Many genes affect polygenic traits, and no single gene is thought to have an overriding influence. The genetic variation in these traits is due to segregation at many loci. Until recently, we knew little about the specific genes affecting these traits – we just know there were lots of them. As long as we cannot identify specific genes, we have to rely on phenotypic performances, predictions of breeding value to characterise the genotypes of animals. There are good grounds for believing that there is a range in the size of effects of genes for any trait, from a few with large effect, down to a large number having very small effects. We will see in this course that the developments in molecular biology now make it feasible to identify individual genes that affect quantitative trait. Information on genetic markers linked to individual genes can be used in selection programmes to improve the accuracy of selection (so-called marker-assisted selection). Once an individual gene has been identified, its biochemical and physiological roles can be studied. The results of these studies will greatly increase our understanding of the nature of genetic variation in traits.

Most traits in animals are polygenic in nature. Some traits, however, are simply-inherited – they are affected by a single or only a few genes. A good example is the horned/pollled character in cattle of European origin (Pollled means naturally without horns). A single gene determines whether a cow is horned or polled. There are also a large number of single-gene disorders that are considered to be serious problems but do not prevent affected individuals from reproducing. Well known examples include the inherited eye disorder is dogs, the malignant hyperthermia syndrome (“halothane gene”) in pigs. Because only a few genes influence simply-inherited traits, selection for simply-inherited traits is different from selection for typical polygenic traits. With simply-inherited traits, we do not deal with breeding values and their predictions, or even with the concept of heritability. Rather, we are interested only in knowing whether an individual possesses the specific allele or alleles of interest, and we select animals based on that knowledge. If the disorder can be detected either by clinical examination or by DNA-testing prior to reproductive age, it is possible to select against the disorder effectively. The detection of the gene for malignant hyperthermia syndrome in pigs and the subsequent development of a DNA-test have greatly increased the opportunity for pig breeders to eliminate the disorder from the population. Malignant hyperthermia in pigs is an autosomal recessive disorder which means that it is not possible to discriminate between a phenotype of animals with two normal alleles (homozygous animals) and animals carrying one defect allele (heterozygous animals, so-called carriers). The power of the DNA-test lies in the fact that it facilitates the detection of carriers - animals that are heterozygous at the gene causing the genetic disorder- prior to reproductive age.

When we think of selection, we normally envision selection of individual animals within a breed. It is also possible to select between breeds. In setting-up a farm or breeding program, we need to choose a breed to work with. Between-breed selection provides a way of using breed differences to make very rapid genetic change. For many traits, breed differences can be very large. By taking advantage of such large differences, between-breed selection can produce genetic change much faster than the gradual change possible from selection within a breed. For example, the milk production of Black and White cattle in The Netherlands has increased enormously in the
1970’s – not through selection within the Dutch Friesian population, but through importation of semen from the more productive Holstein-Friesian in the United States and Canada.

**Mating**

Selection is the first of the two basic tools used by animal breeders to make genetic change. The second tool is mating. Mating is the process that determines which (selected) males are bred to which (selected) females. It is distinctly different from selection. In selection, you choose the group of animals you want to be parents; in mating, you match males and females from the selected group.

There are many different methods for mating animals, and each method can be defined by a set of mating rules: a mating system. There are three reasons for using mating systems: (1) to produce offspring with extreme breeding value, (2) to make use of complementarity, and (3) to obtain hybrid vigour. Extreme phenotypes can be obtained by mating parents with extreme breeding values (high*high and low*low). If an animal of intermediate size is desired, mating large animals to small animals is one way to produce it. The parental genotypes are quite different, and neither one is optimal, but the mating is complementary because the offspring is optimal. Mating a Charolais to an Angus is an example of crossbreeding; the mating of sires of one breed to dams of another. In crossbreeding often used to produce breed complementarity, and in fact, the Charolais x Angus mating is a complementary one. Charolais are large French cattle known for their fast growth and heavy muscling, Angus are smaller British cattle known for their maternal ability, and the crossbred offspring benefit for having both kinds of parents. Another reason for crossing these two breeds is to produce hybrid vigour or heterosis. Hybrid vigour is an increase in performance of crossbred or hybrid animals over that of the pure-breds. Hybrid vigour occurs to a greater or lesser degree in many traits, but it is most noticeable in traits like fertility and survivability.

4. **Multiple trait selection**

In this course, a lot of the discussion of selection and the examples used for illustration will be limited to single-trait selection, selection for just one trait. That is because single-trait selection provides a simple framework within which to learn the principles of animal breeding. But in the real world of animal breeding, selection for a single trait is rare. Breeders are typically interested in improving a number of traits. They practise multiple-trait selection. Dairy farmers select for traits related to milk production, health, reproduction, type and longevity.

Selection for one trait rarely affects just that one trait. Usually other traits are affected as well. Genetic change in a trait resulting from selection on another trait is termed correlated response to selection. Correlated response to selection is probably caused by a number of genetic mechanisms and results in so-called genetic correlation between traits.

Genetic correlations between traits and the correlated response to selection brought about by them can be beneficial. However, if we are unaware of or choose to ignore unfavourable genetic correlations, selection for one trait can lead to undesirable response in others. In cattle, for example, blind selection for growth rate leads to larger birth weights and more dystocia. If we
want faster growth, but cannot tolerate increased dystocia, we must avoid simply selecting for
growth or against dystocia. We need a way to select for growth rate and against dystocia at the
same time. We need a method for multiple-trait selection as introduced in this course.

5. Inbreeding

Inbreeding is the mating of related individuals. That is the simplest definition anyway. Because
all animals within a population are related to some degree, a more technically correct definition
of inbreeding is the mating of individuals more closely related than average for the population.
Inbreeding has a number of effects, but the chief one and the one from which all the others stem
is an increase in homozygosity- an increase in the number of homozygous loci in inbred animals
and an increase in the frequency of homozygote genotypes in an inbred population. Because
inbred individuals have fewer heterozygous loci than non-inbreds, they cannot produce as many
different kinds of gametes. The result is fewer different kinds of zygotes and therefore less
variation in the offspring. This illustrates, as we will see in more detail furtheron in this course,
that inbreeding (more precisely the level of inbreeding in the population) is related to the amount
of genetic variation. A second consequence of inbreeding is the expression of deleterious
recessive alleles with major effects, and it is this aspect of inbreeding, more than any other, that
gives inbreeding a bad reputation. People associate inbreeding with genetic defects. It is true that
defects caused by recessive alleles often surface in inbred populations. But inbreeding does not
create deleterious recessive alleles; they must already have been present in a population.
Inbreeding by itself simply increases homozygosity, and it does so without regard to whether the
newly formed homozygous combinations contain dominant or recessive alleles. It therefore
increases the chance of deleterious alleles becoming homozygous and expressing themselves.
Expression of deleterious recessive alleles with major effects, particularly lethal genes, is a very
visible consequence of inbreeding. It is an example of the effect of inbreeding can have on certain
simply-inherited traits. Less obvious is the expression of unfavourable recessive alleles
influencing polygenic traits. The individual effects of these genes are small but, taken together,
can significantly decrease performance- a phenomenon known as inbreeding depression.

6. Biodiversity

An important issue arises in situations where a breed that is native to a particular area appears to
have lost its function in that area or elsewhere, and consequently is in danger of becoming
extinct. The question to be raised in this situation is whether such a breed should be preserved.
The arguments in favour of preservation are that we do not know what type of animals will be
required in the future, and that we should therefore preserve the available genetic variation
between breeds (bio-diversity) as an insurance against the unknown future. On the other hand, it
is argued that people who aim to earn a living from animals cannot afford to look too far into the
future; they appreciate the arguments in favour of preservation, but are unable to meet the
relatively high cost of preserving populations that they are unlikely ever to utilise during their
own lifetimes. At both the national and international level, e.g. FAO and Rare Breeds
International, concerted efforts are being made to gather relevant data on breeds that seem
threated by extinction, and to act, where possible, to save them. Interestingly, the two areas that
are probably of greatest concern are at the either end of the spectrum of animal improvement. At
one end we have a large variety of locally adapted native populations (often in developing
countries) that are under threat from the influx of “improved” breeds and strains from developed
countries. And at the other end we have an increasing number of poultry selection lines that are discarded when yet another independent poultry breeding company is taken over by a larger and often multinational breeding company.

7. Technology and animal breeding

The face of animal breeding has changed significantly over the past decades. Animal breeding used to be in the hands of a few distinguished “breeders”, individuals who seem to have specific arts and skills to “breed good animals”. Nowadays, breeding in particular in livestock species is dominated by science and technology. In some livestock species, animal breeding is in the hands of a few large companies, and the role of the individual breeders seems to have decreased. There are several reasons for this change. Firstly, the breeding industry has adopted scientific principles. Looking was replaced by measuring, and an intuition was partly replaced by calculations and scientific prediction. Other major developments grew from the introduction of biotechnology.

Biotechnology can be broadly defined as the application of biological knowledge to practical needs. These technologies fall generally into two categories, reproductive and molecular. Not all of this is new. Artificial insemination was introduced in cattle in the fifties. There is no doubt that technology had a major impact on rates of genetic improvement in dairy cattle and is just as important to the structure of animal breeding programs. Nowadays, technologies like ovum pick up, in vitro fertilisation, embryo transfer, cloning of individuals, and selection with the use of DNA-information is all on the ground. Some of the technologies are already applied, others are further developed, or waiting application. Finally, rapid development of computer and information technology has greatly influenced data collection and genetic evaluation procedures in animal populations, now allowing comparison of predicted breeding values across farms, breeds or countries.

It is important to recognise that the introduction and exploitation of new technologies have large social impacts. The introduction of breeding methods typically needs to find the right balance between what is possible from a technological point of view and what is accepted by the decision makers and users within the socio-economic context of the production system. Ultimately it is the consumer who decides which technology is desirable and which is not. In most western societies, consumers are increasingly aware of health, environmental and animal welfare issues. Food safety and methods of food production are part of their buying behaviour. However, price and production efficiency are still major factors determining the sustainability of a livestock sector. Successful animal breeding programs need to find and apply the accepted technologies that help them remain competitive. This course is mostly concerned with the technical issues involved in the application of new technologies in animal breeding.

8. Components of breeding programs

Very generally, the aim of animal breeding is to genetically improve populations of livestock so that they produce more efficiently under the expected future production circumstances. Genetic improvement is achieved by selecting the best individuals of the current generation and by using them as parents of the next generation. A breeding program is the organized structure that is put into place to genetically improve livestock populations. This chapter deals with the set-up and evaluation of animal breeding programs.
A breeding program is the organized structure that is set up in order to realize the desired genetic improvement of the population.

Successful genetic improvement requires breeding programs to have (at least) the following components: i) A system to record data on selection candidates. Without data on selection candidates it is impossible to identify the best individuals. ii) Methods and tools to estimate the genetic merit (breeding value) of selection candidates. This step is referred to as "breeding value estimation" or “genetic evaluation system”. iii) A system to select the animals that become parents of the next generation, and mate them to produce the next generation. iv) A structure to disseminate the genetic improvement of the breeding program into the production population. In most cases, the breeding population and the production population are (partly) separated. Since the aim is to improve livestock production, genetic improvement created in the breeding population should be disseminated into the production population.

**Data recording and collection:** Estimation of breeding values requires phenotypic data on selection candidates. Thus a system has to be set up to routinely record data on selection candidates. The way data is collected depends on the species and the traits in the breeding goal. For example, the product of a dairy cattle breeding company is a straw of semen from a bull. However, milk yield cannot be recorded on bulls. Thus to identify bulls of high genetic merit for milk yield, one has to collect data on daughters of bulls. Dairy cattle breeding schemes therefore have a system to record data on daughters of test bulls. Milk yield of those daughters is recorded on common dairy herds, meaning that farmers are involved in the data recording. In beef cattle breeding, growth performance of bulls can be recorded on the selection candidates themselves, meaning that progeny testing is not necessary. In beef cattle breeding, data collection therefore takes place at testing stations where the performance of selection candidates is recorded. The quality of the data is fundamental to the success of breeding programs. Without high quality data, it is impossible to accurately estimate genetic parameters and breeding values.

**Breeding value estimation:** After data are recorded, breeding values have to be estimated. The common procedure to estimate breeding values in applied livestock breeding is called "BLUP". BLUP and selection index theory have the same theoretical basis; both are based on regression of breeding values on phenotypes. Compared to selection index theory however BLUP has the following advantages; i) It accounts for systematic environmental effects. ii) BLUP is more flexible than selection index theory and therefore more suitable as an operational tool. iii) BLUP takes account of selection.

**Selection and mating:** Selection and mating takes place after breeding values are estimated. Selection refers to the process of choosing parents to produce the next generation, whereas mating refers to the pairing of selected individuals. Thus selection precedes mating. The selection process determines the genetic improvement of the population over time, whereas the mating process determines how maternal and paternally derived alleles are combined within individuals. This chapter will introduce a number of selection and mating procedures and present theory to understand the effects of the different procedures.
Dissemination of genetic progress: In most species, the breeding and production populations are distinct. Genetic progress is created in the breeding population, but the final aim is to improve livestock production in the entire population. Thus genetic improvement created in the breeding population has to be disseminated into the production population.

In dairy cattle, the breeding and production populations are not strictly separated. Superior cows from the production population can enter the breeding population, meaning that they are selected as bull dams. Genetic progress created in the breeding program is transferred to the dairy farms by the sale of semen of progeny tested bulls to the farmers. The sale of semen is the primary source of income for dairy cattle breeding companies. In addition, a limited number of embryos from the breeding population are sold to the dairy farmers.

The situation is different in pig and poultry breeding. Pig and poultry production are based on crossbreeding systems. The breeding populations consist of purebred lines, which are mated together to produce crossbred offspring. Crossbred offspring are sold to fattening farms or egg producers. The breeding and production populations are therefore completely separated; crossbred production animals cannot enter the purebred breeding populations. Dissemination of genetic superiority of the purebred breeding populations takes place by the sale of crossbred offspring.

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A breeding program has the following components: i) a data recording system, ii) methods and tools for breeding value estimation, iii) a selection and mating system and iv) a structure to disseminate the genetic improvement into the production population.

9. Design and evaluation of breeding programs

Design of breeding programs: The structure of breeding programs depends on both the species and the breeding goal. The optimum design of a breeding program will differ between species with large reproductive capacity and species with small reproductive capacity, between breeding programs that aim to improve production or reproduction traits, and low heritable traits versus high heritable traits.

Judging the quality of breeding programs: Choosing the best breeding scheme among a number of alternatives requires yardsticks to measure the quality of breeding schemes. Such yardsticks can be developed only when there is a well-defined breeding goal. Given that the breeding goal is clearly defined, there are three criteria that summarize the quality of a breeding program. These are:

1. Selection response for the breeding goal traits.
2. Maintenance of genetic diversity as measured by the rate of inbreeding.
3. Costs of the breeding program.

Selection response for the breeding goal traits is the revenue of a breeding program, whereas loss of genetic diversity and financial costs are the expenses of a breeding program. Selection response, loss of genetic diversity and financial costs are expressed in different units. The problem therefore is to combine them into a single criterion for the quality of a breeding program.
A comparison of breeding schemes based on selection response and the rate of inbreeding can be done as follows. To avoid long-term loss of genetic diversity an upper limit can be set to the rate of inbreeding. Next, alternative breeding schemes can be judged by comparing their selection response at the same rate of inbreeding. The scheme with the highest selection response at the same rate of inbreeding (e.g. 1%/generation) is the best scheme. It is more difficult to combine selection response and cost into a single criterion. The question is whether the revenues from an increase in selection response, for example in the form of increased market share, makes up for the cost of increased selection response. Hence, this is not a genetic issue but primarily a commercial and business issue.

**Evaluation of breeding programs:** Once a breeding program is operational it is essential to routinely evaluate the results. Evaluation may consist of comparing realized genetic improvement and rates of inbreeding with values expected when designing the breeding program. When there are clear differences between expected and realized selection response and inbreeding, then one needs to find the causes of those discrepancies and if possible improve the breeding program. Reasons that breeding programs do not yield the expected genetic improvement are: i) the use of inappropriate models for breeding value estimation, for example when the models do not include systematic environmental effects that are present in the data; ii) overestimation of the genetic parameters (e.g. \( h^2 \)) resulting in biased EBVs and overprediction of the expected response; iii) preferential treatment among selection candidates resulting in selection of individuals that received "good treatment" instead of genetically superior individuals, and iv) unexpected correlated response in other traits.

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<td>The quality of alternative breeding schemes can be judged by comparing selection response, rate of inbreeding and costs of the alternatives.</td>
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**Methods to design and evaluate breeding programs:** To compare alternative breeding programs we need methods to quantify expected rates genetic improvement and inbreeding of the alternatives. In other words, we need methods to predict rates of gain and inbreeding of breeding programs. From a methodological point of view, quantifying the expected rates of gain and inbreeding can be done in two manners, either stochastically or deterministically. Stochastic simulation is often the easiest way, but in most cases deterministic simulation gives more insight. With stochastic simulation, the breeding program is simulated in detail on a computer. Stochastic simulation consists of the following cycle. 1. Breeding values and phenotypes of individuals in the base generation are simulated. 2. Breeding values are estimated for the base generation animals by performing BLUP analyses on their simulated phenotypes. 3. Based on the estimated breeding values coming from the BLUP analyses, a number of animals is selected to become parents of the next generation. 4. The selected animals are mated and offspring from the matings are simulated. Next, steps 2, 3 and 4 are repeated until the desired number of generations is simulated. Because in stochastic simulation we simulate an entire population of "real" animals, the rates of gain and inbreeding can simply be estimated from the simulated data. Hence, after simulating the breeding scheme, the next step is to analyze the simulated data to quantify the rate of gain and inbreeding of the breeding scheme. Multiple replicates of the population are simulated, and the rates of gain and inbreeding are averaged over replicates.
The advantage of stochastic simulation is that one can mimic the true breeding program in detail, because the individual animal is simulated. Hence, stochastic simulation can be very precise. However, there are two disadvantages related to the use of stochastic simulation to evaluate breeding schemes. First, stochastic simulation is time consuming, particularly when large populations are simulated. Even with modern computers, simulation of a sufficient number of replicates of a large breeding scheme may take several hours or even days. Hence, stochastic simulation is less suited as an operational tool to quickly evaluate a number of alternatives. Second, with stochastic simulation the user often does not gain as much insight into the breeding scheme as with deterministic simulation. For example, with stochastic simulation the user will observe that shorter generation intervals generally go together with higher gain, but the deterministic equation \( \Delta G = \frac{ir_{hl} \sigma_{hl} L}{L} \) directly shows that gain is inversely proportional to the generation interval. Hence, because stochastic simulation does not explicitly model mechanisms like accuracy, generation interval, etc, it can be difficult to extend the result to other breeding schemes that were not simulated themselves.

Instead of using stochastic simulation, one can use deterministic methods to quantify expected gain and inbreeding from alternative breeding schemes. Deterministic methods do not mimic the breeding program on the individual animal level, but use (deterministic) equations to predict gain and inbreeding. For example, prediction of the rate of gain by using the expression that \( \Delta G = \frac{ir_{hl} \sigma_{hl} L}{L} \) is a deterministic methods. Hence, modeling the mechanisms that determine gain and inbreeding as mathematical equations allows us to quantify the expected outcome of a breeding program. To use deterministic methods one needs to know/derive the mechanisms determining gain and inbreeding; it requires more insight into quantitative population genetics than stochastic simulation.

Advantages of deterministic methods are 1). It takes limited computation time, so that many alternatives can be compared within limited time, and 2). Because the mechanisms are modeled explicitly, it gives a lot of insight into gain and inbreeding in breeding programs. In some cases, however, it may be difficult to derive accurate deterministic methods. Hence, there is a risk that deterministic methods are not precise if they do not properly model the mechanisms determining gain and inbreeding in populations. In complicated cases, stochastic simulation may be used to check the accuracy and validity of the deterministic equations. Hence, stochastic simulation may be helpful to validate and improve deterministic models, and in this way we improve our understanding of the mechanisms determining genetic improvement and rates of inbreeding in populations.

In this course we will mainly deal with deterministic models. The reason is that for many important situations deterministic methods are available and they provide more insight than stochastic models.

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<td>The expected selection response and inbreeding of breeding schemes can be determined by using either stochastic simulation or deterministic methods. Deterministic methods provide more insight and are computationally fast. Stochastic simulation is precise and useful to validate deterministic methods.</td>
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10. This course

The course "Animal breeding strategies" introduces the quantitative genetic principles underlying the design and implementation of genetic improvement programs in livestock species. Those principals will also apply to companion animals, populations of endangered breeds and zoo populations. The basic quantitative genetic principles used in this course are handled in Falconer and Mackay (1996)\(^3\).

The lectures start with a general overview of the field. This course focuses on the definition of breeding objectives and the genetic evaluation of breeding strategies. To achieve this, much of the course is devoted to the general principles involved in deriving economic weights of the various traits that might be genetically improved, making selection decisions between animals, designing breeding strategies and determining which strategies will make optimum progress. What is presented is a selection of some of the more common tools used in defining breeding objectives and designing and evaluating breeding strategies. These tools should be adequate to tackle many basic practical problems in animal breeding and provide background to using more complex methods.

Estimation of breeding values using best linear unbiased prediction (BLUP) is an important element in animal breeding but this lies outside the scope of this course (see AnS562). Attention will be paid to selection index theory but the emphasis lies on prediction of genetic gain and not on genetic evaluation of animals.

Lecture notes provide students with detailed knowledge on issues related to the design of breeding programmes for farm animals. Lectures will 'guide' the student through these notes. In addition problems will be supplied.

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