Section D

Genetic improvement methods to support sustainable utilization

1 Introduction

This section gives an overview of genetic improvement methods for sustainable use of AnGR. The first chapter describes the contexts for genetic improvement. As social and economic contexts are discussed extensively in other parts of the Report, they are only briefly described here. The scientific and technology-related context is described in greater detail. The second chapter discusses breeding strategies for genetic improvement, along with the elements of a straight-breeding programme. These elements involve planning, implementation and evaluation, and constitute a continuous and interactive process. Breeding programmes for the main livestock species in high-input systems are then reviewed. This includes a description not only of the breeding goals and the traits making up the selection criteria, but also the organization and the evolution of the breeding sector. This is followed by a description of breeding strategies for low-input systems, and those utilized in the context of breed conservation. This distinction is somewhat artificial as the situations and strategies sometimes overlap. Finally, some general conclusions are drawn.

2 The context for genetic improvement

Genetic improvement implies change. For a change to be an improvement, the overall effects of the change must bring positive benefits to the owners of the animals in question or to the owners' community. Moreover, to be an improvement, the effects of the change should bring positive benefits in both the short and the long term, or at minimum a short-term benefit should not result in long-term harm. As such, it is vital that the planning of genetic improvement programmes takes careful account of the social, economic and environmental context in which they will operate. This can best be achieved by making these programmes an integral part of national livestock development plans, which should establish broad development objectives for each production environment.

2.1 Changing demand

Traditionally, livestock breeding has been of interest only to a small number of professionals: breeding company employees, farmers, and some animal scientists. However, food production is changing from being producer driven to consumer driven. Consumer confidence in the livestock industry has broken down in many countries (Lamb, 2001). Fears about the quality and safety, of animal products have been heightened in recent years by various crises: bovine spongiform encephalopathy (BSE), dioxin, and more recently, highly pathogenic avian influenza (HPAI). Welfare has also become an important element in consumers' perception of product quality especially in Europe (organic products and free-range animals). At the same time, the majority of consumers have become less connected to the countryside, and know less about farming. There is a growing demand for "natural" production, but often without a clear understanding of what this should encompass.

2.2 Diverse production environments

Sustainable production systems need to be tailored to account for physical, social and market conditions. For breeding organizations this raises the question of whether they should diversify their breeding objectives, or whether they should breed an animal that can do well under a wide range of environments (physical environment, management system and market conditions). To date, however, only limited insights into the underlying genetics of phenotypic adaptation to the environment have been achieved.

2.3 Increasing recognition of the importance of genetic diversity

Livestock breeding requires variability within and between populations if it is to improve the traits of interest. Genetic diversity is important to meet present requirements, but is especially important to meet future requirements. For example, a change of emphasis from high-input to low-input production systems will favour different breeds and different characteristics within breeds. More generally, the increasing importance given to factors such as animal welfare, environmental protection, distinctive product quality, human health and climate change, will require a wider range of criteria to be included in breeding programmes. These criteria are often met by local breeds. Thus, it is possible that the most appropriate strategies for managing these breeds may involve only limited genetic change. For example, it may be wise to maintain adaptation to the local environment and disease challenges – and even to maintain the level of a production trait, such as body size or milk production, if this is currently at or near an optimum level.

2.4 Scientific and technological advances

Developments in genetic improvement methods

Quantitative genetics

A breeding scheme aims to achieve genetic improvement in the breeding goal through the selection of the animals that will produce the next generation. The breeding goal reflects the traits that the breeder aims to improve through selection. The rate of genetic improvement (ΔG) with respect to the breeding goal (and the underlying traits) depends on the amount of genetic variability in the population, the accuracy of the selection criteria, the intensity of selection, and the generation interval.

Maintenance of genetic variation is a condition for continuous genetic improvement. Genetic variation is lost by genetic drift and gained by mutation. Therefore, the minimum population size to maintain genetic variation is a function of the mutation rate (Hill, 2000). Selection experiments in laboratory animals have shown that substantial progress can be maintained for many generations, even in populations with an effective size well under 100, but that responses increase with population size (ibid.).

The loss of genetic variation within a breed is related to the rate of inbreeding (ΔF). In the absence of selection, ΔF is related directly to the number of sires and dams. In populations undergoing selection, this assumption is no longer valid because parents contribute unequally to the next generation. A general theory to predict rates of inbreeding in populations undergoing selection has recently been developed (Woolliams *et al.*, 1999; Woolliams and Bijma, 2000). This approach facilitates a deterministic optimization of short and long-term response in breeding schemes.

Research on the optimization of breeding schemes initially focused on genetic gain, while little attention was paid to inbreeding. It is now well accepted that constraining inbreeding is an important element of breeding schemes. Meuwissen (1997) developed a dynamic selection tool which maximizes genetic gain while restricting the rate of inbreeding. From a given set of selection candidates, the method allows the selection of a group of parents in which the genetic merit is maximized while the average coefficient of co-ancestry is constrained. Implementation of this method results in a dynamic breeding programme, in which the number of parents and the number of offspring per parent may vary, depending on the candidates available in a particular generation.

The accuracy of selection depends largely on the quality and the quantity of the performance records that are available. Genetic improvement can only be made if performance and pedigree are recorded. Based on these observations, the genetic merit of an individual is predicted and the animals with the highest predicted merit can be selected as parents.

It is well established that the method of choice for the genetic evaluation of linear traits (e.g. milk and egg production, body size and feed efficiency) is best linear unbiased prediction based on an animal model (BLUP-AM) (Simianer, 1994). The development of algorithms and software has meant that by today, in most countries and for most species, BLUP-AM is routinely used by breeding companies or in national-level breeding programmes. The limitations associated with applying simplistic single-trait models has led to the development of multiple-trait BLUP-AM evaluations based on sophisticated models (including, for example, maternal effects, herd × sire interactions or dominance genetic effects). This has been greatly facilitated by the increasing power of computers, and major advances in computational methods. The tendency now is to use all available information, including single test day records, records from cross-bred animals, and a wide geographical range (across countries). Significant difficulties associated with the use of increasingly complex models are a lack of robustness (especially when population size is limited) and computational problems. The challenge today is to develop tools to systematically validate the models used.

BLUP is optimum only when the true genetic parameters are known. Methods for unbiased estimation of (heterogeneous) variance components with large data sets have been developed. Restricted Maximum Likelihood (REML) applied to animal models is the method of preference. Quite a few important traits are not correctly described by linear models (e.g. traits based on scoring and survival). A wide variety of nonlinear mixed models have, therefore, been proposed: threshold models, survival models, models based on ranks, Poisson models, etc. However, the benefits of using these nonlinear models remain to be proven.

The selection intensity reflects the proportion of animals that are needed as parents for the next generation. Reproductive capacity and techniques have an important influence on the number of parents that are needed for the production of the next generation, and thereby on the rate of genetic improvement. In poultry, high reproductive capacity means that about 2 and 10 percent of the male and female candidates, respectively, are retained as parents. In cattle, the introduction of AI has resulted in an enormous reduction in the number of sires. In dairy and beef cattle, the bulls used for AI and the cows with high genetic merit are the nucleus animals, and form less than 1 percent of the entire population.

The generation interval is the average time between two generations. In most populations, a number of age classes can be distinguished. The amount of information available differs between classes. In general, there is less information about the younger age classes than about older age classes. Consequently, the accuracy of estimates of breeding value is lower in the younger generations. However, the mean level of the estimated breeding value (EBV) of young age classes is higher than that of older age classes because of continuous genetic improvement in the population. Selection across age classes to obtain the highest selection differential is recommended (James, 1972). The fraction of animals selected from each age class depends on the differences in accuracy of the EBV between the age classes (Ducrocq and Quaas, 1988; Bijma *et al*., 2001). The use of reproductive technologies may increase the amount of sib information available, and thereby increase the accuracy of the EBV of younger age classes (van Arendonk and Bijma, 2003). This will change the proportion of parents selected from the younger age classes, and therefore also influence the average generation interval. Thus, generation interval is primarily a result of selection among the available age classes.

Molecular genetics

Molecular genetics in livestock has been subject to extensive study during the last two decades. These studies are related to gene-based selection of Mendelian traits (mainly diseases and genetic defects), marker assisted selection and introgression. Furthermore, molecular information is increasingly used to assist breed conservation programmes and to improve understanding of the origin and domestication of livestock.

Gene-based selection. Increasing knowledge of the animals' genome increases the prospects for applying this technology and provides new tools with which to select for healthy animals. Initial applications are related to Mendelian traits. In cattle for example, DNA diagnosis is routinely utilized to eliminate genetic disorders such as bovine leukocyte adhesion deficiency (BLAD), deficiency of uridine monophosphate synthase (DUMPS) and complex vertebral malformation (CVM), as well as in selection for traits such as milk kappa-casein and double muscling.

In pigs, the best-known gene which has so far been used in commercial breeding is the "halothane" gene. It was known that a number of pigs could not handle stressful situations (e.g. transportation to the slaughterhouse). A (recessive) gene – a natural mutation, called the "halothane" gene – was found to be responsible for this defect. Using a DNA test that detects whether a pig has the "defective form" of the gene, it has been possible to eliminate this gene completely from several breeds (Fuji *et al*., 1991).

Scrapie, the prion disease of sheep, is the most common natural form of transmissible spongiform encephalopathy (TSE), a group of diseases which also include Creutzfeldt-Jakob disease in humans and BSE in cattle. Genetic susceptibility to scrapie is strongly modulated by allelic variations at three different codons in the sheep PrP gene (Hunter, 1997). Breeding for scrapie resistance has, therefore, been considered an attractive option for the control of this disease (Dawson *et al*., 1998; Smits *et al*., 2000). This can be done by selecting for the allele that is associated with the greatest degree of resistance to scrapie (the ARR allele). As described in Part 1 – Section F: 4, breeding programmes to eliminate scrapie can pose a threat to rare breeds that have a low frequency of the resistant genotype.

Marker assisted selection. Most economically important traits in animal production are of a quantitative nature and are affected by a large number of genes (loci), a few of which have major effects, while the majority have small effects (Le Roy *et al*., 1990; Andersson *et al*., 1994). If a gene (locus) with a major effect can be identified, and if a molecular test can be designed, animals' genotypes at the locus can be used for selection. In other cases, a chromosomal region close to the gene of interest may be identified and used as a marker.

Mixed models of inheritance, which assume one or several identified segregating loci, and an additional polygenic component, have been developed. When genotypes at each identified locus are known, they can be treated as fixed effects in standard mixed-model techniques (Kennedy *et al*., 1992). When only genotypes at linked markers are known, the uncertainty resulting from unknown haplotypes and recombination events has to be taken into account (Fernando and Grossman, 1989).

Extra genetic gain is usually to be expected if information on genes with medium to large effects is included in the genetic evaluation process. Numerous studies have investigated this problem in recent years. Results are not always comparable, because selection criteria differed between studies (i.e. from an index based on individual information to animal models), but they all indicate that knowledge of genotypes at quantitative trait loci generally improves short-term response to selection (Larzul *et al*., 1997). Conversely, some discrepancies have been obtained for long-term response to selection – see Larzul *et al*. (1997). In less favourable situations where only genotypes at linked markers are known, results largely depend on the particular circumstances. Large gains can be expected when linkage disequilibrium exists at the population level (Lande and Thompson, 1990), and when traits are difficult to measure (e.g. disease resistance), sex limited (e.g. traits related to egg or milk production), expressed late in the lifespan of the animals (e.g. longevity and persistency in litter size), or measured after slaughtering (e.g. meat quality traits). In other cases, the advantage of marker assisted selection may be questionable.

Genes at the same or at different loci interact with each other in producing a phenotypic effect. It is seldom known how this occurs. When, by using statistical models, an apparent effect is assigned to a particular gene, such interaction is not taken into account. This explains, at least partly, why even when genes with major effects are identified, incorporating them (or their markers) into a selection programme may not achieve the desired results. Because of such interactions, there is often an apparent lack of consistency between different studies related to the use of genetic markers (Rocha *et al*., 1998). To correctly assess the effect of a gene, the average effect over the possible genotypes in the population where the information is to be applied (weighted according to their frequencies) has to be considered.

Introgression is advocated mainly to improve disease resistance in a given population. If markers for the resistance gene(s) (or probe for the gene) are available, marker assisted selection may be used to simplify the process of introgression. Dekkers and Hospital (2002) discuss the use of repeated backcrosses to introgress a gene into a population. If the non-resistant breed is considered the recipient breed, and the breed that carries the resistance gene is considered the donor breed, introgression of the desirable gene from the donor breed to the recipient breed is accomplished by multiple backcrosses to the recipient breed, followed by one or more generations of intercrossing. The aim of the backcross generations is to generate individuals that carry one copy of the donor gene, but that are similar to the recipient breed for the rest of the genome. The aim of the intercrossing phase is to fix the donor gene. Marker information can enhance the effectiveness of the backcrossing phase of gene introgression strategies by identifying carriers of the target gene (foreground selection), and by enhancing recovery of the recipient genetic background (background selection). Generally, it is more feasible and economically sound to mate, in successive generations, pure-bred females of the recipient breed to cross-bred males that carry the desired gene, than to carry out the reverse process.

If the gene for resistance is dominant, its introgression into a population may be effective even without a molecular marker for the gene. If the gene for resistance is recessive (or co-dominant), markers are necessary. In cases where resistance is polygenic, introgression without genetic markers is not likely to be effective; by the time the genetic influence of the donor breed is high enough to give high levels of resistance, the desired characteristics of the recipient breed will probably have been lost. In fact, the development of a composite breed would be easier than the introgression of numerous genes into a recipient breed by backcrossing, even when genetic markers are available. Hanotte *et al*. (2003) mapped QTLs affecting trypanotolerance in a cross between the "tolerant" N'Dama and "non-tolerant" Boran cattle breeds. Results showed that at some of the putative QTLs associated with trypanotolerance, the allele associated with tolerance came from the non-tolerant cattle. It was concluded that "selection for trypanotolerance within an F2 cross between N'Dama and Boran cattle could produce a synthetic breed with higher trypanotolerance levels than currently exist in the parental breeds."

Conceptually, introgression through marker assisted selection could be accomplished even without exposure to the disease agent. It is, however, wise to test the resistance of animals with the desired genotype.

Molecular characterization of genetic diversity is helpful in the planning of conservation programmes and to develop understanding of the origin and domestication of livestock species. Better knowledge of genomic variation, together with the development of new quantitative genetic methods, may provide the means to link marker information to functional variation. For example, combination of molecular methods and pedigree analysis has been used to estimate the degree of genetic diversity in founder populations in thoroughbred horses (Cunningham *et al*., 2001).

Developments in reproductive technologies

Reproductive technology has a direct effect on the rate of genetic improvement. For a given population size, a higher reproduction rate implies a lower number of breeding animals and, therefore, a higher intensity of selection. More offspring per breeding animal also allows more accurate estimation of breeding values. Another advantage of increasing reproductive rates is to disseminate superior genetic stock more quickly.

As reproductive technologies are extensively discussed elsewhere in the report, this chapter focuses only on the use of AI and multiple ovulation and embryo transfer (MOET) in breeding programmes. For other techniques, only a brief description is provided here.

Artificial insemination. The use of AI results in higher selection intensity, more accurate selection of males based on progeny testing and more accurate estimation of breeding value across herds. The latter is a result of exchange of semen between different nucleus herds, which facilitates the establishment of genetic links between them. AI is used by breeding organizations for most species. For species such as cattle that have low reproductive rates, progeny testing based on AI is a prerequisite for an accurate estimation of breeding values for traits of low heritability such as functional traits. AI allows faster dissemination of genetic superiority to the commercial population. Sixty to eighty percent of all the AI performed is carried out in cattle. A male identified as superior can leave thousands of progeny in different populations all over the world.

AI requires technical skills both at the AI centre and on the farm, as well as effective lines of communication between the two. However, in many countries, the majority of producers are smallholder farmers, and existing skills and infrastructure may be insufficient to allow the successful operation of AI services. The farmer has to be able to detect heat and have a means to contact the semen distribution centre, which then has to be able to serve within few hours. For extensive production systems, this is a labour-intensive process. Consequently, AI is unlikely to be used in extensive grazing systems for beef production. Similarly, AI is difficult to perform in sheep, and natural mating using superior males is still the dominant means of diffusing genetic improvement.

Use of AI affects the ownership structure of the breeding sector. Where AI is used, the ownership of the breeding animals is usually transferred to larger breeding organizations, such as cooperatives or private breeding companies. For the last twenty years in the developed world, AI centres have been responsible for the identification of young bulls for progeny testing, and for the marketing of semen from proven sires.

Multiple ovulation and embryo transfer. Increasing the reproductive rate of females by MOET is mainly useful in species with low reproductive rates such as cattle. The benefits are higher selection intensity on the female side, and more accurate estimation of breeding values. As family sizes are larger, there is more information available on animals' sibs. This allows reasonably reliable breeding values to be obtained at a younger age, particularly when the traits are only recorded for one sex (female). In practice, this means that there is no need to wait for a progeny test to select males – they can be selected at younger age based on information on their half-sib sisters. The gain in generation interval is large, and compensates for the loss of selection accuracy that results from replacing a progeny test by a sib test. The ability to select at a young age, even among embryos, is the main reason of the application of MOET in pig breeding. Embryo transfer is also used to disseminate desirable genes from superior female animals with minimum disease risks, as animals do not need to be transported.

The use of MOET is costly and requires highly developed technical skills. The logistical challenge is that at the time of embryo transfer, a group of recipient cows needs to be available and synchronized. This can be done only in large centralized nucleus herds. In many cases, it may be better to invest resources in more basic prerequisites – performance and trait recording, extension and dissemination. This is all the more true as MOET seems less efficient than AI in enhancing genetic progress. In all cases, the introduction of AI and/or MOET has to be cost effective and accepted by the local farmers.

Semen and embryo freezing gives breeding organizations the opportunity to create genebanks as a back-up store of genetic diversity in breeding programmes. Moreover, cryopreservation of gametes and embryos facilitates international exchange and transport of genetic material in ruminants, and is a prerequisite for routine use of AI and ET on a world scale.

Cloning (somatic cells) is a new technology which is currently not being used commercially. This is partly for technical and economic reasons, and partly because there is no public desire for such developments at present. Cloning has potential application in the field of conservation, as other tissues may be easier to preserve than embryos.

Sexing of embryos or semen enables the production of larger numbers of animals of a particular sex. For example, preferences for male or female offspring are obvious in cattle – females for milk production, and males for beef production. Numerous attempts have been made to develop a reliable technology. Currently, it is possible to identify male and female embryos by various methods. However, with a few exceptions, this technology has not yet been widely used by breeders or farmers. Various attempts have been made to separate sperm based on their sex-determining characteristics. However, further advances are required before the technology can be applied on a large scale.

The use of the above-described reproductive and conservation techniques means that there is less need for the transportation of breeding animals. Furthermore, these technologies offer an opportunity to safeguard the health status of flocks and herds even when embryos originate from countries with a radically different health status.

2.5 Economic considerations

Any economic evaluation should consider both returns and costs. As animal breeding is a long-term process, returns on breeding decisions may be realized many years later. This is the case in dairy cattle for example. Furthermore, different costs and returns are realized at different times with different probabilities, and a number of considerations that may not be important for relatively short-term processes are sometimes of major importance in the longer term.

Until the advent of reproductive biotechnologies, the main cost elements of breeding programmes were trait measurement and recording, progeny testing and maintaining the breeding stock. Although the main objective of most recording systems is breeding, it should be noted that once available, the information is useful for other farm management decisions such as culling and predicting future production.

Animal breeding in the developed world has become more and more sophisticated and professionalized, and hence costly. Economic considerations are, therefore, driving most if not all breeding-related activities, and economic theory has been incorporated into this area. The bases for economic evaluation are profit, economic efficiency, or return on investment. When breeding goals have been developed by and for (groups of) producers, emphasis is put on profit maximization. In developing countries, markets are generally more local, but the same mechanism will apply. It is, therefore, advisable to opt for profit maximization, unless there are clear reasons to deviate from this strategy.

A critical economic consideration is: who will pay for the genetic improvement? This question is not particularly important when breeding nuclei, multipliers and commercial herds/flocks are fully integrated. However, in all other situations, where vertical integration does not exist, it is not unusual that those who invested in breeding activities are unable to adequately recoup their investment. This commonly provides justification for public sector involvement in one or more facets of genetic improvement.

Under a free market system, breeding organizations have to adapt to the demands of their customers – the commercial producers, who are normally only prepared to pay for improved breeding animals or semen if this will enhance their profits. However, it is interesting to note that even if a trend in breeding does not appear to be economically justified, it may continue for an extended period of time (Box 80). Under a government subsidized system, all or part of the costs of genetic efforts are paid for by taxpayers. In this case, breeding programmes should be subject to scrutiny to ensure that they truly produce some social benefits. Such benefits could include, for example, providing safer, more nutritious or less expensive products for the consumer, or reducing the negative environmental impacts of livestock production.

3 Elements of a breeding programme

The elements required in a breeding programme depend on the choice of the general breeding strategy. Thus, the first decision is which of the three main genetic improvement strategies should be applied: selection between breeds, selection within breeds or lines, or cross-breeding (Simm, 1998).

- Selection between breeds, the most radical option, is the substitution of a genetically inferior breed by a superior one. This can be done at once (when as in poultry the cost is not prohibitive) or gradually by repeated backcrossing with the superior breed (in large animals).
- Cross-breeding, the second fastest method, capitalizes on heterosis and complementarity between breeds' characteristics. Conventional cross-breeding systems (rotational systems and terminal sire-based systems) have been widely discussed (e.g. Gregory and Cundiff, 1980). The *inter se* mating of animals of newly developed composites has been suggested as an alternative form of cross-breeding (Dickerson, 1969; 1972).
- The third method, within-breed selection, gives the slowest genetic improvement, especially if the generation interval is long. However, this improvement is permanent and cumulative, which is not the case for cross-breeding programmes.

Gradual genetic improvement is the most sustainable form of improvement, as it gives the stakeholders time to adapt the production system to the intended change. When the traits of interest are numerous and/or some of them are antagonistic, different lines may be created, and maintained by within-line selection. These lines can then be crossed to produce commercial animals. This strategy is used in pig and poultry breeding.

Setting up a breeding programme involves the definition of a breeding goal (Groen, 2000) and the design of a scheme that is able to deliver genetic progress in line with this goal. In practice, it involves the management of people and resources as well as the application of the principles of genetics and animal breeding (Falconer and Mackay, 1996). Each aspect of the breeding programme involves many processes, individuals and sometimes institutions. Success depends on how well the available resources are harnessed and managed to achieve the goals of the stakeholders.

The stakeholders of a breeding programme are all those who are affected, in one way or another, by its success. These include the end users of the products of the programme (i.e. livestock producers), commercial companies and others who directly or indirectly invest in the scheme, government departments, breed societies, and those employed to implement the programme. Other stakeholders include ancillary beneficiaries such as suppliers, distributors, and sellers of by-products of the scheme.

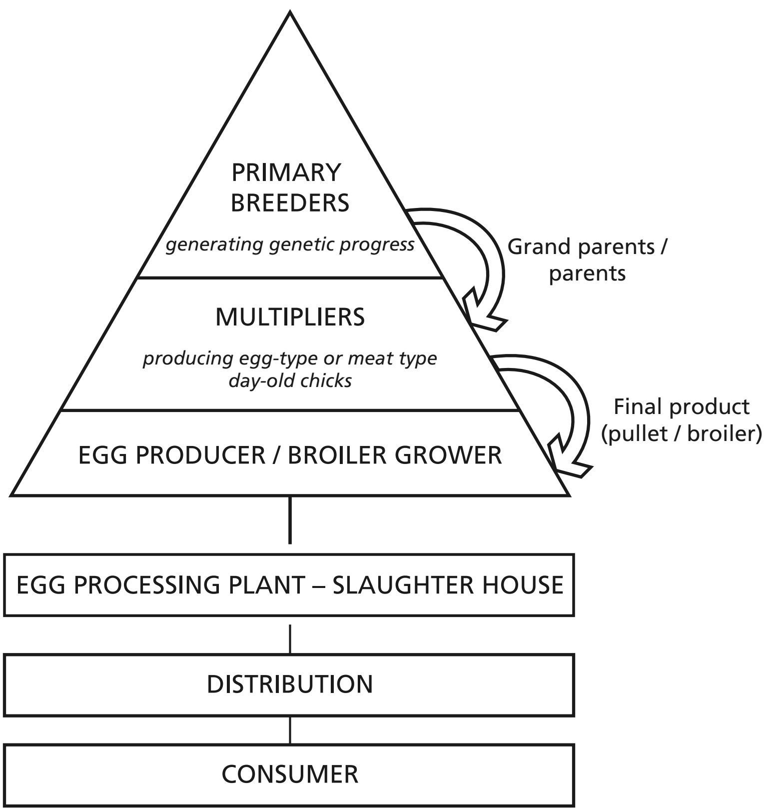
Most programmes have a pyramidal structure (Simm, 1998), with varying number of tiers depending on the sophistication of the programme. At the apex of the pyramid is the nucleus where selection and breeding of the elite pedigree animals is concentrated. The multiplication of stock happens in the middle tiers. This is required when the number of nucleus animals is insufficient to satisfy the demands of commercial farmers. The bottom tier comprises the commercial units where the final product is disseminated. The pyramidal structure of the poultry breeding industry is illustrated in Figure 48.

The activities that constitute a breeding programme can be summarized in eight major steps (Simm, 1998):

- choice of breeding goal;
- choice of selection criteria;
- design of the breeding scheme;
- recording of the animals;
- genetic evaluation of the animals;
- selection and breeding;
- progress monitoring; and
- dissemination of genetic improvement.

These steps will be described in the following subchapters. However, the reader should be aware that planning, implementation and evaluation form a continuous process – the elements should

FIGURE 48
Structure of the poultry breeding industry



be approached interactively rather than step-by-step. A further critical element is the need to document in detail all areas of the breeding plan and its execution over time.

3.1 Breeding goals

The breeding goal is a list of traits to be improved genetically. It should be in line with national agricultural development objectives, and appropriate for the production system for which it is defined and the breeds suited to the production system. A country's development objectives for agricultural production traditionally include economic variables, but should be extended to accommodate ethics, and other social aspects of human well-being. These objectives are used to formulate the breeding goals. Different tools are available to achieve this. The most common is the profit function. In theory, setting up a profit function is straightforward, especially in the case of within-breed selection programmes, as it is a linear function of the relative economic values of the traits to be improved. In practice, however, it is not easy to obtain these economic values, partly because they may vary in time and in space, and partly because of a lack of time, expertise, knowledge, resources, etc. Thus, breeders manipulate the direction of change through trial and error based on perceived market demand and preference. Amer (2006) discusses other tools for formulating breeding goals such as the bio-economic model and the geneflow model.

Livestock improvement is measured relative to a given set of traits, generally referred to as "traits of economic importance". In reality, the traits and their economic importance vary as widely as the breeding programmes. For many livestock species, the traits of economic importance are those that affect the productivity, longevity, health and reproductive ability of the animals.

For most of the traits, the objective is a continuous improvement, but for some traits the goal is to reach intermediate values. Pharo and Pharo (2005) term these alternatives, respectively, breeding for a "direction" and for a "destination". An example of the latter is egg weight in laying hens. The market values eggs within a particular range of weights – for example, between 55 and 70 grams. Smaller eggs are not saleable and there is no premium for bigger ones. Given that egg size is correlated negatively to egg number, shell strength and hatchability, selecting for bigger eggs is not only a waste of selection intensity, it is also counter productive. Another example is body size. For meat animals, size at slaughter is an important determinant of value. Body size has a major effect on nutritional requirements, through its effect on maintenance requirements. It may also affect fertility. The latter (net fertility such as calf crop or lamb crop weaned) is a major determinant of biological efficiency and profitability. Since body size is associated with both costs and benefits, it is difficult to determine an optimum value, especially under grazing systems, because of the difficulty involved in adequately describing forage intake. Another consideration is that most slaughter markets discriminate against animals that fall outside a desired range of carcass (or live) weights. For example, the European market requires a minimum carcass weight, which cannot be met by some breeds (e.g. Sanga breeds from Namibia). Even if the current body size of these cattle is optimum with regard to biological efficiency, larger cattle may be more profitable.

The choice of the breeding goal may be a one-off activity, or one that is revised from time to time. The decision is taken by the breeders, with feedback from all tiers of the breeding pyramid. In poultry and pig breeding, this decision is taken by the top management of the breeding companies (research and development managers in agreement with technical and marketing or sales managers). In cattle breeding, the decision is taken at the apex nucleus, but usually in consultation with people in all other tiers including the commercial tier, in a way that reflects the ownership pattern of the programme.

The outcome of breeding programmes, particularly in dairy and beef cattle, is realized many years after selection decisions are made.

Even in poultry, where the generation interval is shorter, a genetic change implemented in the nucleus will not be noticed at the commercial level in less than three years, at the earliest. This underlines the need to anticipate future demands when defining breeding goals.

In a competitive market like the poultry breeding industry, the identification of traits of interest and the focus of selection efforts is not only highly dependent on signals from the market place (i.e. the commercial producers), but also on the performance of the products of competing programmes.

3.2 Selection criteria

The breeding goal is distinct from the selection criteria that are used to take the decision as to which animals are to become the parents of the next generation. Usually, the decision involves the construction of a "selection index". Measurements are taken in the candidate animals and their relatives, and are weighted according to index coefficients calculated to maximize the correlation between the selection index and the breeding goal. It should be emphasized that some of the breeding goal traits may differ from those used to construct the selection index. For example, pigs are selected for the fatness of their carcass – this is a breeding goal trait. However, it cannot be observed in selection candidates,

Box 80

Changing body size of beef cattle in the United States of America

In 1900 the vast majority of beef cattle in the United States of America were Shorthorn, Hereford, or Angus. The cattle at the time were fairly large. Bulls of 1 100 kg and cows of 730 kg were common. Cattle were finished (fattened) primarily on grass, and there was some interest in producing cattle that would finish at a younger age and lighter weight. A trend developed for selecting for smaller-framed cattle that had greater apparent ability to fatten. Much of the selection was actually based on attempts to win in the show ring. Selection was effective, and major changes were achieved in the cattle population. After a few generations (the late 1920s and early 1930s) the cattle were probably of a more appropriate size for the production conditions under which they were kept. However, selection continued in the same direction, and by the 1950s the cattle in most highly regarded herds were much too small and predisposed to fattening to be profitable under any commercial management programme.

A major change in the United States beef industry began in the mid-1950s, with the development of large feedlots in the Great Plains states. To be profitable in these new feedlots, cattle had to be able to grow at a fairly high rate for a long feeding period (four or five months) without getting too fat. The small early fattening cattle which had previously been popular were not acceptable to the feedlot industry. Charolais and other continental European breeds became popular, and cattle of the British beef breeds were selected for increased size and growth. From the mid-1950s to the late 1960s, larger cattle were favoured as long as they were fairly compact in their conformation. However, by the late 1960s, larger cattle were favoured, even if they were taller and very different in their conformation from the popular cattle of the earlier period. Within a few years, cattle were being selected for larger frame size, even in the continental European breeds. This selection was also quite effective, and extremely large animals were produced.

In the mid to late 1980s, several of the major breeding organizations realized that the trend had gone too far, and moves were made to produce more moderate sized animals. In the last ten years, more breeders have recognized that intermediate size is preferable to extremes in any direction. However, they continue to be in the minority, and extremely large cattle have continued to be favoured in many major herds.

as this would mean that they would have to be slaughtered. A predictor trait, the subcutaneous fat thickness measured ultrasonically, is therefore recorded. Where it is difficult or expensive to acquire information on the relationships between animals, and the traits are sufficiently heritable, selection can be based on individual performance (mass selection). The construction of the selection index is a technical issue, and requires personnel with the necessary expertise.

There are numerous circumstances in which at the moment of selection many traits that are not relevant to breeding goal trait list are considered. This can seriously decrease the actual selection intensity and, therefore, limit the genetic improvement. Sometimes this is acceptable (e.g. a genetic defect is a valid reason for culling). In other cases such criteria are doubtful (e.g. "body volume" as an indicator of productivity) or not recommendable (e.g. frame size or "dairyness").

3.3 Design of breeding scheme

Designing a breeding programme requires taking a range of decisions in a logical order. The designer of the programme should be aware that such a process evolves over time – from the simple to increasing levels of sophistication as organization and capacity develop. Most of the decisions involve determining how best to utilize present population structure to reliably generate the improvement and/or restructuring that is needed. Economic evaluation is an integral part of this process, and should be carried out both for the pre-implementation phase and for evaluating the change being realized when the programme is underway.

Investment decisions in the breeding programme should be assessed with respect to the three components contributing to the rate of genetic change: selection intensity, selection accuracy and generation interval. Based on these components, alternative scenarios are assessed. Theoretical knowledge of quantitative genetics is used to predict the gains to be expected from different scenarios (Falconer and Mackay, 1996). For this purpose, population genetic parameters such as heritability and phenotypic variation of the traits are needed to build up the selection index (reasonable assumptions can also be made) (Jiang *et al*., 1999). A suitable mating plan is then outlined. It must allow sufficient records to be obtained for genetic evaluation, and sufficient elite animals to be produced for the nucleus and for multiplication in the lower levels of the breeding pyramid. Note that in performing these activities, the designer of the programme is already in the optimization phase.

When designing the breeding programme, it should not be forgotten that most aspects are directly influenced by the reproductive rate of the breeding animals. A higher reproductive rate means that fewer breeding animals are needed. More offspring per breeding animal allows more accurate estimation of breeding value.

3.4 Data recording and management

Recording of performance data and pedigrees is the main driving force for genetic improvement. Abundant and accurate measurements lead to efficient selection. In practice, however, resources are limited. The question then is: which traits should be measured and on which animals? Preferably, the traits included in the breeding objective should be measured, but this will depend on the ease and cost of measurement. The nucleus animals, at least, should be measured for performance and pedigree.

The collection of performance data on which to base selection decisions is a vital component of any breeding programme, and it should be regarded as such, rather than as a by-product of recording systems primarily designed to assist short-term management (Bichard, 2002). The task of collecting, collating and using data in genetic evaluation requires good organization and considerable resources (Wickham, 2005; Olori *et al*., 2005). In many instances, special schemes may need to be put in place to generate and record the required data. The cost and complexity of these schemes vary depending on the type of breeding organization, the type of traits, and the method of testing.

Type of breeding organization. pig and poultry breeding companies have in-house facilities for the collection and storage of all required data, whereas other breeding organizations may rely on resources owned by more than one stakeholder. For example, this is the case in a typical dairy cattle breeding programme (see subchapter 4.1).

Type of trait. When body weight of live animals is the trait of interest, all that is needed is a weighing scale. However, to measure feed efficiency in individual animals, more sophisticated equipment may be needed to allow the recording of individual feed intake.

Performance versus progeny or sib testing. In a performance-testing scheme, the traits of interest are recorded directly in every individual. For example, body weight and growth are often recorded over a fixed period during the lifespan of beef cattle, pigs, broiler chickens or turkeys. Basically, a cohort of animals is managed together under similar conditions over a period of time during which individual performance is measured. This can be done on the farm, or at a performance test station where cattle or pigs from different herds or farms are brought together for a direct comparison under the same conditions.

Sometimes, the information of interest may not be measurable directly in the selection candidate, either because the expression of the trait is sex-limited as in the case of milk and egg production, or because the traits can only be recorded after the death of the animal (e.g. carcass composition). In these circumstances, indirect recording by progeny and/or sib testing is required. This is also useful for traits with low heritability, which may require several records to accurately evaluate an individual. Progeny testing refers to a scheme in which an individual is evaluated on the basis of performance records obtained from its progeny. It is mainly associated with males (Willis, 1991), as it is easier to generate large numbers of progeny from a single male than from a single female. Typically, not all males are progeny tested, but only the males born from “elite matings”. Progeny testing is very useful to increase selection accuracy for species with low reproductive rates, and to test genotype–environment interactions.

For many ruminant species, the cost of a central progeny testing facility may be prohibitive. It is, therefore, a common practice to involve as many farmers or commercial producers as possible. The farmers are encouraged to accept semen from a group of young sires to be used on a proportion of their female animals. Because the young sires are not of proven genetic merit, farmers involved in progeny testing often require good incentives to participate (Olori *et al*., 2005). In these circumstances, the total costs (several hundred thousand US Dollars) are often borne by the owners of the young sire under test.

Pedigree information. In addition to performance records, genetic evaluation in a breeding programme requires pedigree information. The quality of pedigree information depends on its depth and completeness. Whether the breeding objective involves genetic improvement or the prevention of extinction resulting from a loss of genetic variation, the pedigree of all breeding animals must be recorded and maintained.

Information systems. When the resources are available, a centralized database with shared access has been shown to be beneficial and cost effective (Wickham, 2005; Olori *et al*., 2005). The provision of comprehensive management-related information from such a system often serves as a stimulus for further participation in data recording schemes. The requirement for small breeding programmes may simply be a single personal computer with adequate spreadsheet, data management and reporting software, while national-level programmes may require a specialized department utilizing modern information technology (Grogan, 2005; Olori *et al*., 2005).

3.5 Genetic evaluation

Progress in a breeding programme requires that animals of superior genotypes for the traits of interest are identified and selected to breed the next generation. Identifying these animals requires disentangling the environmental contribution from the phenotypic observation. This is accomplished by breeding value prediction or genetic evaluation. This is a core activity in every breeding programme.

The genetic evaluation should be reliable. BLUP methodology, applied to a variety of models depending on the traits and data available, has become the standard method for nearly all species. The evaluation should also be available in time to make the best use of the investment in data collection and database management. A genetic evaluation system using BLUP relies on good data measurement and structure. If these prerequisites are in place, investment in BLUP is usually highly cost effective.

Across-herd evaluation has the advantage of allowing fair comparisons of predicted breeding values (PBVs) of animals in different herds, which leads to selection of more animals from the genetically superior herds. To do this, genetic links (usage of animals across herds and across years) are critical. In order to use the information from different herds, an adequate organizational structure is needed. This can be achieved through close collaboration between breeders, their associations, and universities or research centres. Unique identification for all animals that supply data for the breeding scheme is essential. The data analysts, with guidance and assistance from breed association personnel, assign animals to contemporary groups (groups of animals of about the same age that are raised together with the same treatment). This assignment may be critical for accurate genetic evaluation. The breeders submit data to the association, and after checking for obvious errors, the information is forwarded to the evaluation team for analysis. For ruminants, the evaluations are performed once or twice a year, but for pig and poultry meat programmes, where the selection is performed on a monthly, weekly or bi-weekly basis, evaluations are run continuously.

The results of the genetic predictions (PBV and aggregate indices) are typically printed on the animals' registration certificates. It is common to print PBVs in sale and semen catalogues. This means that the end users (farmers) have to understand and accept the EBVs that are produced, and know how to use them. There is no sense in running a genetic evaluation if the results are left untouched by the end users.

A typical genetic evaluation unit requires both qualified staff, and adequate material resources to carry out data analysis and produce suitable reports to facilitate selection decisions. Many large-scale breeding programmes have a dedicated genetic evaluation unit in-house. However, it is also easy to contract this evaluation out to an external institution. Many universities and research centres provide a genetic evaluation service for national and non-national breeding programmes. Such services can cover several different breeds or species, as the principle of genetic evaluation and the software involved will be similar in each case. Perhaps, the most popular genetic evaluation unit with international repute is the International Bull Evaluation Service (INTERBULL). The centre, which is based at the Swedish Agricultural University in Uppsala, was set up as a permanent subcommittee of the International Committee for Animal Recording (ICAR), and provides international genetic evaluation to facilitate the comparison and selection of dairy bulls on an international scale. Another example is BREEDPLAN, a commercial beef cattle genetic evaluation service with an operational base in Australia, which has clients in many countries.

3.6 Selection and mating

Selection should predominantly be based on the selection criterion. From each sex, as few breeding animals as possible should be selected to maximize selection intensity, with the only restrictions being the number of animals required for a minimum population size, and the number needed for reproductive purposes. As reproductive rates of males are generally much higher than those of females, far fewer breeding males than females are normally selected.

Selection candidates may be of different ages, and thus unequal amounts of information may be available about them. For example, older males may have a progeny test, while for younger ones, their own performance, or that of their dam or sibs, will be the only information available. If BLUP is used, such candidates can be easily and fairly compared. Selecting more animals with accurate EBVs, and only the very best animals with less accurate EBVs, is probably the best approach.

It is widely accepted that the use of family information, as occurs in BLUP, increases the probability of co-selection of close relatives, which in turn leads to increased inbreeding. Various methods are used to reduce inbreeding while maintaining high rates of genetic gain. All these methods are based on the same principle – reducing the average relationship between the individuals selected. Computer programmes have been developed to optimize selection decisions for a given list of candidates for which pedigree information and EBVs are available. Ad hoc methods to control inbreeding include selecting a sufficient number of males, as the rate of inbreeding depends on effective population size; not overusing the males within the nucleus; restricting the number of close relatives selected, especially the number of males selected per family; limiting the number of females mated to each male; and avoiding mating between full and half sibs. These simple rules have been quite effective in maintaining a low level of inbreeding in commercial poultry and pig breeding.

Mating of selected animals may or may not be at random. In the latter case, the very best of the selected males are mated to the very best of the selected females – this is known as assortative mating. The average genetic value of the progeny born in the next generation does not change, but there will be more variance among the progeny. When multiple traits are included in the breeding objective, assortative mating may be useful – matching qualities in different parents for different traits.

Any mating strategy will require sufficient facilities. For natural mating, animals to be mated have to be put together in the same paddock, but separated from other animals of reproductive age. AI can be used, but also requires a range of resources and expertise (semen collection, freezing and/or storing, and insemination).

3.7 Progress monitoring

This involves the periodic evaluation of the programme with respect to progress towards the desired goal. If necessary, it leads to a reassessment of the goal and/or the breeding strategy. Monitoring is also important to ensure early detection of undesired effects of the selection process, such as increased susceptibility to diseases or a reduction in genetic variation.

To assess progress, phenotypic and genetic trends are usually obtained by regressing average annual phenotypic and breeding values on year of birth. In addition to this information, breeders run regular internal and external performance testing. An external testing scheme needs to cover a wide range of production environments to ensure that selected animals can perform well under a wide range of conditions. Other sources of information, and probably the most important, are field results and feedback from customers. Ultimately, the customer is the best judge of the work done.

3.8 Dissemination of genetic progress

The value of superior individuals is limited if they do not efficiently contribute to the improvement of the gene pool of the whole target population. The wide impact of genetic improvement depends on the dissemination of genetic material. Reproductive technologies, especially AI, are very important in this respect. However, their impact varies between species. In sheep and goat breeding, the exchange of genetic material largely depends on trade in live animals. In the case of cattle, AI allows bulls selected in the nucleus to be used across the whole population. In principle, there is no problem in allowing an exceptional bull to have many progeny throughout the population. However, performing AI using semen from bulls from the same family very intensively will ultimately lead to inbreeding.

It should be possible to apply the elements described above even under basic conditions. Breeding structures do not necessarily require sophisticated systems of data recording and genetic evaluation, nor do they initially require use of reproductive technologies. The breeding structure should be determined in accordance with what is possible and what is optimum. Environmental or infrastructure restrictions, traditions and socio-economic conditions have to be considered when planning breeding programmes.

4 Breeding programmes in high-input systems

In high-input systems, continuous genetic improvement is generated mainly by straight-breeding within a breed or line. In the case of ruminants, this is largely a result of the strong position and active work of breeding associations, and of the spectacular results obtained by this method. Cross-breeding is used to realize the benefits of hybrid vigour (heterosis) and complementarity. In poultry and pigs, breeders concentrate their efforts on within-breed or line selection, and use cross-breeding to capitalize on heterosis for fitness traits and on complementarity for other traits.

The number of livestock breeding companies in the world is relatively low, but they are of great economic significance. They increasingly operate on a global scale. As the following subchapters will illustrate, the structure, including the ownership, of breeding organizations differs greatly between species.

4.1 Dairy and beef cattle breeding

Selection criteria

In dairy cattle, the average milk, fat and protein production per cow per year has increased enormously in the past decades as a result of the widespread use of breeds such as the Holstein-Friesian and intensive within-breed selection. This increase is also a reflection of the fact that productivity has for many years been an important selection objective, with selection mainly being based on production and morphological traits.

Recent years have seen a growing concern on the part of consumers about animal welfare issues, and about the use of antibiotics in livestock production. Breeding organizations have also realized that selecting solely for product output per animal leads to a deterioration of animals' health and reproductive performance, increased metabolic stress and reduced longevity (Rauw *et al*., 1998). As a result, emphasis on functional traits has increased, and less attention is paid to product output. Selection for functional traits is now based on direct recording of these traits rather than through type traits. Breeding values for a wide range of functional traits have been developed and applied in most countries. This enables breeding organizations and farmers to pay direct attention to these traits in their selection decisions.

Box 81
Calving problems in Belgian White Blue cattle

In beef cattle, the demand for high-quality meat has led to the use of breeds, such as the Belgian White Blue, that have extreme phenotypes. However, this breed has an extremely high rate of caesarean sections (Lips *et al*., 2001). In the short term, this rate cannot be significantly reduced. The extreme muscularity of the Belgian White Blue is mainly caused by the myostatin gene, a single autosomal recessive gene which is located on chromosome 2. It is, therefore, questionable whether a reduction in calving difficulties can be realized while maintaining the extreme muscularity. Because of this, as well as the obvious animal welfare concerns, the future of the breed is questionable.

Box 82
Cross-breeding to address inbreeding-related problems in Holstein cattle

The Holstein breed, which is composed almost completely of American Holstein genes, has largely replaced other breeds of dairy cattle throughout much of the world. Production and conformation traits have been emphasized in the breeding of Holsteins because of moderately high heritability and ease of data collection. However, female fertility, calving ease, calf mortality, health and survival have been ignored until very recently. Problems related to functional traits, coupled with increased inbreeding on an international scale, have resulted in tremendous interest in cross-breeding among commercial dairy producers. Pure-bred sires will continue to be sought to breed almost all dairy heifers and cows for cross-breeding. Most cross-breeding systems with dairy cattle will make use of three breeds to optimize the average level of heterosis across generations.

For further information see: Hansen (2006).

TABLE 99
Breeding objectives in ruminants

Objectives/product	Criteria	Further specification
Production traits		
Milk	Quantity	Milk carrier production
	Contents/quality	Fat percentage, protein percentage, somatic cell count, milk coagulation
Beef	Growth rate	At different ages
	Carcass quality	Fat content, bone/meat ratio
	Meat quality	Tenderness, juiciness
Wool	Quantity Fibre quality	 Length, diameter
Functional traits		
Health and welfare	Genetic defects	BLAD, mule foot and CVM
	Mastitis incidence	
	Udder conformation	Udder attachment, udder depth and teat traits
	Feet and leg problems	
	Locomotion	Indicator of hoof disorders
Reproduction efficiency	Female fertility Male fertility Calving ease Number of live offspring	Showing heat, pregnancy rate Non-return rate Direct and maternal effects, still births
Feed Efficiency	Feed conversion efficiency Milk production persistency	
Workability	Milkability Behaviour	Milking speed
Longevity	Functional herd life	

Breeders face difficulties in two areas – breeding (including recording) and marketing. With regard to breeding, there are problems associated with correlated responses to selection. In most cattle breeding programmes, an aggregate index is constructed that includes traits such as growth, milk yield, fertility, conformation, number of somatic cells in the milk, calving ease and duration of productive lifespan (for more details see Table 99). In dairy cattle, the main focus has been (and is still) put on milk yield, despite the negative genetic correlations between milk yield and reproduction and health-related traits. Undesired side-effects have, therefore, been observed – including lower fertility, and greater susceptibility to mastitis, leg problems and ketosis.

In beef cattle and in sheep, selection for growth has led to higher birth weights and increasing risk of birth problems. Higher growth rates can also be expected to increase the mature size of breeding females. This may result in lower reproductive rates if larger animals are unable to meet their nutritional requirements because of limitations in the quantity or quality of the available forage. These undesired effects can be avoided, or at least reduced, by increasing the weight of functional traits within selection indices. This supposes that these traits can be directly measured. Recording of functional traits often remains an important bottleneck hindering their inclusion in breeding schemes. This is illustrated by the example of efficiency of feed utilization. Recording feed intake in a large number of animals is currently impossible – preventing efficient selection for this trait.

There are also problems related to marketing. For milk, good management practices have been in place in many countries for a long time, and product quality has a direct impact on the price paid to producers. In the case of meat, however, traceability and organization in the production chain has traditionally been poor. This limits opportunities to improve quality. In general, farmers are not rewarded for meat quality, and often only poorly rewarded for carcass quality.

Organization and evolution of the breeding sector

Because of the low reproductive rate, the long generation interval and the large amount of space required to house each animal, cattle breeding has a more complex and more open organizational structure than poultry or pig breeding. Gene flow can occur both from the breeder to the producer and vice versa. Information resources are shared between players at different levels. In a typical dairy cattle breeding programme, pedigree information is often recorded, owned and managed by breed societies, while milk production records are owned by farmers, but collected and managed by milk recording organizations. Information on fertility and reproductive performance are kept by companies that provide AI services, while health information generally resides with veterinarians. Often, these organizations are in decentralized locations and may store information in different systems.

Because cattle production is a major traditional agricultural enterprise and because breeding has a major impact on this enterprise, cattle breeding programmes have more input from government agencies than do poultry or pig breeding, and therefore have a country-specific outlook. Most programmes were either initiated or sustained with support or grants from national government agencies (Wickham, 2005). Organizations such as the Animal Improvement Programs Laboratory (AIPL) of the United States Department of Agriculture (USDA), Canadian Dairy Network (CDN), Cr-Delta in the Netherlands, and l'Institut de l'Elevage (IE) in France, play major roles in cattle breeding programmes in their respective countries, especially in data management and genetic evaluation. This is also the case for breed societies, which have played a major role in maintaining and enhancing the integrity of their respective breeds. The success of the Holstein-Friesian, which is by far the dominant sire breed in most dairy herds in the Western world, is testimony to the activities of the World Holstein-Friesian Federation (WHFF). The formation of

Box 83
Norwegian Red Cattle – selection for functional traits

The Norwegian Red (NRF) is a high-producing dairy cattle breed in which fertility and health have been included in a selection index (known as the Total Merit Index) which has been in operation since the 1970s. The case of the NRF provides a practical illustration that production and functional traits can be successfully balanced in a sustainable breeding programme. This achievement has been based on an effective recording system and a willingness to place sufficient weight on the functional traits. The programme is run by GENO, a cooperative owned and managed by Norwegian dairy farmers. Currently, ten traits are included in the Total Merit Index. The following list shows the relative weight given to each:

Milk index	0.24
Mastitis resistance	0.22
Fertility	0.15
Udder	0.15
Beef (growth rate)	0.09
Legs	0.06
Temperament	0.04
Other diseases	0.03
Stillbirths	0.01
Calving ease	0.01

Key features of the programme include the fact that more than 95 percent of herds participate in the recording system and are on a computerized mating plan, 90 percent of matings are carried out using AI, and there is 40 percent use of test bulls. All diagnosis and health registration is carried out by veterinarians, and databases are maintained for pedigree and AI-related information. About 120 young bulls are tested annually with progeny groups of 250 to 300 daughters – thus enabling the inclusion of traits with low heritability (such as mastitis with a heritability of 0.03 and other diseases with 0.01) while still providing a selection index with high accuracy.

Milk production per lactation in the best herds exceeds 10 000 kg, with the top cows producing more than 16 000 kg. The genetic trend is positive with respect to fertility – the average 60 day non-return rate in the population is 73.4 percent. Between 1999 and 2005 incidence of mastitis in NRF cows was reduced from 28 percent to 21 percent, and it is estimated that of this reduction 0.35 percent per year was the result of genetic improvement. Major calving difficulties are reported in less than 2 percent of calvings, and less than 3 percent of calves are stillborn.

The sustainability of the breeding programme is promoted by a number of factors:

- Both production and function are expressed by many traits, and they are both strongly weighted in the breeding strategy.
- Many different combinations can result in a high total breeding value. This allows for the selection of animals from different breeding lines and, thus, automatically reduces the risk of inbreeding.
- The breeding work is based on data from ordinary dairy herds, which guarantees that the breeding programme produces animals that are well adapted to normal production conditions.

Provided by Erling Fimland.
For further information see: http://www.geno.no/genonett/presentasjonsdel/engelsk/default.asp?menyvalg_id=418

Photo credit: Erling Fimland

herd books with dedicated members and the importance of show ring performance (which are strictly within-breed affairs) have helped sustain pure-breed development and the maintenance of all major breeds of dairy and beef cattle.

The selection programmes conducted by AI centres have developed from local to national schemes, and are increasingly operating internationally. The dissemination of genetic material from "superior" animals is now global. It is predicted that within the next ten to 15 years AI centres will become unified into a few worldwide breeding companies, such as now exist in the pig and poultry sectors. For example, in the early 1990s the "Genus" breeding programme was the major cattle programme in the United Kingdom. Over the years, Genus has merged with ABS genetics from the United States of America to form a global company, which now supplies bovine genetics from a variety of dairy and beef cattle breeds to over 70 countries. More recently, Genus bought Sygen, a biotech company.

Breeding programmes in cattle rely on commercial producers to generate sufficient data for genetic evaluation. Data recording, therefore, takes place in all tiers of the breeding pyramid. This requirement is greatest in the case of dairy programmes, which require large progeny groups for the accurate evaluation of bulls (especially for traits with low heritability), or in beef cattle to be able to estimate direct and maternal effects. The use of AI to disseminate semen across many herds is prevalent, and this helps to facilitate the comparison of animals raised in different environments. AI also enables higher intensity in the selection of males.

Successful selection within dairy cattle breeds is the result of well-organized programmes for the measurement of production, testing of young bulls and effective genetic evaluation. The high level of feeding in commercial dairy production allows a high proportion of a cow's genetic potential to be expressed, which in turn allows selection to be particularly effective.

Cross-breeding studies with dairy cattle have consistently found significant levels of heterosis between dairy breeds for milk production, fertility and survival traits. However, successful long-term selection for high levels of milk production in the Holstein-Friesian has led to the widespread use of straight-bred animals of this breed. However, increasing pressure from commercial producers, who are suffering losses related to poor fertility and longevity, and the need for flexibility in product development is likely in the future to lead to increased development of hybrid cattle at the breeding programme level.

Cross-breeding applied to beef cattle is often undertaken without a well-designed programme. In beef cattle, cross-breeding programmes are difficult to implement in herds that use fewer than four bulls. Even for larger operations, managing the herds separately, as is required in organized cross-breeding programmes, can be difficult (Gregory *et al*., 1999).

In cattle, the introduction of AI has resulted in an enormous reduction of the number of sires and contributed to the exchange of genetic material between regions and countries. Through AI, bulls selected in the nucleus are used in the general population. As a result of the high reproductive rate of sires, the selection of bulls contributes 70 percent to total genetic change in dairy and beef cattle populations.

4.2 Sheep and goat breeding

Selection criteria

Sheep and goats are kept for meat, milk, and wool or fibre (see Table 99 for corresponding breeding goals). Sheep milk is an important product in Mediterranean countries. It is mainly transformed into a variety of cheeses (e.g. Roquefort, Fiore Sardo, Pecorino Romano and Feta). Milk production and quality are important breeding criteria. Milk sheep may also be bred for growth rate, reproductive traits such as twinning rate, and type traits such as udder shape (Mavrogenis, 2000). Conversely, in northwestern Europe, meat is the most significant product obtained from sheep. Specific breeding objectives will depend on the production environment (e.g. mountain vs. lowland), and may include growth rates, carcass quality, reproductive performance and maternal abilities. Commercial wool production is dominated by Australia and New Zealand with their specialized flocks of straight-bred fine-wool sheep of the Merino type. Although the animals all descend from the Merino sheep of Spain, different strains have been developed over the years. The need for animals adapted to specific environmental conditions has shaped breed development. In Australia, for example, different strains of Merino have been bred for their adaptation to the environment in different parts of the country. With respect to wool production, criteria for selection normally include clean fleece weight and fibre diameter. Increasing economic importance of meat relative to wool has led to a shifting of breeding objectives towards criteria such as reproduction rate and sale weight.

In Mediterranean countries, in South Asia, and in parts of Latin America and Africa, goats are mainly kept for their milk. In Mediterranean countries and in Latin America, goat milk is often used for cheese production, whereas in Africa and South Asia, it is consumed raw or acidified. In other parts of Asia and Africa, goats are kept mainly for meat production. In these regions very little supplemental feeding is provided, and browse provides a significant amount of the nutritional requirements. The animals are of moderate to small size, and of moderate to light muscling. An exception is the development of the Boer goat for meat production in South Africa. The breed has been introduced to other countries in Africa and to other parts of the world such as Australia.

Organization of the breeding sector

Major breeding programmes for fine-wool sheep are based in the southern hemisphere (Australia and New Zealand). These programmes are based on straight-breeding. However, in fine-wool sheep operations where a significant part of the income is from lambs (for slaughter), self-contained F1 production has been used. Under this type of programme, all ewes are straight-bred for fine wool. A large fraction of the selected ewes are mated to fine-wool rams to produce replacement females. The remaining ewes are mated to terminal sires and all the lambs are sold.

In the case of meat sheep breeding, the average size of flocks is generally too small to allow intensive within-flock selection. This problem has been overcome through cooperative breeding schemes. Nucleus breeding schemes are well established (e.g. James, 1977), but sire-referencing schemes (SRS) have recently gained popularity. In SRS, genetic links are created between flocks by mutual use of specific rams (reference sires). These connections allow comparable across-flock genetic evaluation, offering a larger pool of candidates for selection for collective goals. About two-thirds of performance-recorded sheep in the United Kingdom, including all of the major specialized meat breeds, now belong to these schemes (Lewis and Simm, 2002).

Cross-breeding is the basis of the stratified sheep industry of the United Kingdom (Simm, 1998). The system functions on the basis of a loose structure involving several breed societies, government agencies and other institutions. Traditional hill breeds such as the Scottish Blackface are straight-bred under the harsh production conditions of the hills. Ewes from these pure breeds are sold to farmers in "upland" areas (where the climate is less harsh and there is better grazing). Here, they are crossed with rams from intermediate crossing breeds such the Blueface Leicester. F1 Females are sold for breeding in lowland flocks where they are mated to terminal-sire breeds such as the Suffolk and the Texel. Most data recording and genetic evaluation aim at improving the terminal-sire breeds to produce rams of superior genetic quality. Data recording and genetic evaluations are carried out by commercial operations such as Signet or by research institutions supported by public funds.

Most dairy goats are in developing countries. However, breeding programmes are concentrated mainly in Europe and North America. The French selection programme, based on AI with frozen semen and oestrus synchronization (60 000 goats inseminated/year), and the Norwegian programme, based on rotation of sires in several herds (buck circles), are examples of organized progeny testing programmes. They include a formal definition of selection objectives and organized mating to produce young sires and their progeny. Probably, the best example of a structured meat goat breeding programme is that run by the Boer Goat Breeders' Association of Australia. Cashmere and mohair production is based on straight-breeding of the respective breeds. There is almost no cross-breeding involving Angoras.

4.3 Pig and poultry breeding

Selection criteria in pigs

As in the case of ruminants, pig breeding programmes have been very successful in achieving genetic improvement of economically important traits, especially daily gain, backfat thickness, feed efficiency and, during the last decade, litter size (for more details see Table 100). At present, the goal is to breed for more robust and efficient animals to meet different environmental conditions. This implies finding an adequate strategy to deal with genotype × environment interaction, and the placing of more emphasis on secondary traits which have up to the present been of negligible economic importance. Secondary traits include piglet survival, interval between weaning and first oestrus, longevity of sows, conformation (especially legs), vitality of pigs until slaughter weight, meat colour and

TABLE 100
Breeding objectives in pigs

Objectives	Criteria	Further specification
Production traits		
	Growth rate	At different ages
	Carcass weight	
	Carcass quality	Uniformity, leanness of carcass
	Meat quality	Water holding capacity, colour, flavour
Functional traits		
Health and welfare	General resistance	Robustness
	Vital piglets Survival of pigs	Maternal ability, teat number
	Stress	Elimination of stress (halothane) gene in dam lines, and where possible, in male lines
	Congenital effects	Examples: atresia ani, cryptorchism, splay leg, hermaphrodism and hernia
	Leg problems	Leg weakness and lameness.
Efficiency	Litter size	Number of slaughter pigs per sow per year
	Feed conversion efficiency	
Longevity	Functional herd life	Lifetime production with minimal health problems

TABLE 101
Breeding objectives in poultry

Objectives/product	Criteria	Further specification
Production traits		
Egg	Egg number	Number of saleable eggs per hen
	External egg quality	Average egg weight, shell strength and colour
	Internal egg quality	Egg composition (yolk/albumen ratio), firmness of albumen and freedom from inclusions (blood and meat spots)
Meat	Growth rate	Weight gain; age at market weight
	Carcass quality	"Yield" in terms of valuable parts, especially breast meat; select against breast blisters and other defects to reduce condemnation rate
Functional traits		
Health and welfare	Disease resistance	Not routinely used
	Monofactorial genetic defects	
	Leg problems in broilers and turkeys	
	Osteoporosis in laying hens	
	Heart and lung insufficiency	Incidence of "sudden death syndrome" and ascites in broilers and "round heart" in turkeys
	Cannibalism, feather pecking	
Feed efficiency	Feed consumption per: • kg egg mass in laying hens, • kg weight gain in broilers and turkeys	
	Residual feed consumption	
Longevity	Length of productive life	

drip loss. The health of the pigs is becoming more important. This means not only improving the sanitary status in breeding farms, but also selecting for general disease resistance under commercial conditions.

As in the case of ruminants, there are some difficulties involved in implementing efficient selection for "functional" traits. There are still no appropriate tools to select for better resistance to diseases or to reduce metabolic disorders. Sufficient knowledge of the genetic aspects of welfare is lacking. Stress recording methods need to be improved – for example, through the use of non-invasive methods for measuring stress-indicating parameters, determination of catecholamine levels, and heart-rate recording on under-skin chips. Improved knowledge of the cognitive abilities and coping strategies of pigs might enable individual characteristics to become indicative of ability to adapt to various housing conditions and social challenges, and could be included in selection criteria. Additionally, there is a need for further assessment of the impact of selection for specific disease resistance and welfare objectives.

Selection criteria in poultry

Laying hens have been selected mainly for productivity. Over several decades, breeding programmes were refined, and more and more traits were included in the selection objectives. Today, the main selection objectives are: the number of saleable eggs per hen housed per year, efficiency of converting feed into eggs, external and internal egg quality, and adaptability to different environments (for more details see Table 101).

For poultry meat, substantial genetic improvements in terms of market weight at a younger age and correlated feed efficiency have been achieved by simple mass selection for juvenile growth rate and "conformation". During the 1970s, direct selection for efficient feed conversion was introduced. During the last two decades, the emphasis of selection has shifted increasingly to traits that are of primary importance to processing plants – breast meat yield, total carcass value, efficiency of lean meat production, uniformity of product, and low mortality and condemnation rates. The development of specialized male and female lines, and the introduction of controlled feeding of parents, are effective tools to overcome the negative correlation between juvenile growth rate and reproductive traits.

The most obvious challenges for the poultry industry are related to diseases. Primary breeding companies have eliminated egg-transmitted disease agents such as leucosis virus, mycoplasms and *Salmonella* from their elite stock, and continue to monitor freedom from these problems. Other diseases such as Marek's disease, *E. coli*, *Campylobacter coli*, and highly pathogenic avian influenza are more difficult to control.

In the field of animal welfare, the main challenges for breeders are to adapt laying hens to alternative management systems – for example, to reduce feather pecking and cannibalism in non-cage systems (pecking and cannibalism are also serious problems for turkeys and waterfowl), and to reduce the incidence of cardio-vascular insufficiencies (sudden death syndrome and ascites) and leg problems in broilers and turkeys. However, the causes of these problems are probably multifactorial, and further research is required.

Organization and evolution of pig and poultry breeding sectors

The modern poultry industry has a typical hierarchical structure with several distinct tiers. Breeding companies based mainly in Europe and North America, with subsidiaries in major production regions, own the pure lines. They have to keep the whole production chain in mind – hatcheries, egg and meat poultry growers, processing plants, retailers and consumers. Hatcheries (multipliers) are located near population centres around the world. They receive either parents or grandparents from the breeders as day-old chicks, and produce the final crosses for egg producers and broiler, turkey or duck growers. Today, egg processing plants, slaughterhouses and feed suppliers have developed contractual relationships with egg producers and poultry growers, which provide the latter with better financial security, but at the cost of reduced initiative and freedom.

The pig sector has a similar pyramidal structure, which is largely the result of the introduction of cross-breeding, AI and specialized breeding farms. However, some differences exist between the pig and the poultry sectors. For example, a pig producer will typically obtain the "commercial" animals by mating sows from a specialized dam line and boars from a specialized sire line – both genders being bought from the breeding company (and not from a multiplier as in poultry).

In contrast to poultry, there are still breeding associations for pigs, and national genetic evaluation is performed. While genetic evaluations for the large breeding companies may be performed in-house, genetic evaluations at the pure-breed level are conducted by governmental institutions (e.g. by the National Swine Registry in the United States of America) or breed associations.

Pig and poultry breeding schemes are sometimes referred to as "commercial" breeding programmes because of the corporate ownership structure of these companies. Over the years, these programmes have amalgamated to become large corporations. In poultry, for example, only two to three groups of primary breeders account for about 90 percent of the layers, broilers and turkeys produced annually. Furthermore, some of these companies are owned by the same group. The pig breeding industry has more breeding companies and fewer large ones (such as PIC and Monsanto), but is following the same trend. The recent entry of the giant Monsanto into this sector is a clear indication of this tendency. Because of the competitive nature of the business and the high level of investment, "commercial" breeding companies are usually at the forefront in the application of technologies. These leading companies are on the verge of incorporating genomic information in their breeding programmes, at a time when many breeders are merely discussing the feasibility of the approach.

The activities of these commercial breeding companies are characterized by the following features:

- Pedigree selection occurs in the nucleus only.
- Selection is strictly within specialized lines (or breeds). These lines are designated as sire and dam lines and are selected with different intensities. In poultry bred for meat and in pigs, male lines are selected for growth and lean meat production, while female lines are selected for reproduction. New lines are constantly developed either by crossing between existing lines or by further selection in a given direction.
- The final product is a cross between two or more pure-bred lines.

For economic reasons, each breeding company will sell under several trademarks (accumulated through acquisitions and fusions), but will in fact only have a limited number of differentiated products. Indeed, pig or poultry breeding companies develop lines to meet few (two or three) breeding goals, which vary depending on the extent of their global market share and the degree of variation in the production environments in which the clients operate. For example, a breeder may develop a high-yielding, fast-growing line for use under high-input conditions where superior-quality feed allows the expression of the animals' full genetic potential, and a line for more challenging environments that is more "robust", but has lower performance for production traits.

5 Breeding programmes in low-input systems

5.1 Description of low-input systems

Many of the world's livestock will continue to be kept by smallholders and pastoralists. These producers often have limited access to external inputs and to commodity markets. Even if external inputs are locally available, there is usually little cash available for their purchase. To quote LPPS and Köhler-Rollefson (2005):

> *"Cash products are often of secondary importance, especially in marginal and remote areas. Traditional breeds generate an array of benefits that are more difficult to grasp and to quantify than outputs of meat, milk, eggs or wool. These include their contribution to social cohesion and identity, their fulfilment of ritual and religious needs, their role in nutrient recycling and as providers of energy, and their capacity to serve as savings bank and insurance against droughts and other natural calamities."*

The livestock owned by smallholders and pastoralists may be autochthonous or originate from early introductions of exotic breeds to the area. Traditional livestock keepers have no technical training in genetics and many are illiterate. However, they possess valuable local knowledge about breeds and their management. They have breeding goals and strategies even if they are not "formalized" or written down. For example, they may share breeding males (they

Box 84
Community-based sheep management in the Peruvian Andes

Agriculture in the central Andes of Peru is severely limited by low temperatures and drought, and most rural households depend on livestock for their income. Rangeland sheep are economically the most important species, and are used as a source of food, as a means of obtaining goods through exchange, and to generate cash through the sale of live animals or wool. To a lesser extent they are also used for cultural activities, recreation and tourism. Criollo sheep represent 60 percent of the Peruvian sheep population. They are mainly raised on family farms and by individual farmers, who value the local breed highly. A dual-purpose breed, developed from a cross between Criollo sheep and Corriedale sheep imported from Argentina, Australia, Chile, New Zealand and Uruguay between 1935 and 1954, is also available. Peasant farmers maintain both the Criollo and the composite breed.

In this part of Peru, peasant communities have organized themselves independently to improve the management of their sheep, with little support from the government. Multicommunal and communal enterprises, cooperatives, as well as family and individual farms, are common. Farmers exchange genetic material, experiences and technologies. Multicommunal and communal enterprises have far higher production rates than individual farmers. They have successfully set up participatory breed improvement programmes based on open-nucleus schemes, are technically efficient, keep their pastures in good condition, and use some of their profits to improve the social well-being of their members – for example, by buying school materials, selling milk and meat at reduced prices, and providing assistance to the elderly.

Provided by Kim-Anh Tempelman.
For further information see: FAO (2007).

seldom have more than one of a given species) with their neighbours or the entire community.

In conclusion, formalizing genetic improvement in these conditions is a challenging, but definitely not an impossible or inappropriate, task.

5.2 Breeding strategies

It is important to keep in mind that whatever strategy is considered, it will be successful only if certain conditions are met. Meeting these conditions does not guarantee success, but neglecting them will certainly lead to failure. The owners of the livestock should be involved as much as possible, and preferably from the very beginning of the programme. The social structure of the region and the objectives of the producers should be carefully taken into consideration. The whole system, and not only one element of it, needs to be considered. For example, when considering a cross-breeding scheme in a remote area, it is necessary to ensure that the progeny of cross-bred animals are viable in these conditions.

The programme should be as simple as possible. In some cases it may be feasible to cross-breed individual females to males from other breeds that are available in the vicinity, but programmes that require continuous use of males of more than one breed are not feasible under low-input systems.

Breeding strategies

Determining the breeding objectives is the most important and difficult task in any genetic improvement programme, and there is even less margin for error in low-input systems. The questions that need to be considered under these conditions include: what (if anything) should be changed, and what would actually be an improvement in these conditions?

A low-input system is also a low-output system, but this does not necessarily mean low productivity.

Box 85
Genetic improvement of an indigenous livestock breed – Boran cattle in Kenya

The Boran, a medium-sized cattle breed of East African origin, is the breed most widely kept primarily for beef production in the semi-arid zones of Kenya. Commercial ranchers prefer the Boran to *Bos taurus* breeds because of their relative adaptability to the local environment – achieved through generations of natural and artificial selection in conditions of high ambient temperature, poor feed quality, and high disease and parasite challenge. Boran genetic material is recommended as a means of improving beef production in other indigenous and exotic breeds in the tropics. Genetic exports to Zambia, the United Republic of Tanzania, Uganda, Australia and the United States of America occurred from the 1970s to the 1990s. Export of Boran embryos to Zimbabwe and South Africa took place during 1994 and 2000.

This market potential has been an incentive for farmers to improve the breed. By the 1970s, the Boran had undergone cross-breeding with *B. taurus* types, backcrossing, and within-breed selection (which was mainly based on visual appraisal guided by experience). During the 1970s a recording scheme was initiated. Producers sent animal performance records routinely to the Livestock Recording Centre (LRC) for genetic evaluation. However, because of inconsistency and delays in the release of evaluation results, and the expenses associated with recording, most producers opted out of the scheme. In 1998, a bull performance testing project was implemented by the National Beef Research Centre in an attempt to evaluate bulls across various herds. However, the performance testing could not be sustained because of a lack of funds.

Recently, breeding objectives for Boran production systems have been developed. Systems are classified according to the sale age of the animals (24 or 36 months), levels of input (low, medium or high), and final goal (beef or dual purpose). Traits of economic importance have been identified, and genetic parameters have been estimated for some of them. These traits include sale weight for steers and heifers, dressing percentage, consumable meat percentage, milk yield in dual purpose production systems, cow weight, cow weaning rate, cow survival rate, post-weaning survival rate, and feed intake of steers, heifers and cows.

Genetic improvement of the Boran in Kenya is facilitated by the Boran Cattle Breeders' Society (BCBS). Membership of the society is restricted to farmers keeping Boran cattle, and other interested stakeholders. At present, the activities of the society focus on administration, maintaining breed standards, and searching for new markets for both beef and genetic material. Farmers are still independent with respect to selection and genetic improvement. Occasional exchange of genetic material between herds as a means of preventing inbreeding is probably the only form of interaction between farms. On most farms, selection focuses largely on weaning weights and calving interval. To evaluate their animals, some farmers have purchased various computer programmes to enable them to re-orientate on-farm performance recording to suit their management purposes.

The BCBS is among the most active breeders' associations in Kenya. It is not at present subsidized financially, but is involved in strategic cooperation with the LRC which stores and evaluates performance records for those producers still participating in the recording scheme. The BCBS also cooperates with the National Agricultural Research System in the exchange of information – especially on nutrition and breeding. Research aimed at developing appropriate genetic improvement programmes for the Boran and updating the current ones is ongoing.

Provided by Alexander Kahi.
For more information on Boran cattle and BCBS see: www.borankenya.org

Box 86
A llama breeding programme in Ayopaya, Bolivia

In the high Andes of Bolivia, llama keeping is an important and integral part of the mixed farming practised by rural households. Llamas provide smallholders with dung, meat and fibre; they are used as pack animals and also play an important social role. Llamas, as an autochthonous species, contribute to maintaining the ecological balance of the fragile local ecosystem. There are two main types of llama – the "Kh'ara" type, and the wool type known as "Th'ampulli".

The region of Ayopaya (department of Cochabamba) where the breeding programme takes place is situated at 4 000 to 5 000 metres above sea level in the eastern Cordillera of the Andes. Because of the geographical conditions and very basic infrastructure, the region is difficult to access.

In 1998, a breeding programme for llamas was jointly initiated by the 120-member local producers association ORPACA (Organización de Productores Agropecuarios de Calientes), the NGO ASAR (Asociación de Servicios Rurales y Artesanales) and two universities (University Mayor de San Simon, Cochabamba, and University of Hohenheim, Germany). Initial funding was assured by the above-mentioned institutions. Continuation of the programme critically depends on securing external funding.

Llamas in Ayopaya region

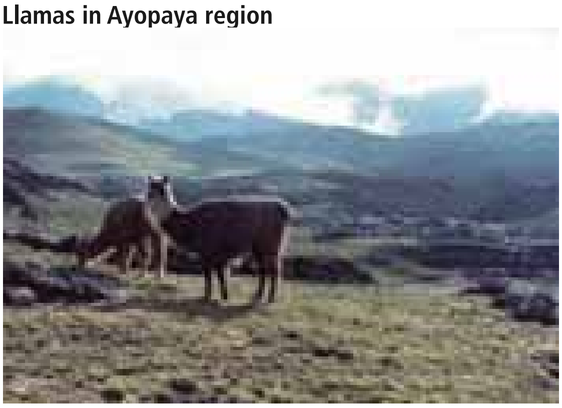


Photo credit: Michaela Nürnberg

Restraining llamas for transport

Photo credit: Michaela Nürnberg

As a first step, the production system was studied by participative observation and the use of questionnaires. The phenotype of 2 183 llamas of the Th'ampulli type was also characterized. The process revealed that the llamas possess fibre of extraordinarily high quality – 91.7 percent fine fibres and a fibre diameter averaging 21.08 μm. This fibre quality is unmatched by other llama populations in Bolivia. The animals, therefore, constitute a unique genetic resource. Interviews with representatives of the textile industry and traders provided information on the economic potential of the fleece. The performance of identified llamas was recorded and breeding parameters estimated. A mating centre run by ASAR to which members of ORPACA bring their females for service was established in Calientes in 1999. Selected males are kept at the centre during the mating season. The phenotypic evaluation of the males aims to identify animals with uniform fleece colour; a straight back, legs and neck; testicles that are of equal size and not too small; and no congenital defects. Six communities within a radius of about 15 km are served by the mating centre. Performance data for the offspring are recorded by trained farmers.

● *continues*

Box 86 *cont.*

A llama breeding programme in Ayopaya, Bolivia

Functions of llamas and breeding objectives are being recorded, ranked and valued jointly with the llama keepers. In a stepwise procedure, the breeding programme is being adapted to meet the breeders' preferences, the market conditions, and the biological constraints. Genetic progress has not yet been evaluated because of the llama's long generation interval.

Linear measurements on llamas

Photo credit: Javier Delgado

Provided by: Angelika Stemmer, André Markemann, Marianna Siegmund-Schultze, Anne Valle Zárate.

Further information can be obtained from the following sources: Alandia (2003); Delgado Santivañez (2003); Markemann (forthcoming): Nürnberg (2005); Wurzinger (2005), or from: Prof. Dr Anne Valle Zárate, Institute of Animal Production in the Tropics and Subtropics, University of Hohenheim, 70593 Stuttgart, Germany.
E-mail: inst480a@uni-hohenheim.de

Llama herd (of Emeterio Campos) in Ayopaya region

Photo credit: André Markemann

Deworming during sire selection at Milluni

Photo credit: André Markemann

Box 87
Pastoralists' breeding criteria – insights from a community member

The East African pastoralists of the Karamoja cluster [4] keep a range of livestock including Zebu cattle, Small East African goats, Persian Black Head sheep, grey donkeys and light brown dromedaries. Some also keep indigenous chickens. Uses of livestock are diverse, and include food; a store of wealth, and a currency against which other commodities can be valued; a source of recreation and prestige; a means for the payment of debts, fines and compensations; a means of transport and agricultural traction; a source of skins and fibres; and a source of dung for fuel, fertilizer or building. Livestock also have many cultural roles such as being given to the bride's family at the time of marriage. They are also slaughtered at the time of rituals associated with births; funerals; the onset of transhumance; rain-making; averting bad omens, epidemics or enemy attack; cleansing ceremonies; or curing an ailment on the prescription of a village herbalist.

Criteria for breeding decisions are multifaceted, and reflect the interaction of social, economic and ecological factors. They include not only productivity, but also the taste of meat, blood, and milk; agreeable temperament; coat colour; religious requirements; disease and parasite resistance; mothering instincts; walking ability; tolerance of droughts; survival on meagre feed; and tolerance of extremes of temperature or precipitation.

Criteria for breeding decisions (in order of importance)

A breeding bull should:

- be active and agile – so as to serve all the females in the herd in a given breeding period (it is considered that such bulls are tolerant of diseases and parasites, and that diseases in them are easily detected);
- produce offspring that can maintain their body weight (and milk yield in the case of females) even during periods of feed shortage;
- have large body size and weight – important for marketability and status, but be not too heavy to perform its breeding functions;
- be tall, with a wide chest and straight back – again to meet breeding functions;
- have the coat colour or horn configuration identified with the owner[5] or the community;
- have a coat colour and quality suitable for marketing or other uses;
- have good temperament – aggressive[6] towards predators, but not towards other livestock or humans;
- bulls kept to breed offspring for draught purposes should have large body weight, and be strong and tractable;
- breeding bulls should stay in the owner's herd, graze well, and not be fond of roaming or fighting other bulls.

• *continues*

[4] "Karamoja Cluster": The entire Ateker people in Uganda, Kenya, Ethiopia and the Sudan who generally share a common livelihood. "Ateker" people: (variously called "Ngitunga/Itunga" = the people). The people with a common origin living in Uganda (NgiKarimojong including Pokot, Iteso), Kenya (NgiTurukana; Itesio, Pokot); Ethiopia (NgiNyangatom/NgiDongiro) and in the Sudan (NgiToposa) and their neighbours; who speak similar languages and refer to their clans as Ateker (pl. Ngatekerin/ Atekerin). Some clans of Ateker people are spread all over Karamoja cluster.

[5] Pastoralists also base their own name on the colour or horn configuration of their favorite bulls. This is typical in the Karamoja Cluster. Such names have the prefix Apa- which means "the owner of the bull with a ... coat colour/horn configuration". For instance, the name "ApaLongor" means "the man with a bull with a brownish coat colour". The favourite breeding bull receives many privileges from the owner such as being adorned with a bell, or prompt treatment when ill.

[6] Indiscriminate aggression is unacceptable in livestock, even if other traits are favourable.

Box 87 *cont.*
Pastoralists' breeding criteria – insights from a community member

Female breeding animals should:

- have a stable high milk yield that is not only tasty and has ample butterfat content, but is also able to maintain healthy and quick growth of the offspring;
- be able to calve regularly and produce quick-growing offspring;
- be tolerant of disease, heat, cold and long droughts;
- survive on little feed and maintain high milk yield, particularly in the dry season when the feed quantity and quality is low;
- the udder should be wide and the teats always complete;
- cows should be docile to humans and other livestock, but aggressive towards predators;
- small stock (goats, sheep) should regularly give birth to twins[7].

The world should appreciate the role pastoralists play in sustainably utilizing their uniquely adapted breeds. Not only do these animals provide food and income security for their keepers, but they also contribute to the maintenance of genetic diversity, thereby providing a resource for future genetic improvement programmes. In this regard, pastoralists need appropriate support from livestock services provided by national governments, civil society organizations and the international community.

Provided by Thomas Loquang (member of the Karimojong pastoralist community).
For further information see: Loquang (2003); Loquang (2006a); Loquang (2006b); Loquang and Köhler-Rollefson (2005).

For the low-input system, it is inadequate to think of genetic improvement only in terms of increases in output traits, such as body weight, milk or egg production, or fleece weight. Efficiency is also a key criterion. Unfortunately, very little is known about the genetic improvement of intrinsic efficiency. Increased efficiency is usually measured in terms of increased gross efficiency. The increased gross efficiency observed in high-producing animals results from the fact that a lower proportion of the animals' nutrient intake is used for maintenance, and a correspondingly higher proportion is used for production. This does not mean that the animal needs less feed to achieve a given level of performance.

Selection based on residual feed intake (RFI) has been proposed as a means of improving intrinsic efficiency. This is an important criterion for all species and all production systems. Genetic selection to reduce RFI can result in animals that eat less without sacrificing growth or production performance (Herd *et al*., 1997; Richardson *et al*., 1998). For example, in contrast to the ratio of weight gain/feed intake, residual feed consumption is relatively independent of growth. RFI is therefore a more sensitive and precise measurement of feed utilization (Sainz and Paulino, 2004).

[7] Please note that it is a taboo for small ruminants to deliver twins at the first delivery. It is allowed only in the subsequent births. Similarly, it is a taboo for cattle to deliver twins whether at the first or subsequent delivery. Any such situations (births of twins) would lead to the animals concerned being slaughtered by stoning or beating. An animal in this situation is said to have become a witch and as such should be promptly eliminated!

Box 88
The Bororo Zebu of the WoDaaBe in Niger – selection for reliability in an extreme environment

This example refers to cattle breeding in a specialized pastoral system in Niger. The WoDaaBe are full-time cattle keepers. Marketing livestock is the cornerstone of their livelihood strategy. Their herds contribute a substantial proportion of national cattle exports, particularly to the large markets of Nigeria where Bororo animals sell at a premium.

"Extreme environment" here refers to a combination of a harsh ecosystem characterized by stochastic events, and comparatively poor access to both primary resources and external inputs. WoDaaBe herders exploit a semi-arid territory characterized by erratic and unpredictable rainfall. In an ordinary year, fresh grass is available for only two to three months at any given location. Access to forage, water and services requires a degree of purchasing power and negotiation with neighbouring economic actors competing for these resources. The WoDaaBe are usually on the weaker side in these transactions.

It has been proposed that the concept of "reliability" is key to understanding the management strategies of pastoralists under such conditions (Roe *et al*., 1998). "High-reliability" pastoral systems are geared to the active management of hazards rather than their avoidance, with the aim of ensuring a steady flow of livestock production. In these systems, breeding has to be closely interconnected with the environment and the production strategy. The main goal of the WoDaaBe is to maximize the health and reproductive capacity of the herd throughout the year. Their management system aims to ensure that the animals eat the highest possible amount of the richest possible diet all year round (FAO, 2003). This involves specialized labour, focusing on managing the diversity and variability of both grazing resources and livestock capabilities.

Photos credit: Saverio Krätli

• *continues*

Box 88 *cont.*
The Bororo Zebu of the WoDaaBe in Niger – selection for reliability in an extreme environment

The nutritional value of the range is maximized by moving the herd across zones that show spatially and temporally heterogeneous distribution of fodder. Additionally, the animals' capacity as feeders is stretched beyond the natural level. While feeding capacity has in part a genetic base (for example the enzymatic system or the size and conformation of the mouth), it can also be greatly affected by learning, based on individual experience and imitation between social partners (for example efficient trekking and grazing behaviour and diet preferences). Animals' feeding motivation is manipulated through optimizing their digestive feedback, and ensuring best fodder quality and preferred foraging conditions. A carefully diversified diet of grasses and browse is favoured, in order to correct nutritional imbalances which, particularly during the dry season, could keep feeding motivation low by triggering negative digestive feedback. The dry-season watering regime is also tailored in order to hone cattle's digestive performance to meet the herders' long-term strategic goal of maximizing reproduction.

The production strategy is very demanding on both people and the herd. With the onset of the dry season, while other pastoral groups sharing the same ecosystem move closer to water points, where water is more accessible but pasture is poor, the WoDaaBe move in the opposite direction, trying to keep their camps close to prime fodder. This results in long-distance mobility and a watering regime which, at the peak of the hot season, often involves journeys of 25–30 kilometres to reach the well, with the herd drinking every third day.

It is, therefore, essential to the WoDaaBe's production strategy that functional behavioural patterns are maintained within the herd. Consequently, their breeding system focuses on fostering social organization and interaction within the herd. It encourages sharing of animals' feeding competence across the breeding network, and tries to guarantee the genetic and "cultural" continuity of successful cattle lineages within the network. These lineages have proved capable of prospering under the WoDaaBe's herd management system, and over a long enough period to have included episodes of severe stress. The breeding strategy focuses on ensuring the reliability of the herd's reproductive performance, more than on maximizing individual performance in specific traits.

Breeding involves selective mating of cows with matched sires, and a marketing policy that targets unproductive cows. Less than 2 percent of the males are used for reproduction. Close monitoring of the herd allows early detection of oestrus and ensures that more than 95 percent of births result from match-making with selected males. A different sire is used for almost every oestrus of a particular cow, with an overall ratio of about one sire every four births. Pedigree sires are borrowed across large networks of (often related) breeders. Sire borrowing remains frequent (affecting about half the births) even when a breeder owns pedigree sires of his own. Match-making with non-pedigree sires, owned or borrowed, affects about 12 percent of births. Both practices are maintained explicitly in order to preserve variability. Matrilineal genealogies and the sire of each animal in the herd are usually remembered, together with pedigrees of special sires, and the identity and owner of all borrowed sires.

A cow's productivity depends heavily on how well the animal responds to the management system. By adopting a production strategy that manipulates the animals' experience of the ecosystem, the herder exposes his animals to diverse natural environments involving particular combinations of favourable and unfavourable foraging and watering conditions. Over the years, some cows prosper and produce a numerous progeny while others die or struggle and are sold. In this way, the WoDaaBe are able to harness natural selection pressure for their breeding purposes.

Provided by Saverio Krätli.
For more information see: Krätli (2007).

Box 89
Community-driven breeding programmes for local pig breeds in north Viet Nam

In the mountainous areas of Northwest Viet Nam, livestock breeding and management programmes, can contribute to improving rural livelihoods if they respect the production objectives, intensity and resource-availability of the area's resource-poor smallholder mixed farming systems. The local Ban pig which shows considerable hardiness, but has a low reproductive and growth performance is increasingly being replaced by higher-yielding Vietnamese Mong Cai sows from the Red River Delta.

In a collaborative project between the National Institute of Animal Husbandry (NIAH) Hanoi and the University of Hohenheim, Germany[8], community-based pig breeding programmes have been established in seven villages, differing in terms of their remoteness and market access.

A total of 176 households currently participate in the programmes. On-farm performance testing schemes have been developed. Farmers are provided with data sheets on which they record the performance of their pigs (mainly date of farrowing and number of piglets). Vietnamese and German researchers cross-check data and collect additional data by weighing and identifying animals when they visit the villages. Specially trained farmers enter the data into the project databank using the PigChamp® software and researchers analyse the data.

Farmers in Viet Nam often receive money for their participation in projects; in the case of this project, compensations are gradually being reduced. Results are fed back to farmers at seminars/training modules, and are further used to optimize breeding (gilt selection and optimization of mating plans). In order to ensure long-term sustainability, local partners such as the province Department of Agriculture and Rural Development (DARD) and the sub-Department of Animal Health of Son La province, are actively involved and trained. Cooperation with provincial extension services will be strengthened in the current project phase. In earlier phases, the service's strong orientation towards intensive management in favoured regions meant that exchanges were limited. Financial support for the future of the project seems to be available thanks to NIAH's official mandate to carry out projects on AnGR conservation. Moreover, the marketing element of the current project is aimed at ensuring long-term economic viability.

Initial performance testing results indicate that Mong Cai and their cross-bred offspring (sired by exotic boars) are more suited to semi-intensive, market-oriented production conditions, where the higher levels of inputs needed to achieve higher production can be provided. They seem to be less robust in the harsh upland climates and under conditions of low and varying input intensity. Ban pigs are only suited for the extensive conditions of subsistence-oriented resource-poor farming. As the project continues, efforts are being made to further develop breeding goals, to optimize stratified breeding programmes, and to implement marketing programmes. Close to town, lean meat is produced from the cross-bred offspring of Mong Cai sows. Production of Ban pigs continues in remote locations with pure or cross-bred animals marketed as a branded speciality – contributing to the "conservation through use" of this local breed.

Provided by Ute Lemke and Anne Valle Zárate.
Further information can be obtained from the following sources: Huyen, *et al.* (2005); Lemke, (2006); Rößler. (2005), or from: Prof Dr Anne Valle Zárate, Institute of Animal Production in the Tropics and Subtropics, University of Hohenheim, 70593 Stuttgart, Germany.
E-mail: inst480a@uni-hohenheim.de

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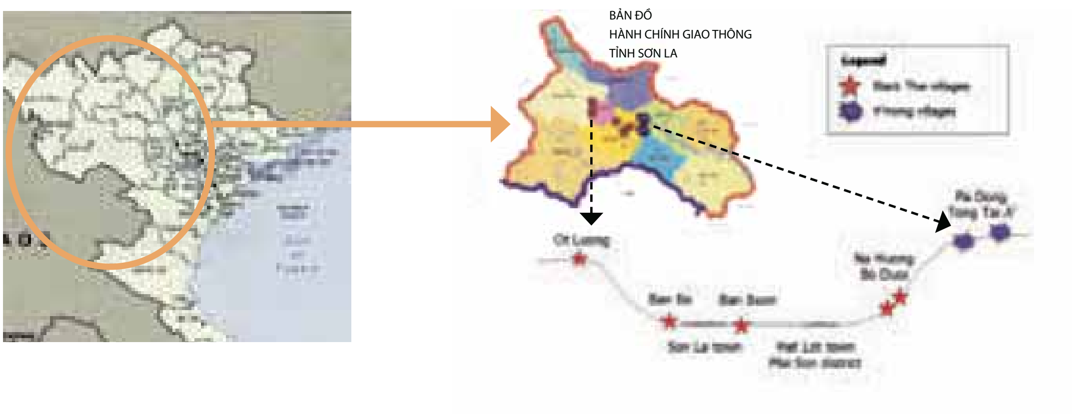
[8] Funded by the German Research Association (DFG) in the frame of the Thai-Vietnamese-German collaborative research programme SFB 564 and by the Ministry of Science and Technology, Viet Nam.

Box 89 *cont.*

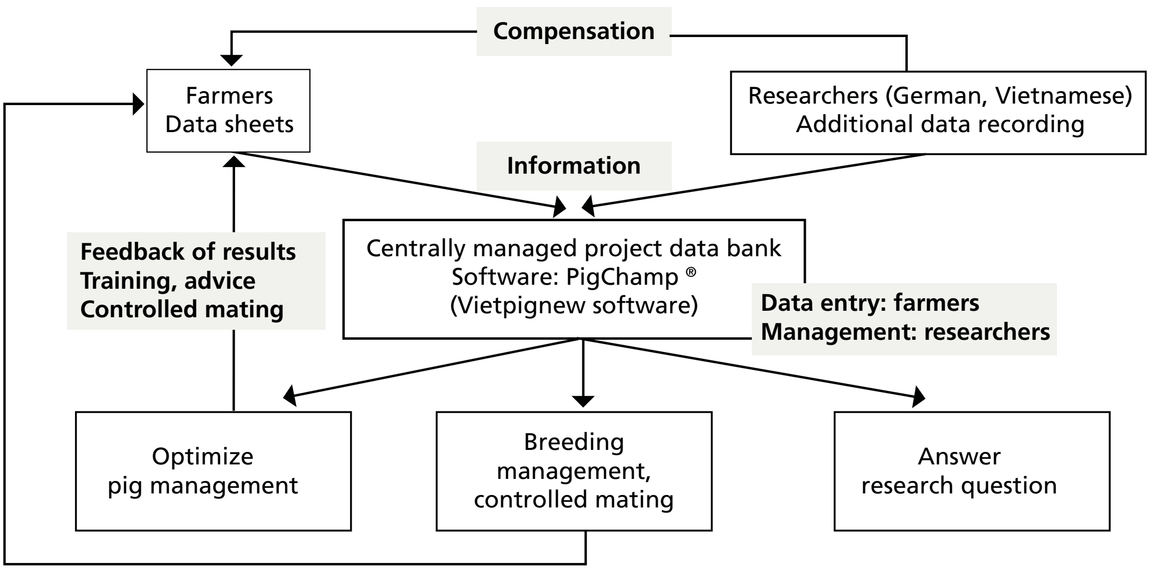
Community-driven breeding programmes for local pig breeds in north Viet Nam



Mong Cai sow

Ban fatteners

Photos provided by Ute Lemke



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Box 89 *cont.*
Community-driven breeding programmes for local pig breeds in north Viet Nam

Pigs in Song Ma district

Photo credit: Pham Thi Thanh Hoa

Weighing pigs in Pa Dong, Mai Son district

Photo credit: Regina Rößler

Data recording in low-input systems

The absence of a credible recording scheme and resources for adequate data storage and management hinder the development of sustainable breeding programmes in low-input systems. Running a computerized database can be expensive and may require specialized skills. The absence of technical skills and financial resources has been identified as the main obstacle to the establishment of sustainable animal recording systems in many African countries (Djemali, 2005). Continuous advances in information technology mean that data recording devices are becoming cheaper and offer greater potential for recording in low-input systems. The use of hand-held devices, laptops and the Internet could make it easier for small numbers of people to gather and transmit large amounts of data from remote locations to a central database. Such a database could be based in a university or a government department. Provision of facilities of this type is one way in which governments or donor agencies could facilitate the development of breeding programmes for low-input systems in developing countries.

Breeding schemes

If genetic change is justified, how can it be achieved? The choice is between straight or cross-breeding, but choosing the appropriate option is far from simple.

In low-input systems, adaptation to the environment is a prerequisite for improved efficiency. This is a matter of great importance, as intervention to reduce environmental stresses (supplementary feeding, parasite treatments or other management inputs) is often unaffordable. In these circumstances, straight-breeding to improve well-adapted indigenous breeds may be an option. Implementing a straight-breeding programme is a long-term undertaking, requiring considerable resources, good organization, and (most of all) commitment of all stakeholders. These requirements tend to be lacking under low-input systems in the developing world, and programmes that do exist are only of a very limited scope. For example, most controlled breeding of the West African Dwarf Goat has been in research institutions (especially in those in Nigeria) (Odubote, 1992).

Cross-breeding with an exotic breed may appear to be a more rapid means to improve performance with a minimal increase in inputs. However, the higher performance of the cross-breeds is accompanied by higher nutritional and management requirements (disease control, housing, etc.). Therefore, any system that incorporates higher-performing cross-bred animals will require (among other needs) more feed resources – which in many cases can only be achieved by maintaining a smaller number of animals.

If, after careful analysis, cross-breeding is considered to be a better option than straight-breeding the local breed, the programme should be developed in a way that can be sustained with locally available inputs. Cross-breeding with an exotic (non-adapted) breed presents particular difficulties. Even if the F1 animals are sufficiently adapted, the pure-bred exotic males will usually be under environmental stress, and this will often result in a reduced reproductive life. Even if the male of the exotic breed can be successfully maintained, the backcross resulting from mating F1 females with the exotic males will almost always lack adequate adaptation to the area. Therefore, the F1 females should preferably be mated to adapted-breed sires.

One option under these conditions is to use F1 males, generation after generation. Under such a system, the original local females are mated to F1 males, resulting in offspring that are 1/4 exotic. These quarter-blood females are, in turn, mated to F1 males, resulting in females that are 3/8 exotic. After a few generations the animals would be very close to half exotic. This system introduces exotic influence into the population, but never uses or produces any animals that are more than half exotic.

Another option for cross-breeding under low-input systems is to cross different breeds that are well adapted to the production conditions. The obvious advantage of such programmes is the ability to maintain and produce the breeding stock in the area without additional inputs. It

Box 90
The cost of heterosis

Heterosis has sometimes been referred to as a free opportunity for increased profitability. Although it may be worth more than it costs, heterosis is not free. It involves at least two types of costs.

First, there is the cost involved in meeting the nutritional requirement for the additional performance. The higher performance of the cross-bred animal tends to reduce the cost per unit of production, because the cost for maintenance becomes a smaller fraction of the total requirement, but there is a cost for the extra production.

A second type of cost is associated with potential changes in population structure. These costs may include (1) reductions in the size (and a corresponding increase in the level of inbreeding) of an original pure-bred population which occurs because of the need to accommodate the cross-bred population, and (2) a reduced opportunity to select for female productivity in a population where some of the cross-bred females are not considered to be candidates for selection (as in any terminal-sire system).

Box 91
Nigeria's Village Poultry Improvement Scheme

A Village Poultry Improvement Scheme aimed at upgrading the indigenous breed of chicken with improved exotic breeds (Rhode Island Red, Light Sussex and Australorp) was initiated in Nigeria around 1950 (Anwo, 1989). The strategy was to cull all indigenous males and replace them with improved imported breeds in a "cockerel exchange programme" (Bessei, 1987). This scheme failed because the cross-bred chicks, though better in performance, could not survive in the semi-wild extensive backyard production system under which the indigenous chickens were raised. Another major drawback was that breed replacement resulted in a rapid loss in genetic variation and narrowing of the available AnGR.

Box 92
A community-based and participatory dairy goat cross-breeding programme in a low-input smallholder system in the eastern highlands of Kenya

FARM Africa's Meru project in Kenya provides an example of a comprehensive and flexible cross-breeding programme. Improved goat genotypes accompanied by improved husbandry practices have been adopted by very poor farmers with incomes well below US$1 per person per day. The local goats (Galla and East African) were proving difficult to maintain on small and declining farm sizes (0.25 to 1.5 acres), and the farmers had started to abandon goat production. Consequently, the cross-breeding programme aimed to provide more docile and productive animals. Sixty-eight female and 62 male British Toggenburg goats were imported from the United Kingdom and crossed with indigenous goats: the Toggenburgs providing the dairy potential and the local goats providing adaptability. Previous introductions and trials had indicated that Toggenburgs were better adapted than other exotic dairy breeds such as Saanens or Anglo-Nubians.

The project adopted a group and community-based approach. The farmers established the project's rules, by-laws and mechanisms. It was linked to the government, NARS, and international research institutes, which provided training in husbandry (housing, nutrition, fodder production, record keeping and healthcare), group dynamics, marketing and entrepreneurship.

Farmer groups initially comprised 20 to 25 members, but some lost members over time while others grew. Four such groups were linked in a unit (mainly for administrative and monitoring purposes), with representatives being elected to a larger body the Meru Goat Breeders' Association (MGBA). Small (one buck and four does) breeder units were provided (as a loan to be paid back in kind) to one group member, who produced the Toggenburgs (T) needed for breeding stock. One pure-bred Toggenburg buck was provided to each farmer group and kept in a buck station, maintained by another group member. Local does were brought to the buck station for service. The resulting F1 female cross-breeds were backcrossed to unrelated Toggenburg bucks to produce ¾ Toggenburg and ¼ Local (L) animals. These were evaluated, and superior males selected to start new buck stations, where they were used to serve unrelated females of similar genetic composition (¾ T and ¼ L). Initial trials had shown that such does produced adequate amounts of both milk and meat, and were reasonably adapted to the local conditions. Through the MGBA, which also registered the cross-breeds with the Kenya Stud Book, groups rotated the bucks every 1 to 1.5 years to avoid inbreeding. Farmers who wished to further upgrade towards the Toggenburg had the

Project statistics 1996 to 2004

	1996	1997	1998	1999	2000	2001	2002	2003	2004
New farmer groups	10	34	20	6	12	10	7	18	8
New buck stations	10	34	10	11	6	16	14	3	22
New breeders units	5	20	25	10	12	6	2	4	7
Buck services		809	1 994	3 376	3 936	3 892	3 253	5 660	6 500
Families participating	250	1 100	1 125	1 400	1 550	1 700	2 050	2 050	2 650
Cross-breeds produced		990	2 894	3 241	3 817	3 736	4 187	5 865	7 200

Source: FARM-Africa Dairy Goat and Animal Healthcare Project; six-monthly reports January 1996–June 2004.

• *continues*

Box 92 *cont.*
A community-based and participatory dairy goat cross-breeding programme in a low-input smallholder system in the eastern highlands of Kenya

opportunity to do so by further backcrossing the ¾ T females to unrelated pure T bucks.

Two years after FARM Africa's pull-out the number of operating groups has continued to increase. In 2006 the MGBA has 3 450 members, all of whom keep improved goats which produce between 1.5 and 3.5 litres of milk per day. The group produces about 3 500 litres of milk daily, some of which is processed and packaged for sale. Member families own more than 35 000 improved goats of which 30 percent have reliable pedigree and performance records. The performance records are used for calculating growth rates and milk yields. These data were formerly processed by FARM-Africa. After the phasing out of the project, MGBA has been encouraged to establish collaboration with universities and research institutions to support them in data processing. Most of the owners of the improved goats are no longer "poor". Some have used profits from goat production to purchase one or two dairy cows, build better houses and educate their children. Production of yoghurt and fresh pasteurized milk (adding value) is indicative of scope for further developments..

The features that made the scheme successful include:

- a farmer-based approach since its inception;
- an emphasis on capacity building so that farmers can manage the programme;
- availability of locally produced breeding material;
- a group approach – farmers train each other and share experiences;
- capacity building for extension staff, farmer-centred extension messages, and participatory approaches; and
- the community-based establishment of breeder units and buck stations.

The scheme has ensured that after the end of "the project", farmers are not reliant on government services. Breeding stock is supplied by farmers themselves, and a parallel animal healthcare service has also been established by training community-based animal health workers, with links to more qualified paraveterinarians and veterinarians. An integrated fodder and reforestation programme was also established.

Provided by Okeyo Mwai and Camillus O. Ahuya.
For further reading see: Ahuya *et al.* (2004); Ahuya *et al.* (2005); Okeyo (1997).

would be logical to assume that such crosses would produce less-productive animals and/or exhibit less heterosis than crosses between a local and an exotic breed. However, Gregory *et al*. (1985) report estimates of heterosis for weight of calf weaned per cow of 24 percent between Boran and Ankole cattle, and 25 percent between Boran and Small East African Zebu.

With any cross-breeding scheme it is important to consider the whole system and all outputs produced. Commenting the value of the European dairy x Zebu F1 cow for milk production in the tropics, LPPS and Köhler-Rollefson (2005) write "in India, many owners of cross-bred cows cannot see a use for male calves, so let them die."

6 Breeding in the context of conservation

Conservation programmes for AnGR are discussed in greater detail elsewhere in this report. The following discussion, therefore, focuses on aspects of breeding that need to be considered when implementing conservation measures. A conservation programme may simply aim at ensuring the survival of a population through monitoring and maintaining its integrity, or a programme may also have the objective of improving the performance of the population.

6.1 Methods for monitoring small populations

FAO has produced several publications on the management of at-risk small populations – see for example FAO (1998). These documents provide a more extensive review of the subject. Where the Where the objective is merely to ensure the survival of the population and the maintenance of its integrity (as a pure population), the conservation strategy is limited to monitoring the population, and ensuring that inbreeding and effective population size are within acceptable limits.

Inbreeding is the result of mating related animals. In a small population, all animals in future generations will come to be related to each other, and mating among these animals will result in inbreeding. The genetic effect of inbreeding is increased homozygosity – the animal receives the same alleles from both its parents. The degree of inbreeding and homozygosity in future generations can be predicted from the population size.

As there is almost always a much smaller number of breeding males than breeding females, the number of breeding males is the more important factor determining the amount of inbreeding. The effective population size (N_e) is a function of the number of breeding males and breeding females. If N_m represents the number of breeding males and N_f represents the number of breeding females, effective population size can be calculated as:

$$N_e = (4N_mN_f) / (N_m + N_f)$$

If the number of breeding males is the same as the number of breeding females, the effective population size is the same as the actual population size; if the numbers of males and females are different, the effective population size is less than the actual population size. If the number of breeding females is much larger than the number of males, the effective population size will be slightly less than four times the number of males.

A decrease in effective population size in livestock populations can be observed in two situations. The first and most obvious case is when the actual population size decreases. This can result from the replacement of a significant proportion of a breed with breeding animals of another breed, or from cross-breeding a significant fraction of the breed.

The second situation is when a particularly popular sire and his sons and other descendants are heavily used. From the time of the first establishment of breed societies up to the mid-1900s, much of the popularity of particular sires came about as a result of success in the show ring. In more recent times, predicted genetic value for particular traits has been the decisive factor. In dairy cattle, selection was for many years almost entirely focused on milk yield. Hansen (2001) reports that although over 300 000 head were registered by the Holstein Association USA Inc. in 2000, the effective population size was only 37 head. Using pedigree records of cattle born in 2001, Cleveland *et al*. (2005) report an estimated effective population size in the American Hereford of 85 head. The American Hereford Association registered over 75 000 head in 2001.

The level of inbreeding in a given population is dependent on effective population size rather than actual population size. The increase in the level of inbreeding per generation is expected to be $1/2N_e$. This is the increase expected per generation if each animal produces an equal number of offspring, and the animals in the initial population are not related to each other. If these assumptions are not met, the degree of inbreeding will be higher. Based on this relationship, Gregory *et al*. (1999) recommend that at least 20 to 25 sires be used per generation. This would also be a reasonable number to be used in the conservation of a breed. The use of 25 sires per generation would result in a rate of increase in inbreeding of about 0.5 percent per generation.

While the loss of effective population size is an important issue in the conservation of AnGR, it is interesting to note that successful breeders have always accepted some level of inbreeding in their programmes. These breeders established herds or flocks that met their standards – the animals produced in these closed herds or flocks inevitably came to be closely related, and inbreeding resulted (Hazelton, 1939).

6.2 Conservation through breeding

The objectives of a conservation programme may include not only ensuring the survival and integrity of the target population, but also improving its reproductive rate and performance while maintaining its specific adaptive features. Much of the above discussion of breeding strategy for low-input systems is likely to be applicable in these circumstances. This subchapter focuses on the potential risks associated with cross-breeding in the context of breed conservation.

One option to safeguard a breed is to use it as one of the components of a cross-breeding programme. However, any use of pure-bred females to produce cross-breeds will reduce the population size unless there is a reproductive surplus of females. In many cases, the environmental and management conditions do not allow for much reproductive surplus – especially in cattle, which have low reproductive rates. As such, most of the females that are raised must be retained as breeding animals in order to maintain the size of the population. In fact, the largest effect comes from the requirement for a smaller number of indigenous breeding males, brought about by the smaller number of indigenous females that are being used to produce pure-bred offspring. A logical starting point for consideration of a cross-breeding programme is, therefore, to estimate the amount of reproductive surplus in females. This can be measured in terms of the fraction of young females that are available for slaughter or for sale out of the programme (or region). As an example, for fairly well-managed beef herds in temperate areas, about 40 percent of the heifer calves are needed for replacements in order to maintain the size of the herd.

With knowledge of the reproductive surplus of females, and knowledge of the fraction of the total population that is currently made up of cross-breeds, the fraction of pure-breeds that can be utilized to produce F1s without further decreasing the population size of the pure breed can be calculated. As an example, if there is a 20 percent reproductive surplus of females and the current population is composed of 50 percent pure-breeds and 50 percent cross-breeds (includes any pure-bred females that are currently being used for cross-breeding), the population could move towards a composition of slightly more than 50 percent pure-breeds producing pure-breeds, slightly more than 20 percent pure-breeds producing F1s, and slightly less than 30 percent F1 females, without any further reduction in the size of the pure-bred population that is producing pure-breeds. These values assume that none of the females produced by the F1 females are retained as breeding females; in reality, this would probably never occur.

7 Conclusions

Breeding methods and organization vary greatly between industrialized commercial production systems and subsistence-oriented low external input systems. The current organization of the breeding sector is a result of a long evolutionary process. The latest development is the spread of the industrialized breeding model, characteristic of the poultry sector, to other species.

The industrialized breeding model uses state of the art techniques for genetic improvement. Breeding programmes are based mainly on straight-breeding and vary according to the characteristics of the species. Breeding companies market their animals worldwide. This tendency, which is well established among "commercial" pig and poultry breeders, is increasingly the case for beef and dairy cattle. To select for robust animals that are able to cope with different environments, breeders run selection programmes across different environments and management systems. However, it is not possible to have animals that produce well everywhere and under all conditions. As such, different breeds or lines may be developed to meet demands in high-input systems. To date, little is known about the genetic aspects of adaptation. Scientists and breeding companies are expected to explore these matters further in their research and their breeding programmes in the coming years.

In low external input production systems, animals kept by smallholders represent an important element of household food security and of the social fabric of village communities. To a large extent, smallholders and pastoralists keep local breeds. Genetic improvement in these conditions is a challenging, but not impossible, task. Detailed guidelines for the design and execution of sustainable breed utilization and improvement programmes for low external input systems are being developed and validated. Straight-breeding to adjust a local breed to the changing needs of producers is the most viable option not only to keep it in production and hence safeguard it, but also to improve food security and alleviate poverty. Another option is to use it as a component of a well-planned cross-breeding programme. In conjunction with the introduction of a breeding programme, attention should be given to the improvement of management conditions and husbandry practices.

A common tendency in research related to breeding programmes for all species is an increasing focus on functional traits – in response to the growing importance given to factors such as animal welfare, environmental protection, distinctive product qualities and human health. Examples of functional traits include robustness, disease resistance and behavioural traits, fertility, efficiency of feed utilization, calving ease and milkability. Generally, considered as secondary traits in high-input systems, functional traits are of great importance in low-input systems. Recording of functional traits, however, still remains an important bottleneck which hinders their inclusion in breeding schemes. Information is lacking on the genetic basis of disease resistance, welfare, robustness and adaptation to different environments. Nevertheless, the dairy cattle and pig industries have started to use DNA typing of single genes and genomics (SNPs) to screen breeding animals. This will support the expected shift towards breeding for functional and lifetime productivity traits.

Because of the tendency for reduced use of chemical medications in the developed world, animals are required to have better resistance, or at least tolerance, to particular diseases and parasites. However, for economic and animal welfare reasons, it is very difficult to select for such animals using classical quantitative genetic approaches. High expectations are therefore placed on genomics. Some applications are already in use to eliminate genetic disorders with Mendelian inheritance. In the case of the more complex resistance traits for which genetic markers have been identified, such as Marek's disease in poultry and *E. coli* in pigs, few if any breeding companies have implemented DNA-based selection.

Welfare has become an important element in consumers' perception of product quality, especially in Europe. The main challenges for breeders are to select for better temperament, and reduce foot and leg problems and the incidence of cardio-vascular problems (in poultry kept for meat production). The causes of these problems are multifactorial.

The increasing importance of functional traits will require inclusion of a wider range of criteria in breeding programmes. Some of these criteria may be best met by local breeds. Characterization (phenotypic and molecular) and assessment of these breeds for important traits may allow the detection of some that have unique features. Their further development through breeding programmes would ensure that they remain available for future generations. Unfortunately, the reality is a continuous loss of breeds and lines. The developed world (where the majority of concerted genetic improvement efforts are occurring) contributes directly or indirectly to this loss by concentrating on a very small number of breeds. The deletion of genetic lines that accompanies the worldwide reduction in the number of breeding companies via buy-outs has also played a major role.

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