

Section C

Breeding strategies and programmes

1 Introduction

This section serves as an update of the overview of the state of the art in genetic improvement methods presented in the first report on *The State of the World's Animal Genetic Resources for Food and Agriculture* (first SoW-AnGR) (FAO, 2007a).¹ The importance of appropriate breeding strategies and programmes is highlighted throughout the Global Plan of Action for Animal Genetic Resources (FAO, 2007b), particularly in Strategic Priority Area 2, Sustainable Use and Development. The material presented in the first SoW-AnGR included an overview of the “context for genetic improvement”, which described both the factors influencing the objectives of breeding programmes (market demands, wider societal concerns about the nature and impacts of livestock production, the need to provide animals suitable for a diverse range of production environments, growing recognition of the importance of maintaining genetic diversity in livestock populations, etc.) and the latest scientific and technological developments in the field. This was followed by a description of the various activities or “elements” that make up a breeding programme and then by a review of the current state of breeding programmes by production system (high input vs. low input) and by species. Much of this material remains relevant. While the livestock sector is continuously evolving (see Part 2), the challenges that breeding programmes have to contend with remain broadly similar to those that existed at the time the first SoW-AnGR was prepared (2005/2006). Similarly,

the basic constituent elements of a typical breeding programme have not changed.

This update largely follows the same structure as that described above for the first SoW-AnGR. Emphasis is given to recent developments, but each subsection aims to provide sufficient background information (where relevant, a short recapitulation of the material presented in the first report) to make it comprehensible, in standalone form, to the non-specialist reader. High-input systems are again treated separately from low-input systems. These terms can be defined in various ways, but for the purposes of this section, “high-input systems” is used to refer to systems in which external inputs such as supplementary feeds, veterinary medicines and advanced breeding and reproductive technologies are relatively easily obtainable and widely used (precise levels of use will depend on the particular circumstances) and “low-input systems” to systems where the use of such technologies is more limited, often because of factors such as inaccessibility, unaffordability, lack of relevant knowledge or lack of organizational capacity. Departures from the structure of the first SoW-AnGR include separate subsections on sheep and goat breeding in high-input systems and the addition of a subsection on rabbit breeding in high-input systems. The issue of breeding in the context of conservation programmes is addressed in Part 4 Section D. As indicated above, the broad context for breeding programmes (trends in the livestock sector) is addressed in Part 2.

¹ FAO, 2007a, Part 4 Section D (pages 381–427).

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2 Scientific and technological advances

2.1 Quantitative genetics

Since the time the first SoW-AnGR was prepared (2005/2006), there have been few technological advances in the field of quantitative genetics. The standard method for estimating breeding values and ranking animals according to their genetic merit continues to be traditional BLUP (best linear unbiased prediction). This method uses phenotypic information on animals and their relatives to predict the genetic potential of each animal. Existing tools for controlling inbreeding in herds and populations (e.g. Meuwissen, 1997) have become more widely utilized. From a given set of selection candidates, these tools allow the selection of a group of parents in which the genetic merit is maximized while a measure of genetic variation (e.g. the average coefficient of coancestry) is constrained.

Many breeding organizations, particularly in the dairy cattle, pig and chicken industries, have long been using mate selection software to minimize the effects of inbreeding in their breeding populations (Weigel and Lin, 2000). Over recent years, the various algorithms have been made more efficient (e.g. Kinghorn, 2011) and their value in the control of genetic defects has been recognized (Van Eenennaam and Kinghorn, 2014). Not surprisingly given the increasing use of genomic information in breeding programmes (see Subsection 2.3 and Subsection 4), software for managing inbreeding in the context of increasingly available genomic data has also been developed (e.g. Schierenbeck *et al.*, 2011).

2.2 Molecular genetics

Knowledge of the biology of traits is being enhanced by the availability of an ever increasing amount of genetic information, much of it unavailable only a few years ago. Genotypes can now be obtained much faster and at a lower

Box 4C1

Reduction of genetic variability and its consequences in cattle breeds

Intensive selection may reduce the genetic diversity of livestock populations even if the number of animals remains high. A study of Holstein, Jersey and Angus cattle (very widely used international transboundary cattle breeds) undertaken by de Roos *et al.* (2008) used single nucleotide polymorphism (SNP) markers to investigate linkage disequilibrium (non-random association between alleles). Information on linkage disequilibrium can be used to trace the evolution of effective population size (N_e) over past generations. Several historical episodes of reduction in N_e were identified, including one 10 000 generations ago – corresponding to the time of cattle domestication – during which N_e fell to a few thousands. Another reduction occurred over recent generations, during which time effective population sizes fell to close to 100 as a result of the introduction of new breeding techniques.

Low N_e does not yet seem to have affected the selection potential of widely used transboundary breeds. However, other effects – related to the spread of inherited disorders or to a reduction in fitness associated with inbreeding depression – have been observed. A recent study estimated that in Holstein and Jersey cattle a 1 percent increase in inbreeding, as indicated by pedigree or genomic information, was associated with a decrease of 0.4-0.6 percent of the phenotypic mean for milk, fat and protein yields and an increase of 0.02-0.05 percent for calving intervals. Inbreeding depression can be managed either by minimizing overall inbreeding within the breeding scheme or by targeting specific regions of the genome associated with inbreeding depression.

Based on de Roos *et al.* (2008) and Pryce *et al.* (2014).
See also Part 1 Section F Table 1F1.

cost than they could just five years ago. A simple biological sample (usually blood, hair, tissue or semen) from an individual animal can be used to determine its entire DNA sequence. Of particular interest are the areas where the sequence differs, at a single point, from that of the common reference sequence for the respective species. Such differences are referred to as single nucleotide polymorphisms (SNPs). Combined with enhanced computational capacity, these developments mean that researchers can analyse the genome for more complex traits than ever previously thought possible. It is likely that genotyping costs will continue to decline and that computational capacity will continue to improve – and that therefore the use of these tools will become ever more widespread in the coming years (see Part 4 Section B).

2.3 Gene-based selection

As knowledge of molecular genetics and trait biology has improved, it has been possible to improve breeding programmes through the use of various types of gene-based selection. Most traits of economic importance in livestock are so-called quantitative traits, the phenotypes of which are the result of the combined small effects of many genes. In some instances, however, individual genes can have substantial effects. Molecular genetics can be used to detect the presence of these genes and this information can be used in concert with phenotypic information from animals and their relatives in a process generally referred to as marker-assisted selection (MAS), where “marker” refers to a polymorphic locus either directly responsible for the genetic differences observed or “linked” to the causative locus by being situated nearby on the same chromosome. Most commonly, MAS is applied using linked loci rather than the causative gene, although some accuracy is lost by doing this.

At the time the first SoW-AnGR was prepared (2005/2006), several countries had incorporated MAS into their national breeding programmes for dairy cattle (e.g. Liu *et al.*, 2004; Boichard *et al.*, 2006) and other species. The application of MAS

was judged to be profitable in dairy cattle even with only moderate linkage between the marker and the causative gene. However, for species lacking the complex system of artificial insemination (AI) and progeny testing that is in place for dairy cattle, MAS was considered to be a profitable strategy only in the case of highly informative markers located very close to the causative loci (Boichard *et al.*, 2006).

In recent years, the availability of genomic information has greatly increased and continues to accumulate at a rapid pace. Cost-efficient DNA sequencing methods have facilitated the development of assays that can provide genotypes for tens to hundreds of thousands of SNPs for only a few tens or hundreds of dollars per animal. Thus, nearly all genes with effects on phenotypic traits can be marked by a SNP. It has become possible to apply genome-wide approaches that are more comprehensive than simple MAS based on a few markers.

Researchers have established ways of incorporating information on the genetic make-up of individual animals into breeding programmes for complex traits influenced by many genes, a process known as genome-enabled selection. There are two general approaches to this: genome-enhanced BLUP (Garrick, 2007; VanRaden, 2007; Zhang *et al.*, 2007) and SNP-effect models.

Whereas genetic evaluations based on traditional BLUP utilize average relationships based on animals’ pedigrees, genome-enhanced BLUP utilizes the actual genomic relationship between the animals. For example, with traditional BLUP, two animals with the same sire are assumed to have exactly one-quarter of their genes in common. In reality, this proportion is not a fixed quantity, but rather ranges from zero to one-half. Genome-enhanced BLUP allows this proportion to be estimated more precisely. The approach can be extended – via a method known as single-step genome-enhanced BLUP – to incorporate phenotypes from individuals that are not genotyped (Aguilar *et al.*, 2010; Christensen and Lund, 2010).

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Simple genome-enhanced BLUP is based on the assumption that all regions of the genome have an equal influence on the phenotype being evaluated. Although this assumption facilitates the statistical analysis and generally yields satisfactory results, our knowledge of biology tells us that this assumption is not strictly true; only certain genes have actual physiological effects on a given trait. Computational methods such as Bayesian regression allow differential weighting of specific genomic regions that have a particularly large statistical association with the trait of interest, in other words where findings are consistent with the presence of a quantitative trait locus (QTL) affecting the trait.

In SNP effect models, effects on phenotype are simultaneously estimated for all genotyped SNPs in a so-called “training population” for which full phenotypic information is available (Erbe *et al.*, 2010). The output is referred to as a “SNP-key” and can be used to predict the breeding value of animals that are genotyped, but for which no phenotypic data have been recorded. Such predicted breeding values are obtained by summing the estimated effects at each genotyped SNP. To incorporate information from individuals that have not been genotyped, the resulting genomic prediction is “blended” with an estimate of breeding value derived using traditional BLUP. This blended estimate is used as the final genetic index value for each animal.

Another distinction to note is that between high- and low-density genotyping. High-density genotyping involves analysing 50 000 to 1 million SNPs. Low-density genotyping only analyses a few hundred to a few thousand SNPs. The cost of high-density genotyping is more than twice that of low-density genotyping. Costs can be reduced via a process known as “imputation”, in which high-density genotyping is conducted only in a base population of animals that have many descendants (usually AI sires) and the information obtained is then used to develop a system for inferring or deducing the missing information for animals that have been subject only to low-density genotyping. The correlation between

low-density and high-density genotyping has been shown to be approximately 0.95 (Hickey *et al.*, 2012).

If genomic information is used alone (i.e. is based exclusively on historical phenotypic data), the genetic improvement resulting from selection may not exceed that achieved using traditional BLUP with phenotypes for selection candidates (Dekkers, 2007; Muir, 2007). Moreover, because of the effects of selection and recombination, the accuracy of genomic estimated breeding values (GEBVs) decreases as the number of generations from the training population increases. All available phenotypic and genomic information should be incorporated into GEBVs to ensure that they are as accurate as possible.

Studies have attempted to predict GEBVs for one breed based on the phenotypes of a training population belonging to another breed. The value of this approach has been found to be small or non-existent (Hayes *et al.*, 2009a; Erbe *et al.*, 2012). In numerically small breeds that have adequate phenotyping, multibreed genomic selection may, in future, prove to be an interesting option (Hozé *et al.*, 2014), especially for breeds with a shared genetic history. However, in developing countries, a lack of routinely recorded reference populations is likely to be a significant barrier for the foreseeable future (see Subsection 5.3). Development of genome-enabled selection strategies that can alleviate the constraints imposed by low population sizes and limited phenotypic data is therefore a priority.

Genome-enabled selection can be expected to improve the accuracy of EBVs, particularly for young animals for which phenotypic data are not available (Meuwissen *et al.*, 2001). Increasing EBV accuracy proportionally increases the expected rate of genetic gain. Having more accurate EBVs at a younger age allows selection decisions to be made earlier, which reduces the generation interval and increases genetic gain per unit of time.

In general, genome-enabled selection is beneficial because it can be used to increase the accuracy of the EBVs of animals without direct phenotypic measurements. This general rule applies not

only with respect to young animals, but also to sex-limited traits, traits that are difficult or impossible to measure in the live animal, traits measured at the end of an animal's productive life and as yet undetermined traits that are not currently measured but may become important in the future. In the latter instance, data collected in the future could be used to obtain EBVs for animals that are no longer living but from which cryopreserved semen or other germplasm is available. Genetic material from these animals could thus potentially be used to enhance the trait in the *in vivo* population.

Genome-enabled selection has been implemented in some animal breeding programmes, including programmes for pigs and dairy cattle. In pigs, generation intervals are already low, and hence the greatest effect of genome-enabled selection is on the accuracy of selection for traits that are difficult to measure or measured late in life, such as disease resistance (difficult to define and measure systematically), feed efficiency (expensive to measure directly) and longevity (sow longevity is a sex-limited trait that is not recorded until the animal is culled from the herd).

In addition to quantitative traits (and arguably to an even greater degree) the use of genomic information has increased our ability to manage Mendelian traits, i.e. those traits controlled by a single or small number of genes. In particular, genomic approaches have been used to identify causative mutations or genomic regions associated with deleterious recessive traits, and genetic markers have been developed to help eliminate these genetic defects or attempt to fix beneficial traits within a population.

Deleterious recessive traits are often characterized by a completely homozygous chromosomal region that includes the mutation responsible for the defect and flanking regions on either side of it. Such completely homozygous regions can be relatively simply detected by sequencing or genotyping a small group of affected animals (even as few as ten) and comparing their genotypes to those of unaffected animals (Charlier *et al.*, 2008). For example, in dairy cattle, a rare recessive genetic defect affecting cow fertility has

been identified in the Holstein breed. The defect, known as brachyspina syndrome, is caused by a 3.3 kb (kilo base pair) deletion in the so-called *FANCI* gene (Charlier *et al.*, 2012). Despite the low incidence of brachyspina syndrome (thought to be less than 1 in 100 000), the frequency of the carrier state may be greater than 7 percent. The large discrepancy between the low incidence and relatively large percentage of carriers is accounted for by the fact that almost all homozygous mutant calves die during pregnancy. Identifying this mutation would not have been possible without state of the art genomic tools. Producers can now select against animals carrying a single copy of the gene and thereby improve fertility in the Holstein breed.

Arachnomelia is a monogenic recessive defect affecting skeletal development in cattle. The causative mutation, mapped to chromosome 5, was identified using array-based sequence capture and parallel sequencing technologies (Drögemüller *et al.*, 2010), state of the art genomic tools at the time. A healthy, partially inbred cow known to be carrying one copy of the mutation was re-sequenced and a single heterozygous position was identified. As in the case of brachyspina syndrome, homozygous recessive offspring die before birth, which negatively affects fertility. Again, animals carrying the gene can be selected against in order to improve the fertility of the population.

Genomic information can also be utilized to correct pedigree errors (Seroussi *et al.*, 2013) and reconstruct pedigrees when parentage data have not been recorded (Kirkpatrick *et al.*, 2011). Using genomic information in this way not only increases the accuracy of genome-enhanced BLUP (Munoz *et al.*, 2014), but can also improve traditional BLUP EBVs. Correcting pedigree errors allows more accurate understanding of the true relationships among individuals in the herd. This is important when establishing contemporary groups to estimate breeding values.

2.4 Reproductive technology

The state of the art in the use of reproductive technologies has not changed greatly in recent

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Box 4C2

Genetically modified animals in agriculture

Technologies related to genetic modification (GM) have advanced significantly in recent years. Classical gene transfer techniques have been complemented by new tools such as genome editing, a technique that allows the identification and modification (small insertions or deletions) of a specific DNA sequence instead of the insertion of a foreign DNA sequence into the cell (Carlson *et al.*, 2013).

Many transgenic animals have been developed, both for biomedical purposes (production of biomolecules, xenotransplantation, medical models, etc.) and for potential use in agriculture, including in the improvement of economically important traits such as growth rate, wool growth, feed conversion, milk composition, meat quality, disease resistance and survival. One example is the development of a transgenic chicken expressing a short-hairpin RNA (an RNA sequence whose structure can be used to silence the expression of specific genes) that interferes with H5N1 propagation and thereby confers resistance to avian influenza (Lyall *et al.*, 2011).

In comparison to conventional breeding, transgenic strategies may allow faster introduction of new alleles and genes of interest. However, the production of GM animals is labour intensive and costly. Moreover, unforeseen negative pleiotropic side effects (when a

gene influences multiple unrelated phenotypes) are a possibility. It also has to be borne in mind that genetic progress often involves a multiplicity of genes and that in such cases transgenesis is of little interest.

In a large majority of cases, the development of GM animals for potential use in food production is only at the research stage. A few cases are close to final approval. As yet, no GM animals have been approved for commercial use in food production.

There are still many unresolved ethical issues related to the use and development of GM animals, including concerns related to the invasiveness of procedures and their effects on welfare and health and those related to intellectual property issues. Attitudes towards GM animals vary from country to country. In Europe, for example, the development of GM animals is subject to many restrictions. However, some developing countries have adopted a more permissive approach. For instance, Argentina and China have invested massively in the development of GM animals for food production. Such animals may play a growing role in the coming years. The extent to which this occurs is likely to depend on consumer attitudes to the use of GM technology.

For more information see Forabosco *et al.*, 2013; Jonas *et al.*, 2014.

years, at least in terms of application in the field. One area of advancement has been increased commercial use of semen sexing, predominantly in cattle and particularly in dairy cattle (see Boxes 3E6 and 3E7 in Part 3 Section E). This process involves the use of a molecular biology technology known as flow cytometry to sort X and Y sperm cells (Johnson and Welch, 1999). The obvious advantage is that sexed semen can be used to obtain offspring of the desired sex (more than 90 percent accuracy can be achieved). This allows the rate of genetic improvement to be increased, as selection intensity can be increased and the generation interval shortened. Given that

in some production systems young animals of the undesired sex often suffer from neglect, the use of sexed semen can also indirectly enhance animal welfare.

Challenges associated with the use of sexed semen include a slight decline in conception rate (a fall to 80 or 85 percent of the rate obtained using conventional semen) and the fact that sexed semen is not available from all potential sires (Van Doormaal, 2010). These challenges are likely to be overcome as more experience is gained in the use of sexed semen and as companies make sexed semen routinely available for all sires. Another challenge is that semen sexing does

not work well in all species. In cattle, for example, overall semen and sperm volumes are low and the technology works well. Pigs, however, have relatively large semen and sperm volumes, which means that a lot of time (up to a day per sample) is needed to sort a single semen collection into X and Y sperm cells. To enable widespread use of semen sexing in this species, flow cytometry technology will need to be improved so as to allow sorting to be done much more quickly, as many commercial boar studs collect semen from as many as 100 boars in a day.

Reproductive technologies targeting the female animal (multiple ovulation, embryo transfer, *in vitro* fertilization and cloning) have been available for most major livestock species for some time (all had already been developed at the time the first SoW-AnGR was prepared – 2005/2006). Active research into these technologies continues to improve their success rates and their efficiencies, hence decreasing their costs. Nevertheless, cost remains a major constraint to their more widespread use. Genomic developments could, however, help change this. As discussed above, genome-enabled BLUP and related approaches have increased the accuracies of EBVs. In particular, the EBVs of female animals, especially young females, have become more accurate. This improved accuracy has increased the monetary value of the best females (Pryce *et al.*, 2012). In theory, this increases the expected return on investments in reproductive technologies that increase the number of offspring per female.

Cloning and genetic modification (GM) have been available for many years, but have not gained widespread commercial use. This is largely for economic reasons, but there are also potential ethical concerns. Among livestock species, cloning is most frequently undertaken in horses, where individual animals can have extremely high values because of their earning potential in racing and other riding competitions. Since the first SoW-AnGR was prepared, technologies involving “genome editing” have been developed. These techniques tend to be much more efficient than more traditional GM approaches. Moreover, as genome editing does not involve

transfer of genes across species, it may also raise fewer ethical questions. Research on this technology is increasing and has the potential to have a significant effect on animal production and the management of AnGR (see Box 4C2).

3 The elements of a breeding programme

Genetic improvement strategies fall into three main categories: selection between breeds; selection within breeds or lines; and cross-breeding. The choice of which strategy to pursue will depend on the characteristics of the production system and of the types of animal available (i.e. already present in the local area or potentially introduced). To reduce the risk of costly failures, any options under consideration need to be thoroughly assessed. Detailed advice on planning a breeding strategy is provided in the FAO guidelines *Breeding strategies for sustainable management of animal genetic resources* (FAO, 2010).

All within-breed selection programmes (straight-breeding programmes) have a number of common elements. Setting up a breeding programme involves defining a breeding goal and the design of a scheme that is able to deliver genetic progress in line with this goal. This requires, *inter alia*, the identification of selection criteria, recording of animals’ performances and pedigrees, genetic evaluation, selection and mating, progress monitoring and dissemination of genetic improvement.

A breeding goal is a list of traits to be targeted by the breeding programme, including their relative importance, and a description of how they should be changed genetically (increased, decreased or maintained the same). Breeding goals inevitably shift over time in response to the changing requirements of livestock producers and ultimately the demands of consumers and society at large. For many years, production traits were the primary target. Later, traits affecting function such as longevity, health and reproductive ability were added, as it was observed that selection for production had led to deterioration in these

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traits. Today, as a result of societal pressures, increasing attention is being given to behaviour, well-being and other novel traits. For example, in response to the elimination of gestation stalls in pig husbandry, the breeding industry has started to select for more docile sows, which it is hoped will be more tractable in situations where animals are housed in groups during gestation.

As breeding objectives become broader, breeders increasingly have to deal with antagonisms between different sets of traits. When the genetic correlation between two traits is favourable, selecting for one trait can bring a correlated beneficial response in the other trait. However, when traits are antagonistically correlated, selecting for one trait will lead to an undesirable response in the other. In such cases, it is common practice to include both traits in the selection objective and select animals with desirable attributes for both traits. This strategy allows all traits to be improved over time (Neeteson-van Nieuwenhoven *et al.*, 2013). Typically, the most efficient way to select for multiple traits is to combine them into a “selection index” (Phocas *et al.*, 2013). Traits are weighted according to index coefficients that consider the economic importance of traits and their genetic relationships and maximize the correlation between the selection index and the breeding goal.

The outcomes of breeding programmes, particularly in species with long generation intervals, are realized many years after selection decisions are made. Even in poultry, a genetic change implemented in a breeding nucleus will take at least three years to have a noticeable effect at commercial level. This underlines the need to anticipate future demands when defining breeding goals. Breeders and breeding organizations need to be tuned into societal pressures and how they are likely to affect future demand.

Animal identification and the recording of animals’ performance and pedigrees are the driving forces of genetic improvement. Detailed advice on the development of animal recording systems is provided in the FAO guidelines on the *Development of integrated multipurpose animal*

recording systems (FAO, 2015). Abundant and accurate measurements lead to efficient selection. As described above (Subsection 2), developments in the field of genome-enabled selection are creating significant new opportunities to improve animal breeding. A key prerequisite is to have sufficient phenotypic information recorded for the traits that potentially benefit the most from the use of this technology (e.g. health traits, sex-limited traits and traits that are difficult or impossible to measure in live animals).

Genetic evaluation is the process of determining which animals have a superior genotype for the traits of interest so that decisions can be taken as to which animals should be used to breed the next generation. As performance is influenced both by the animal’s genetics and by its environment, genetic evaluation involves separating environmental components from genetic components. As described above in Subsection 2, genetic evaluation methods based on information on the performance of animals and their relatives are now being supplemented by methods that involve the use of molecular genetic information. The extent to which these new methods have moved beyond the research level and into commercial production varies from species to species (see Subsection 4 and also Part 3 Section E).

Capacity to store performance and pedigree data for use in genetic evaluations is continuously increasing as more sophisticated computer hardware becomes more widely available. It is likely that technology will continue to improve and that capacity to run yet more complex genomic evaluations will not be limited by hardware availability. The greatest limitation may prove to be a lack of progress in the development of software for these types of analysis because of a lack of trained personnel in the field of animal breeding and genetics and a lack of labs working on the development of the specialized software required.

Family information in genetic evaluation increases the probability of co-selecting close relatives, which in turn leads to increased inbreeding. Various methods are used to reduce inbreeding

while maintaining high rates of genetic gain. All are based on the principle of 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 (Weigel and Lin, 2000). Other mating rules or methods for reducing the accumulation of inbreeding in a population were outlined in the first SoW-AnGR² (see also Part 4 Section D and FAO, 2013). These rules have been utilized in commercial poultry and pig breeding to maintain inbreeding at relatively low levels. Many breeding companies have moved towards using programs such as “Mate Select” to control inbreeding more systematically.

The progress achieved in a breeding programme is usually assessed by regressing average phenotypic and breeding values on year of birth. In addition, 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. Frequently, companies test their products against those of their competitors.

The impact of a breeding programme depends on the dissemination of genetic progress to customers or into the wider livestock population. Reproductive technologies, particularly AI, play an important role in many species. They allow genetic material to be transported around the world and greatly increase the number of offspring that can be obtained from a superior breeding animal. As discussed above (Subsection 2.3), recent years have not seen major technological advances in this field. However, the use of reproductive technologies is becoming more widespread in many countries (see Part 3 Section E).

Despite the ever-increasing sophistication of breeding technologies, it is important to recall

that all the elements of a breeding programme can be implemented even under very basic conditions. Success is possible without the use of elaborate data recording and genetic evaluation systems, without genomic tools and without the use of reproductive technologies (see Subsection 5 for further discussion of breeding programmes in low-input systems).

4 Breeding programmes in high-input systems

4.1 Dairy and beef cattle

The characteristics of the cattle breeding industry highlighted in the first SoW-AnGR³ included:

- a relatively decentralized structure (compared to the pig and poultry sectors), with different organizations performing complementary tasks in the breeding scheme (identification, performance recording, genetic evaluation, selection and commercialization of genetics), the most distinctive feature being the role played by commercial producers in the provision of data used in genetic evaluation;
- (in the dairy sector) a historical emphasis on production traits (milk yield and components) that had led to a great increase in milk output, but also to a deterioration in so-called functional traits, i.e. those related to the animal's health and fertility; this had led breeding organizations to increase the weight of functional traits in selection indices;
- (in the beef sector) a focus on increasing growth rates that had caused an increase in calving problems associated with calf size, as well as creating potential fertility problems associated with heifers being unable to meet higher nutritional demands associated with a larger size;
- a need to improve the recording of functional traits, particularly in beef cattle;

² FAO, 2007a, page 395.

³ FAO, 2007a, pages 396–400.

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- a lack of capacity to implement direct selection for feed efficiency, resulting from a lack of capacity to obtain feed-intake data for sufficient numbers of animals;
- a lack of market mechanisms that reward producers for improved meat quality;
- (in the beef sector) a lack of well-organized cross-breeding programmes;
- a major role played by breeders' associations, along with significant input from public institutions in terms of data management and genetic evaluation; and
- a trend towards the internationalization of AI companies.

These characteristics have changed little in the years since the first SoW-AnGR was prepared (2005/2006). Decentralization remains a common theme. Ownership of individual animals remains with private livestock keepers, particularly in the case of female animals, although there is a general trend towards concentration. Breed associations continue to play a major role. The trend towards globalization continues, both in terms of the organization of AI companies and the use of breeds in a transboundary manner. Cross-breeding is a routine practice in dairy cattle as a means of increasing profitability by improving functionality and fitness. As discussed in more detail below, the adoption of genomic selection has been nothing short of revolutionary. The evaluation, acquisition and marketing of AI bulls have been transformed, with a much greater emphasis now given to younger bulls with no progeny.

The breeding objectives listed in the first SoW-AnGR⁴ are still relevant to most selection programmes worldwide, but some changes have occurred. In many countries, selection indices for dairy cattle have been adjusted so as to reduce the emphasis given to production traits and to accentuate functional traits such as fertility, longevity and udder health. The major obstacle to including more health traits and novel traits such as feed efficiency in selection programmes is a lack

of reliable phenotypic records, either because of logistical problems or because of high costs. The automation of milking procedures has become significantly more widespread during the past decade and is generating a large volume of new records that could potentially be used to expand the portfolio of traits evaluated. The practice of breeding companies establishing contracts with the owners of large herds to collect data on novel traits is foreseen to become more common in the future and to play an increasingly important role in genetic evaluation of these traits. These practices may increase the accuracy of genetic evaluation, but perhaps only for the specific standardized environment in which they are recorded. In beef cattle, growth and carcass traits continue to be the main selection objectives, although calving and fertility traits are receiving increasing attention. Difficulties with reliable recording are even more acute in beef than in dairy operations. Assessing the sophisticated carcass classification data collected by slaughterhouses (e.g. the EUROP carcass classification system)⁵ for genetic evaluation purposes would improve the selection process. However, it would require a consistent animal identification infrastructure, from birth to slaughter (or, perhaps, much more widespread reliance on DNA-based measures of animal identification and genetic relationships) that would allow the development of consolidated databases. Current breeding objectives in dairy and beef cattle are summarized in Tables 4C1 and 4C2.

The development of technologies that allow fast, accurate and affordable determination of SNPs has enabled the AI industry to make efficient use of genetic markers for selection purposes and represents the most significant advance in cattle breeding since the adoption of AI (see Subsection 2 for a general description of the role of genetic markers in animal breeding). The completion of the bovine genome sequence and reference assembly (Elsik *et al.*, 2009) enabled the

⁴ FAO, 2007a, Table 99 (page 397).

⁵ See Commission Regulation (EEC) No 2930/81 of 12 October 1981 adopting additional provisions for the application of the Community scale for the classification of carcasses of adult bovine animals (available at <http://tinyurl.com/qejooac>).

TABLE 4C1
Selection criteria in dairy cattle

Traits		Comments
Production traits	Milk quantity	More frequently the quantity of protein and/or fat
	Milk quality	Concentration of protein and/or fat
	Feed efficiency	Rarely measured directly
Reproduction traits	Conception rate	For males, it may be calculated based on mates or daughters
	Ease of calving	Often used for mating, rather than selection
Robustness traits	Survival	Measured as longevity
	Mastitis resistance	Either directly based on incidence or indirectly based on somatic cell concentration in milk and udder conformation of daughters
	Leg soundness	Usually based on conformation traits and observed mobility
	Body conformation	Decreased body size has a positive association with feed efficiency and longevity

Note: This table updates and expands upon information provided in Table 99 of the first SoW-AnGR (FAO, 2007a).

TABLE 4C2
Selection criteria in beef cattle

Traits		Comments
Production traits	Body size	Ideal size depends on environment
	Growth rate	Weight at various ages (e.g. birth, weaning, one year of age)
	Milking ability	Measured indirectly based on growth, has an intermediate optimum because high milk production results in waste
	Carcass quality	Carcass yield, loin muscle area
	Feed efficiency	
	Meat quality	Marbling (intramuscular fat), tenderness
Reproduction traits	Male fertility	Measured by using scrotal circumference
	Mothering ability	
	Ease of calving	Based on scores provided by breeders
	Calving interval	Seasonal production requires regular yearly calving
Robustness traits	Survival	Longevity
	Conformation	Leg soundness is important for function in rangeland conditions
	Temperament	To improve safety and increase ease of management

Note: This table updates and expands upon information provided in Table 99 of the first SoW-AnGR (FAO, 2007a).

identification of the several thousands of SNPs used to develop low-cost SNP chips. Genomic screening of a large proportion of the population facilitates the discovery of haplotypes associated with economically important traits such as recessive disorders, reproductive performance, coat colour and polledness. Carriers of such haplotypes

are now regularly identified among genotyped cattle (Table 4C3).

Adoption of genomic selection has been extremely rapid in the dairy sector and has already replaced the progeny testing schemes that were the state of the art for several decades. Males, and a rapidly increasing number of females, are

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TABLE 4C3

Recessive haplotypes tracked in the genomic evaluation system in the United States of America

Breed	Haplo-type	OMIA 9913 ID ¹	Gene name	Condition/trait	Frequency (%)	Chromosome	Reference
Ayrshire	AH1	001934	<i>UBE3B</i>	Conception rate	13.0	17	Cooper <i>et al.</i> , 2014, Venhoranta <i>et al.</i> , 2014
Brown Swiss	BH1	001825	—	Abortion	6.67	7	VanRaden <i>et al.</i> , 2011
	BH2	001939	—	Abortion	7.78	19	Schwarzenbacher <i>et al.</i> , 2012
	BHD	001247	<i>SPAST</i>	Spinal dysmyelination	2.19	11	Hafner <i>et al.</i> , 1993, Thomsen <i>et al.</i> , 2010
	BHM	000939	<i>KDSR (FVT1)</i>	Spinal muscular atrophy	3.61	24	El-Hamidi <i>et al.</i> , 1989, Krebs <i>et al.</i> , 2007
	BHW	000827		Progressive degenerative myeloencephalopathy (Weaver syndrome)	1.56	4	McClure <i>et al.</i> , 2013
Holstein	HBR	—	<i>MC1R (MSHR)</i>	Black/red coat colour	0.8	18	Lawlor <i>et al.</i> , 2014
	HDR	—		Dominant red coat colour	0.04	3	Lawlor <i>et al.</i> , 2014
	HH0	000151	<i>FANCI</i>	Brachyspina	2.76	21	Agerholm <i>et al.</i> , 2006, Charlier <i>et al.</i> , 2012
	HH1	000001	<i>APAF1</i>	Abortion	1.92	5	Adams <i>et al.</i> , 2012
	HH2	001823	—	Abortion	1.66	1	VanRaden <i>et al.</i> , 2011, McClure <i>et al.</i> , 2014
	HH3	001824	<i>SMC2</i>	Abortion	2.95	8	Daetwyler <i>et al.</i> , 2014, McClure <i>et al.</i> , 2014
	HH4	001826	<i>GART</i>	Abortion	0.37	1	Fritz <i>et al.</i> , 2013
	HH5	001941	—	Abortion	2.22	9	Cooper <i>et al.</i> , 2013
	HHB	000595	<i>ITGB2</i>	Leukocyte adhesion deficiency, type I (BLAD)	0.25	1	Shuster <i>et al.</i> , 1992
	HHC	001340	<i>SLC35A3</i>	Complex vertebral malformation	1.37	3	Agerholm <i>et al.</i> , 2001
	HHD	000262	<i>UMPS</i>	Deficiency of uridine monophosphate synthase (DUMPS)	0.01	1	Shanks <i>et al.</i> , 1984
	HHM	000963	<i>LRP4</i>	Syndactyly (mule foot)	0.07	15	Eldridge <i>et al.</i> , 1951, Duchesne <i>et al.</i> , 2006
	HHP	000483	<i>POLLED</i>	Polled/horns	0.71	1	Medugorac <i>et al.</i> , 2012, Rothammer <i>et al.</i> , 2014
	HHR	001199	<i>MC1R (MSHR)</i>	Red coat colour	5.42	18	Joerg <i>et al.</i> , 1996
	Jersey	JH1	001697	<i>CWC15</i>	Abortion	12.10	15
JH2		001942	—	Abortion	1.3	26	VanRaden <i>et al.</i> , 2014

Note: ¹ Online Mendelian Inheritance in Animals (<http://omia.angis.org.au/>) identification number for *Bos taurus* (National Center for Biotechnology Information species code 9913).

Source: Cole *et al.*, 2015.

genotyped at very young ages and not used as breeding animals if their GEBVs do not meet the selection criteria. In combination with advances in multiple ovulation and embryo transfer (MOET), genomic selection has shortened the generation interval to such an extent that the sires of the currently active AI bulls do not yet have any recorded progeny. The replacement of progeny testing has been a revolution in dairy cattle breeding, but yet another paradigm shift is now taking hold. The relatively low reproductive capacity of cattle and the rates of involuntary culling have traditionally meant that the female offspring from all cows were needed as replacements within a given herd. Therefore, genetic improvement via the dam-of-daughters pathway has been negligible. Now, the combination of sexed-semen technologies and low-density, low-cost SNP chips has increased both the selection intensity and the selection accuracy within this pathway, thus creating a new opportunity for additional genetic improvement.

Because the accuracy of GEBVs is highly dependent on the size of reference populations (Hayes *et al.*, 2009b), even the largest cattle populations greatly benefit from international exchanges of genomic data. Exporting countries took the lead in adopting genomic technologies and formed consortia to share genotypes. Interbull, a subcommittee of the International Committee for Animal Recording (ICAR), has continually adapted its activities to account for the use of genomic information in genetic evaluation. The market has become polarized into two major blocks, the importers and the exporters of genetics. The technological gap between these two blocks has widened rapidly, both because of the investments required and because of a relative lack of expertise in the importing countries. Poor results from multibreed genomic predictions have hindered genomic applications in smaller, non-mainstream, populations and the hegemony of the Holstein has been increasing at a greater speed. The potential uses of genomics are seemingly limitless. New actors coming from sectors not directly related to dairy or beef breeding (e.g. pharmaceutical companies) have started to

take the lead and supply innovative and customized services to dairy breeders in a manner similar to that already pertaining in the poultry and pig industries. Data ownership has become a key issue and control over the genetic-improvement process may shift from breeders to corporations (Dürr, 2013).

Genomic selection has advanced more slowly in the beef sector. This is mainly because of differences in population structure (in dairy breeds, the large number of offspring produced per bull through AI improves the precision of genomic selection), the fact that major production traits such as growth rate can be measured in all animals relatively early in life and the lack of large phenotypic and animal-pedigree databases for beef cattle.

4.2 Sheep

The first SoW-AnGR presented an overview of the state of sheep breeding in high-input systems, noting the selection criteria utilized and describing the organization of the breeding sector in different parts of the world.⁶ Table 4C4 summarizes the traits most commonly considered in current sheep breeding programmes. While the broad characteristics of the sheep breeding industry remain similar to those described in the first SoW-AnGR, breeding programmes for high-input systems have undergone considerable change in the past decade. Although developments in genomic prediction are exciting and have attracted considerable research investment in a number of countries, structural and economic effects are also very important.

While in general, sheep breeding programmes have typically aimed to improve production and reproduction traits, identification of molecular markers for major genes that directly affect sheep health has led to the incorporation of selection for health traits. Selection for the ARR haplotype at the *PRNP* locus and against the VRQ haplotype has been used in several countries to reduce susceptibility to scrapie (Hunter, 2007). Selection

⁶ FAO, 2007a, pages 400–402.

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TABLE 4C4

Selection criteria in sheep

	Traits	Comments
Production traits	Body size	Ideal size depends on environment
	Growth rate	Weight at various ages (e.g. birth, weaning, one year of age)
	Meat yield	Proportion of fat in the carcass and lean distribution across carcass regions
	Meat quality	Marbling (intramuscular fat), tenderness
	Wool quantity and quality	Fleece weight, fibre diameter, advanced processing characteristics (e.g. coefficient of variation of fibre diameter, staple strength)
	Milk yield and quality	
Reproduction traits	Litter size	Twinning rate, larger numbers of offspring may be detrimental
	Mothering ability	Number of lambs weaned, milk yield, early growth
	Weaning rate	Number of lambs weaned, combining effects of litter size and lamb survival
Robustness traits	Survival	Longevity
	Parasite resistance	Helminths, blowfly strike
	Scrapie resistance	Based on molecular tests
	Mastitis resistance	Trait indirectly selected for based on somatic cell concentration in milk
	Udder conformation	

Note: This table updates and expands upon information provided in Table 99 of the first SoW-AnGR (FAO, 2007a).

against day blindness in Awassi sheep is being undertaken via the *CNGA3* locus (Reicher *et al.*, 2010) and resistance to maedi visna infection has been shown to have favourable alleles at the *TMEM154* locus (Heaton *et al.*, 2012).

In the very intensive sheep-farming systems of Europe and the Middle East, where high prolificacy is economically important, use of genetic technologies such as introgression of the *FecB* mutation with the aid of molecular genotyping (Gootwine *et al.*, 2008) and the advent of genomic selection (Larroque *et al.*, 2014) have created substantial opportunities to increase the rate of genetic progress. Breeding programmes for improving milk production traits are in place in several European countries. Most milk recording is carried out in France, Italy and Spain, where large-scale use of AI facilitates breeding work. According to an ICAR survey reported in 2013 (Astruc, 2014), there are about 2 million sheep under recording, almost exclusively in European countries.

The potential to exploit genomic selection is less in small milking ruminants than in dairy cattle breeds such as the Holstein, which have larger values per animal, longer generation intervals in progeny testing schemes, smaller effective population sizes and larger numbers of historical individuals with accurately recorded phenotypes and genotypes. However, because genomic selection simplifies the AI cooperative structure, a shift towards genomic breeding strategies is occurring, at least in some French milking sheep breeding programmes (Duchemin *et al.*, 2012; Larroque *et al.*, 2014) (see Box 4C3).

In the meat and wool sectors, programmes such as the National Sheep Improvement Program in the United States of America⁷ and LAMBPLAN⁸ in Australia evaluate records of on-farm performance

⁷ www.nsip.org

⁸ <http://www.sheepgenetics.org.au/Breeding-services/LAMBPLAN-Home>

Box 4C3

Adoption of genomic selection in French dairy sheep breeds

Given the importance of ewe-milk production in France, there is growing interest in implementing genomic selection in dairy sheep breeds. The reliabilities of genomic breeding values for the Lacaune and Blond-Faced Manech sheep breeds are similar to those of the Montbéliard and Normande dairy cattle breeds, as they all have reference populations of a similar size (Duchemin, 2012; Baloche *et al.*, 2014). A simulation study of the Lacaune has indicated that genomic selection could increase annual genetic gain by 15 percent as a result of an increase in the intensity of selection of young rams (Buisson *et al.*, 2014). The simulation predicted that the increased income obtained would compensate for the extra costs of genotyping. Based on this information, Lacaune breeders decided, in 2015, to shift to a genomic breeding programme. It is assumed that genotyping costs will continue to decrease in the future, thus increasing the potential economic benefits of genomic selection. Breeders of the Blond-Faced Manech breed are planning to adopt routine genomic selection in the near future.

records and provide the industry with EBVs for many traits for elite and young rams belonging to a range of breeds. Some EBVs are combined to calculate indexes for specific breeding goals.

Breed shifts and the introduction of composite breed types have been transformational in New Zealand and Australia over recent decades. This has been driven, at least partly, by shifts in focus from wool production to meat production. Interestingly, in New Zealand, although higher performance composites rapidly took substantial market share following the introduction of novel breeds from Europe, much of this market share has since been recovered by breed types (including lower-performance composites) identified by farmers as having higher levels of robustness in breeding ewes. Sheep flocks in New Zealand are

increasingly being forced into harsher production environments due to rapid expansion of the dairy industry (Morris and Kenyon, 2014). The three test sites of the country's central progeny testing structure, widely recognized as a key facilitator of accelerating rates of genetic progress, have recently been supplemented by two additional sites, both of which are commercial farms operating in very harsh production environments.

Despite considerable investment in genomic approaches, there are still challenges to the integration of these technologies into breeding programmes. Both the Australian approach, based on a very large reference population with intensive phenotypic recording, and the New Zealand approach, based on industry sires as the training resource, have produced relatively modest improvements in selection accuracy compared, for example, to those achieved in Holstein cattle (Dodds *et al.*, 2014; Swann *et al.*, 2014). To date, adoption of genomic selection approaches in both countries has been limited to highly progressive breeders who wish to be at the forefront of technology and are content with marginal gains in the rate of genetic progress. Work on how to integrate genomic predictions into novel breeding programme structures and attempts to reduce testing costs per animal and per breeding scheme via two-stage selection strategies (Sise *et al.*, 2011) and combination with reproductive technologies (Granleese *et al.*, 2013) have been identified as keys to increased adoption. Research is also being undertaken into higher-density chips and gene sequences, although there is little evidence of practical benefits. Exploiting the ever-decreasing costs of genome sequencing remains an exciting challenge for the future.

Formal industry structures and coordinated provision of genetic improvement services such as databases and genetic evaluation systems are critical to the success of genetic evaluation systems. However, even where such systems exist, rates of adoption of new technologies may be poor and rates of penetration into the commercial sector by rams from flocks in which the latest technologies are used may be very low (Amer *et al.*, 2007). An

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example of steps that can be taken to overcome challenges of this kind is provided in Box 4C4.

4.3 Goats

The first SoW-AnGR provided a short review of the state of goat-breeding programmes in high-input systems, noting that such programmes were mainly concentrated in Europe and North America and focused mainly on dairy breeds. Breeding programmes for meat goats were described as being present in a few countries with well-developed goat-meat sectors, such as Australia, South Africa and the United States of America.⁹ This overall picture has not changed greatly in the recent years. Well-structured goat breeding programmes are generally found only in developed countries where the production, processing and commercialization of goat products are well organized. Table 4C5 lists the most important traits considered in contemporary breeding programmes for dairy and meat breeds.

All effective goat breeding programmes are based on straight-breeding. They rely on the existence of well-characterized breeds and breeders' associations that can manage herd books and performance-recording systems. As with other

⁹ FAO, 2007a, page 402.

Box 4C4

Improving the system of sheep breeding in Ireland

In Ireland, a new and modern support structure has been put in place to support sheep breeding. The initial challenge has been to engage with a breeding sector that historically relied on basic phenotypes and physical type traits as primary selection criteria, and to overcome the barrier of having many small breeder flocks with low levels of genetic connectedness among them. A central progeny testing scheme has been established, which originally had the goal of increasing levels of genetic connectedness. More recently, the focus has switched to identifying sires of sires that excel for a balance of maternal and carcass traits (Pabiou *et al.*, 2014). If these sires get used through AI in a large number of flocks that market rams for natural service, it will be possible to multiply the elite genetic material across a substantial proportion of the industry. This strategy is less reliant on widespread uptake of recording by all breeders, for many of whom ram production and marketing is a secondary source of income. In addition, interest is growing in Ireland in the potential of genomic selection, and also imported genetics, to accelerate genetic progress.

TABLE 4C5

Selection criteria in goats

	Traits	Comments
Production traits	Body size	
	Growth rate	Weight at various ages (e.g. birth, weaning, one year of age)
	Meat quality	Marbling (intramuscular fat), tenderness
	Milk yield and quality	
	Fibre quantity and quality	Fleece weight and fibre diameter (for mohair and cashmere producers)
Reproduction traits	Litter size	Twinning rate, larger numbers of offspring may be detrimental
	Mothering ability	Number of kids weaned, combining effects of litter size and kid survival
Robustness traits	Survival	Longevity
	Mastitis resistance	

Note: This table updates and expands upon information provided in Table 99 of the first SoW-AnGR (FAO, 2007a).

species, goat breeds are monitored for inbreeding, and the selection and diffusion of AI bucks is modulated to minimize inbreeding (Colleau *et al.*, 2011; Palhiere *et al.*, 2014). Obtaining EBVs that are sufficiently reliable for efficient selection requires the recording of pedigree information and at least a minimum of genetic connection between herds. Schemes based on progeny testing and the collective use of sires have become somewhat more common in recent years. In addition to the French and Norwegian programmes noted in the first SoW-AnGR (the former involving the use of AI and the latter the sharing of sires among cooperating breeders), examples now include selection schemes for Spanish dairy breeds (Murciano-granadina, Malagueña, Florida and Payoya), based on progeny-tested males and the use of their semen for planned matings throughout the whole selection nucleus (Seradilla, 2014). Although some of these schemes have achieved a degree of success (Menendez-Buxadera *et al.*, 2014), several constraints to their further development remain to be resolved, particularly with regard to their economic sustainability (Serradilla, 2008).

There have also been some notable developments in Latin America. In Brazil, selection schemes for improving meat and milk production have been implemented in small selection nuclei of imported and locally adapted breeds (Lôbo *et al.*, 2010). In Mexico, a small selection nucleus has been organized by a group of breeders from the state of Guanajuato, which also progeny tests sires through AI and undertakes genetic evaluation of sires and dams (Torres Vázquez *et al.*, 2009).

The main technological innovation in recent years has been the development of tools for the exploitation of molecular genomics in advanced selection schemes. Gene-assisted selection is currently applied in France and Norway to improve milk protein content (Manfredi and Ådnøi, 2012). The International Goat Genome Consortium¹⁰ has worked with a private company to develop a commercially available SNP chip for goats (Tosser-Klopp, 2012). France has investigated the

adoption of genomic selection and has established reference populations for the popular Alpine and Saanen breeds (Larroque *et al.*, 2014). Study of these populations suggests that the reliability of genomic evaluation would be less than in dairy cattle breeds with large populations, but similar to that in cattle breeds with equivalent population sizes (*ibid.*). In addition, in contrast to the findings of most studies in dairy cattle (e.g. Kemper *et al.*, 2015), joint genomic evaluation of goat breeds tends to improve the accuracy of GEBVs (Carillier *et al.*, 2014).

4.4 Pigs

The basic structure of the pig breeding sector remains similar to that described in the first SoW-AnGR.¹¹ In the typical breeding programme, pedigree selection occurs only within pure-bred lines (designated as sire or dam lines) in the nucleus (i.e. the top layer of the production pyramid). Sire lines are selected for growth and carcass traits, meat quality and robustness. Dam lines are also selected for reproduction traits. New lines are regularly developed by crossing existing lines and/or by specialized selection in a particular direction. A breeding organization's final products are parent sows (two- or three-way crosses) and parent boars (pure lines or two-way crosses). These parent animals are used by producers to breed pigs for slaughter.

The pig-breeding sector is less concentrated than the poultry sector (see Subsection 4.5). There are still many breed associations and many countries have some kind of national, often semi-governmental, genetic evaluation scheme (e.g. the National Swine Registry in the United States of America, the Canadian Centre for Swine Improvement Inc. and LGPC-IFIP-INRA¹² in France). These schemes compete with pig-breeding companies that may be owned by cooperatives (e.g. Topigs, Danavl, Nucléus and ANAS) or by families (e.g. ACMC, Grimaud, Hendrix and JSR) or may be

¹⁰ <http://www.goatgenome.org/>

¹¹ FAO, 2007a, pages 402–405.

¹² Livres Généalogiques Porcins Collectifs - Institut de la Filière Porcine - Institut National de la Recherche Agronomique.

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corporations (e.g. PIC). Over the years, pig-breeding companies have tended to amalgamate into larger and more cost-efficient entities.

Pig-breeding programmes have been very successful in improving economically important traits (e.g. Chen *et al.*, 2002; Tribout *et al.*, 2010), with growth and carcass performance (growth rate, leanness and feed efficiency) having been targeted since the 1970s and greater attention given to reproductive performance (litter size, piglet survival and farrowing interval) and meat quality (water binding capacity, colour and intramuscular fat content) from the 1990s onwards. Since the 2000s, the focus has been shifting towards breeding for more robust and efficient animals to meet the needs of a more diverse range of production environments (Merks *et al.*, 2012). This has required strategies for dealing with genotype by environment interactions. One popular approach is the combined cross-bred and pure-bred selection (CCPS) scheme, which involves recording the cross-bred progeny of AI nucleus boars under commercial conditions and using the data to estimate the breeding values of

pure-bred relatives that are selection candidates in the nucleus (Wei and Van der Steen, 1991). This approach implies increasing the emphasis given to robustness traits such as survival rates, leg soundness, disease resistance, stress susceptibility and longevity. Table 4C6 presents a summary of current selection objectives in pig breeding. Recent changes have been quantitative rather than qualitative: a gradual shift towards robustness traits and efficiency. An important development for the late 2010s will be the introduction of boar taint as a breeding goal trait in the European Union, where piglet castration is likely to end in 2018.

With ongoing intensification of the production sector, pig health is becoming ever more important. This requires, in the first place, improving sanitary status and biosecurity at the breeding-farm level, so that diseases are not introduced from the breeding farms into the production pyramid. It has also triggered attempts to breed for disease resistance and against metabolic disorders. However, this work is only in its initial stages. Globally, pig

TABLE 4C6

Selection criteria in pigs

Traits		Comments
Production traits	Growth rate	At various ages
	Carcass quality	Carcass yield, carcass leanness, uniformity
	Feed efficiency	
	Meat quality	Water-holding capacity, colour, intramuscular fat content
Reproduction traits	Litter size	
	Piglet survival	Mothering ability of the sow, viability of the piglets, litter uniformity
	Farrowing interval	
Robustness traits	Stress susceptibility: halothane sensitivity	Allele eradication at a single gene; still relevant in a few extreme sire lines only
	Congenital defects	Atresia ani, cryptorchidism, splayleg, hernias, hermaphrodites, etc.
	Leg soundness	Osteochondrosis and many other aspects
	Disease resistance	Specific <i>Escherichia coli</i> strains
	Survival	Piglet viability (effect of the sire); postweaning survival rates
	Sow longevity	

Note: This is an updated version of Table 100 of the first SoW-AnGR (FAO, 2007a).

production is gradually shifting from temperate to warmer climatic zones and this has created requirements for animals that are resilient to hot conditions. This has led to the introduction of novel breeding-goal traits such as lactation feed intake (Renaudeau *et al.*, 2014). In Western societies, increasing attention to animal welfare is leading to the introduction of novel housing systems, which in turn is leading to the adoption of a new set of breeding-goal traits, mainly related to various aspects of animal behaviour. Growing concern about environmental efficiency (e.g. greenhouse gas emission, phosphorus retention and nitrogen excretion) is likely to increase the emphasis given to feed efficiency in genetic improvement programmes.

Because of the competitive nature of the industry and its high levels of investment, commercial breeding companies usually spearhead the use of technologies. Many use MAS in one form or another and a handful have implemented full-scale genomic selection (Van Eenennaam *et al.*, 2014). These are expensive technologies, and studies have been undertaken to evaluate their financial feasibility in various breeding systems (e.g. Abell *et al.*, 2014). Another important innovation has been the development of optimization routines that balance between genetic improvement and inbreeding in the planning of selection and mating schedules at nucleus level (see Subsections 2.1 and 3). At present, a major focus of development is accommodating genomic information in mate-selection procedures.

4.5 Poultry

The first SoW-AnGR provided an overview of the poultry-breeding industry, noting its hierarchical structure, often referred to as the “breeding pyramid”, and its concentration in the hands of a small number of companies.¹³ It also discussed the main selection criteria in poultry breeding programmes, noting a trend towards the inclusion of ever more traits in breeding objectives.

A typical poultry breeding programme includes a biosecure breeding nucleus from which genetic improvement is disseminated to the wider industry through multiplication tiers at great-grand parent, grandparent and parent levels. Improved birds are multiplied and crossed, in three or four steps, in the lower tiers of the breeding structure to produce broiler or layer birds (see Table 4C7). It is important to note, however, that the traditional portrayal of the structure of the poultry industry as a pyramid, with the breeding programme at the apex, is something of an over simplification (Laughlin, 2007). The structure can more accurately be represented by two pyramids: a small supporting pyramid at the base, representing the specialized breeding programmes, and a larger inverted pyramid above, representing the other tiers of production, with the consumer at the top (see Figure 4C1). The supporting pyramid contains all the elements needed to maintain a breeding programme: experimental lines, test lines and pure lines, along with the various support systems of modern genetics, including a strong research

¹³ FAO, 2007a, pages 404–405.

TABLE 4C7

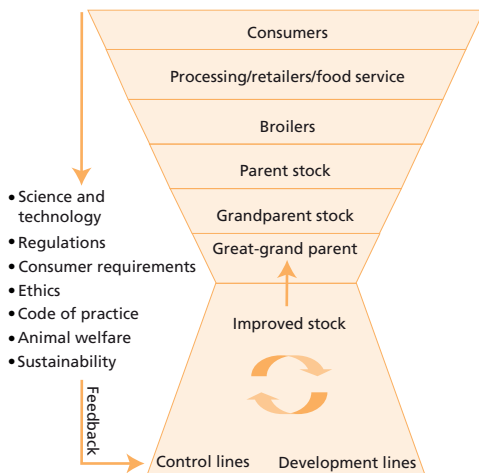
Cross-breeding scheme and relative numbers in a typical broiler breeding programme

Level in breeding pyramid	Paternal lines		Maternal lines	
Pedigree stock	A♂ × A♀	B♂ × B♀	C♂ × C♀	D♂ × D♀
Great grand parents	1 A♂ × 10 A♀	10 B♂ × 100 B♀	3 C♂ × 30 C♀	25 D♂ × 250 D♀
Grand parents	250 A♂ × 2 500 B♀		1 500 C♂ × 12 500 D♀	
Parents	62 500 AB♂ × 625 000 CD♀			
Broilers	87 million ABCD			

Source: Adapted from Hiemstra and Napel, 2013.

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FIGURE 4C1

Structure of the poultry breeding industry

and development base geared towards responding to feedback from every tier of the industry and from society.

The poultry-breeding industry remains concentrated in few hands. Fewer than five groups of primary breeders dominate the market for breeding stock (Fuglie and Heisey, 2011) and some of these are involved in the production of more than one poultry species. Most breeding companies are based in Europe or North America, with subsidiaries in major production regions.

The main breeding objectives and selection criteria in commercial poultry breeding are summarized in Table 4C8. Since the 1960s, breeding goals have evolved from a narrow starting point emphasizing production traits to now encompass a very broad range of considerations, including reproduction, animal health, product quality and environmental impact. This expansion has been particularly notable during the last two decades (Neeteson-van Nieuwenhoven *et al.*, 2013). The trend has been driven by the need for efficiency, including in environmental terms, as well as by the need for robustness and adaptability to varying production environments.

Poultry breeding is a global business and poultry are raised in production environments that vary substantially in terms of ambient temperature, humidity, altitude, disease exposure, feed quality and management capacity. Many regions where poultry are produced are highly vulnerable to climate change, and the development of resilient strains able to cope with climate change-affected production environments has become a focus of many breeding programmes. The high cost of recording and the need to maintain strict biosecurity mean that breeding companies typically undertake selection at a limited number of sites, rather than at many sites spread around the world. There is therefore a high potential for genotype \times environment interactions (Neeteson-van Nieuwenhoven *et al.*, 2013). To reduce the problem, poultry breeders have developed crosses that are robust to minor changes in the production environment. This is achieved by testing the siblings of selection candidates, different lines or different cross-bred progeny in multiple production facilities and field environments. The field data are then combined with data obtained in the breeding nucleus.

Increasing attention is also being paid to the need to reduce the carbon footprint of poultry production systems. This has led to an increased focus on the efficiency of production and a consequent shift in breeding objectives. Life-cycle analyses have indicated that the feed supply chain contributes a large proportion of the poultry sector's share of global greenhouse gas emissions (Pelletier *et al.*, 2014). Improving feed efficiency is thus a key factor in reducing the environmental impact of poultry production (Olori, 2010; Pelletier *et al.*, 2014). It has been estimated that an improvement in feed efficiency resulting in a saving of 15 g feed per kg body weight gained would reduce global poultry feed requirements by around 1.85 million tonnes per year, freeing up about 4 000 km² of arable land¹⁴ (Neeteson-van Nieuwenhoven *et al.*, 2013). Feed intake, feed conversion ratio and residual feed intake are included in breeding objectives in

¹⁴ Based on 2010 harvest yield of 466 tonnes of wheat per km².

TABLE 4C8

Selection criteria in poultry

Traits		Comments
Egg production	Egg number Hen house production Hen-day percentage	Chickens, ducks and geese: number of saleable eggs per bird
Egg weight	Egg weight/size, shape index	
Egg quality – external	Shell breaking strength Shell thickness Shell porosity/egg weight loss Shell colour, egg shape	Broiler and layer chickens: shell breaking strength, puncture score, dynamic stiffness, resonance frequency; egg weight loss between setting and transfer as a measure of shell porosity
Egg quality – internal	Haugh unit, albumen height, yolk percentage	
Meat production	Growth rate Body weight at various ages Breast meat percentage Leg meat percentage Fat percentage Eviscerated yield percentage	Chickens, turkeys and ducks: high emphasis on selection against fat in meat-type ducks; fat percentage assessed on live birds using multidimensional ultrasound measures as well as condition scoring
Feed efficiency	Feed intake Residual feed intake Feed conversion ratio	Feed conversion ratio is feed intake per kg weight gain in meat-type birds and per kg egg mass in layers
Health, welfare and metabolic fitness	Liveability, leg health and walking Gait, bone strength Gut health Heart and lung function Feather-pecking behaviour Feather cover End of lay condition score	Selection for improved robustness, disease resistance and liveability traits and for decrease of (for example) tibial dyschondroplasia assessed with a lixoscope, valgus/varus, osteoporosis, toe defects, footpad dermatitis, femoral head necrosis and hockburn; heart and lung function assessed by measuring blood oxygen saturation using an oximeter
Reproductive efficiency	Fertility and hatchability Early and late embryo mortality Chick viability (survivability beyond day of hatch)	Broiler and layer chickens and turkeys: hatchability in terms of hatch of fertile eggs or hatch of set eggs
Plumage	Plumage colour Feather quality	

Note: This is an updated version of Table 101 of the first SoW-AnGR (FAO, 2007a).

the turkey, layer and broiler sectors. To account for group dynamics in feeding, some breeding programmes have invested in feed recording systems based on transponder technology that allow continuous recording of the feed intake of individual birds in housed groups (Bley and Bessei, 2008; Howie *et al.*, 2010; Tu *et al.*, 2011). This technology also allows the genetic basis of feeding behaviour under competition to be studied (Howie *et al.*, 2009; Howie *et al.*, 2010).

One problem that has been highlighted by some authors (e.g. Dawkins and Layton, 2012) is the risk that rapid growth potential may pose to the welfare and the fertility of breeding birds. Feed management has been effective in optimizing

reproductive performance while avoiding obesity and associated welfare problems in breeding birds. However, welfare concerns about hunger have also been raised (D'Eath, 2009). Recent research has focused on behavioural and neuro-physiological measures of hunger (Dixon *et al.*, 2014; Dunn *et al.*, 2013) and the development of feeding strategies that optimise reproductive performance while avoiding both obesity and hunger (Van Emous, 2015).

Reproductive ability is not only vital to the profitability of the breeding companies' customers, it also affects the intensity of selection within the breeding nucleus. Increased longevity, egg fertility and hatchability, chick viability and persistency of

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performance are therefore key breeding objectives. These traits are significantly affected by hen age. New methodologies based on random regression models are now used to evaluate these traits (Wolc *et al.*, 2009; 2010) and this facilitates examination of the persistency of performance over time.

Livability (survival to the end of the production cycle) and persistent performance require healthy birds that are free of physical and physiological defects. Breeding objectives therefore include traits that contribute to the health and welfare of the birds. For example, in the egg-layer sector, efforts are made to minimize cannibalism and feather pecking in group-housing systems. Traits monitored include feather coverage at various ages. Some companies select breeding stock while the birds are housed in groups, particularly in the case of broilers. A strategy based on group selection using so-called social interaction models has also been shown to be feasible (Bijma, 2010) and is being evaluated (Ellen *et al.*, 2011). However, it is generally difficult to estimate genetic parameters for such effects, especially when group sizes are large, and this may limit the use of such methods. Livability also requires reduction in the incidence of cardio-vascular problems (sudden death syndrome and ascites) and leg problems in broilers and turkeys. However, the causes of these problems are multifactorial and have been the focus of research efforts for decades. Many breeding programmes regularly select against contact dermatitis (foot pad and hock burn) (Kapell *et al.*, 2012a) and for improved clinical and subclinical leg health (Kapell *et al.*, 2012b), as well as for measures of heart rate and oxygen saturation as indicators of ascites and sudden death.

Poultry breeders have adopted genomic selection (see Subsection 2.3) as a means of increasing selection accuracy and reducing generation intervals (Avendano *et al.*, 2010; Avendano *et al.*, 2012; Sitzenstock *et al.*, 2013; Wolc *et al.*, 2014). The greatest benefit from genomic selection is expected to be seen in the improvement of traits expressed in only one sex and/or at a late age (e.g. egg production, fertility and hatchability), carcass traits that hitherto required the sacrifice of potential selection

candidates, and disease-resistance traits that could otherwise only be meaningfully selected for on the basis of challenge tests (i.e. tests involving exposure to disease). It is now clear that despite these developments traditional data recording remains important, as the accuracy of genomics-predicted breeding values relies on accurate phenotypic data. Further statistical and technological developments that reduce the cost of genotyping individual birds will be key to the widespread application of genomic selection and its contribution to poultry breeding in the coming decades.

4.6 Rabbits

Intensive rabbit-meat production is based on three-way or four-way cross-breeding (Baselga and Blasco 1989; Lebas *et al.* 1997). In maternal lines, litter size remains the most common selection criterion because of its high economic value (Prayaga and Eady, 2000; Cartuche *et al.*, 2014). However, functional traits, such as doe longevity, kit survival, maternal traits and genetic resistance to bacterial disease, are emerging as criteria in breeding programmes targeting more sustainable production (Piles *et al.*, 2006; Eady *et al.*, 2007; Garreau *et al.*, 2008a; Sanchez *et al.*, 2008). Paternal lines are commonly selected for post-weaning daily gain or for weight at a point close to market age (Rochambeau *et al.*, 1989; Lukefahr *et al.*, 1996; Piles and Blasco, 2003; Larzul *et al.*, 2005). These criteria are easy to record and have a favourable genetic correlation with feed conversion index (Piles *et al.*, 2004), which is very important for efficient production, as feeding accounts for the highest proportion of total costs. In Europe, demands from slaughterhouses mean that carcass yield is becoming increasingly important. Disease resistance has also become a major issue. Thus, in addition to weight at slaughter age or average daily gain, some paternal lines are now selected for carcass traits and against susceptibility to digestive disorders (Eady *et al.*, 2007; Garreau *et al.*, 2008b). Breeding objectives in rabbits are summarized in Table 4C9.

Meat-rabbit selection schemes are found mainly in France, Spain, Italy, Hungary, Egypt and Saudi

TABLE 4C9
Selection criteria in rabbits

	Traits	Comments
Meat production	Growth rate or weight at slaughter	
	Carcass yield	
	Thigh muscle volume	Using computerized tomography
Reproductive efficiency	Litter size	
	Litter weight	
	Individual weaning weight	Direct and maternal effects
	Number of teats	
Longevity	Length of productive life	
Health and welfare	Homogeneity of birth weight	Indirect criterion for kit survival
	Genetic resistance to diseases	Mainly digestive disorders
Fibre production	Total fleece weight at each harvest (every 80-120 days)	
Fur size	Live body weight	
Fur density	Density of fibres per skin unit area	
Fur structure and composition	Bristliness or guard-hair content	
Fur priming	Scoring extent of the moult and hair follicle activity	

Arabia. Pedigree selection occurs strictly in specialized paternal and maternal lines, mainly using the BLUP methodology. Genetic improvement is diffused from the breeding nucleus into the wider population via pyramidally structured multiplication units. Some public research organizations are deeply involved in meat-rabbit breeding, either providing scientific and logistic support to private breeding companies (e.g. the Institut National de la Recherche Agronomique in France) or directly managing breeding nuclei (e.g. the Polytechnic University of Valencia and Instituto de Investigación y Tecnología Agroalimentarias in Spain and the University of Kaposvar in Hungary).

In contrast to meat-rabbit breeding, fibre (Rafat *et al.*, 2008) and fur production in rabbits is based on pure-bred selection in specialized breeds: Angora for fibre and Rex for fur. Genetic improvement of fibre and fur production in rabbits targets:

- increasing production of fibre or fur to give greater economic return per animal and production unit; and

- improving the quality of the fibre or fur so that it can be processed into superior end-products and thus attract a higher unit value.

Functional and adaptation traits (reproduction, health, growth and maternal traits) are also taken into consideration, but to a lesser extent than in meat production. BLUP methodology is used for genetic evaluation. Programmes are mainly located in France and China and are operated by public organizations and some private companies.

The main objectives of selection in commercial rabbit lines (i.e. prolificacy and feed efficiency) have not changed in recent years. However, research has provided information on the feasibility of improving traits such as the length of does' productive lives (Sanchez *et al.*, 2008; Larzul *et al.*, 2014), homogeneity of litter weight at birth (Garreau *et al.*, 2008a), carcass dressing percentage, heat tolerance (Sanchez and Piles, 2013), resistance to pasteurellosis and diseases causing digestive disorders (Garreau

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et al., 2008b; Eady *et al.*, 2007), and efficient production of semen doses for AI (Tusell *et al.*, 2012). As a consequence, new breeding programmes targeting kit and doe survival, carcass dressing percentage and digestive health have been implemented in commercial lines, with successful results. In addition, new selection criteria for improving prolificacy (ovulation rate and litter size – Ziadi *et al.*, 2013) and feed efficiency (residual feed intake and daily weight gain under feed restriction – Drouilhet *et al.*, 2013) have also been introduced. Results from experiments on Angora rabbits have shown that selection for total fleece weight, a simple trait that is easy to measure on-farm, positively affects both quantitative and qualitative traits in wool production (Rafat *et al.*, 2007; Rafat *et al.*, 2008).

Future priorities in rabbit breeding relate to the intensification of production to cope with the expected growth in global demand for animal protein in a way that is economically, environmentally and socially sustainable and to the need to adapt to changing environmental conditions. Breeding for improved disease resistance (robustness) has become a major challenge because of the effect that some infectious diseases (e.g. epizootic rabbit enteropathy and pasteurellosis) have been having on efficiency and productivity, the safety of rabbit products, animal welfare and public perceptions of rabbit production. Research objectives are increasingly focusing on quantifying the genetic control of the host–pathogen interactions, as well as on identifying SNPs associated with resistance.

The recent development of high-throughput genomic tools and statistical methods for dealing with massive amounts of data could allow selection based on SNPs associated with resistance traits. The rabbit genome has been sequenced (Carneiro *et al.*, 2014) and the implementation of gene-based and genomic selection is an emerging area of research in rabbit breeding. Its suitability in this species is still under discussion. As with other species, the use of genomic information could also lead to better understanding of

the biological processes underlying important traits.

The design and implementation of recording systems for specific difficult-to-measure traits, such as individual feed intake, would allow consideration to be given to new breeding strategies for improving the efficiency of production. The development of advanced statistical models and procedures involving, *inter alia*, direct and indirect effects (e.g. social effects for traits recorded in animals raised in groups), genetic × environment interactions and the use of information from cross-bred animals in commercial farms is also a major issue for future research.

5 Breeding programmes in low-input systems

The first SoW-AnGR provided an overview of the various challenges involved in establishing breeding programmes (including those involving cross-breeding) in low-input systems.¹⁵ It highlighted the importance of involving livestock keepers from the outset in the planning and implementation of such programmes and of paying attention to traits related to the efficiency of production (i.e. taking input use into account rather than simply targeting increased output). This subsection provides an updated account, beginning with a short description of the main options currently available for establishing breeding programmes in low-input systems and then addressing the specific considerations that need to be taken into account in the implementation of such programmes.

5.1 Breeding strategy options

As noted above (Subsection 3), a genetic improvement strategy can involve selection among breeds, cross-breeding and/or within-breed selection. In a low-input system it is particularly important to ensure that any breeds introduced

¹⁵ FAO, 2007a, pages 405–419.

and any crosses produced are able to thrive in the local production environment. As in all circumstances, breeding strategies for low-input systems should be based on careful assessments of the current state of the targeted production systems, the trends affecting them and the needs and objectives of the local livestock keepers and of society more broadly (FAO, 2010).

A properly implemented cross-breeding scheme offers the opportunity to combine the positive attributes of two different breeds. In a low-input system, this will often involve an attempt to combine the adaptive qualities of a locally adapted breed with the higher production potential of an exotic breed. There are several different types of breeding schemes that can be considered:

- pure-bred or terminal crossing systems – mating of animals from separate pure-bred populations over one or two generations to produce a generation of cross-bred animals that “terminates” the system, i.e. has desirable qualities in production terms, but is not used for breeding;
- rotational crossing – producing an initial two-way cross and then, in each subsequent generation, alternating the sire breed used (can include the incorporation of additional breeds); and
- creation of a new synthetic breed – crossing two or more breeds in order to achieve a desired proportion of each, followed by *inter se* mating of these animals.

The two first options have the advantage of continuously producing a heterosis effect. However, they may present logistical difficulties, and maintaining an exotic parental line in low-input conditions may be problematic (see Serradilla, 2001 for discussion of this issue in goats). As with any other kind of breeding scheme, determining what is possible in the specific local circumstances is a key element of planning a cross-breeding strategy. It has to be emphasized that if cross-breeding efforts are not carefully planned, or if plans are not properly followed, activities of this kind may create serious problems, both in terms of producing animals that are not well suited to local conditions

and in terms of eroding the existing locally adapted animal genetic resources. Uncontrolled cross-breeding is regarded as major threat to animal genetic resources in many countries (see Part 1 Section F).

Meta-analyses of studies on dairy and beef cattle in tropical environments (Burrow, 2006; Galukende *et al.*, 2013) have shown that in most cases F1 crosses perform better than other genotypes. For instance, Galukende *et al.* (2013) showed that 50 percent *B. taurus* × *B. indicus* cross-breeds had on average 2.6, 2.4 and 2.2 times higher milk yield than local *B. indicus* in highland, tropical wet and dry and semi-arid climatic zones, respectively. However, harsher production environments can lead to increasing problems with a lack of adaptedness (including reproductive problems) in cross-bred animals and particularly in exotic parental lines. When evaluating a programme involving cross-breeding with exotics, it is therefore important to consider a multiyear time horizon, accounting both for the lifetime profitability of individual animals (i.e. considering input costs, lifespan, reproductive success, etc., in addition to product output) and the costs of maintaining the various populations needed to keep the programme operating in the long term.

Improving a breed through straight breeding is a long-term commitment. In low-input systems it generally involves either a programme based on a central nucleus or a community-based breeding programme. Central nucleus schemes involve genetic improvement in a nucleus flock or herd and subsequent dissemination of improved genetic material directly or indirectly (via a multiplier layer) into the base population. The scope of the operation is, in principle, the whole population of the respective breed. The nucleus may be “closed” (gene flow occurs in one direction only – from the nucleus to the base population) or “open” (gene flow can also occur in the opposite direction, i.e. superior animals from the base population may be used to supplement the nucleus).

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The advantage of a programme based on a central nucleus is that it allows the use of advanced genetic evaluation methods (BLUP) and hence rapid genetic progress. Performance and pedigree recording is usually limited to the nucleus. A weakness is that such schemes depend heavily on organizational, technical and financial support (Mueller *et al.*, 2015). They also tend to be hierarchical rather than participatory in their planning and operation and hence often fail adequately to address the needs of livestock keepers in low-input systems (e.g. Gizaw *et al.*, 2013). Over the years, schemes of this type, entirely managed and controlled by governments or state operators – and with minimal, if any, participation on the part of livestock keepers – have been established in many developing countries (Wurzinger *et al.*, 2013a). A large proportion of them have failed. Such schemes have proven to be effective only when governments and other funding agencies have a long-term perspective and continue to provide technical and financial support until the programmes have achieved self-sustainability (Wurzinger *et al.*, 2011).

Community-based schemes (Mueller; 2006; Mueller *et al.*, 2015) operate at the scale of a single community rather than at the scale of the whole breed population. As well as operating at community scale, they are also community-based in the sense that livestock keepers are the main players in their design and operation, although support of various kinds may be provided by external stakeholders. A number of different types of structure are possible (Haile *et al.*, 2011; Gizaw *et al.*, 2013). Schemes may operate with or without a nucleus and, if present, the nucleus may be open or closed. The nucleus may also have a “dispersed” character, i.e. rather than being maintained as a single unit the nucleus animals are maintained in several different flocks or herds. Table 4C10 contrasts the typical characteristics of conventional and community-based breeding programmes.

The number of community-based breeding programmes implemented in low-input systems

has increased in recent years (e.g. Kosgey *et al.*, 2006; Mueller, 2006; Pastor *et al.*, 2008; Wurzinger *et al.*, 2008; Tadele *et al.*, 2010; Valle Zárate and Markemann, 2010; Wurzinger *et al.*, 2011; Abegaz *et al.*, 2013). A review prepared by Mueller *et al.* (2015) describes eight case studies of community-based programmes. An overview of the main characteristics of these programmes is provided in Table 4C11, along with some additional examples.

Experience indicates that establishing a successful community-based programme requires the involvement of a range of stakeholders (livestock keepers, local government, NGOs, universities, etc.) (Wurzinger *et al.*, 2013a). Adopting a participatory approach from the start of the planning process will help to ensure commitment and ownership and to clarify the roles and responsibilities of the various stakeholders involved.

5.2 Specific challenges involved in establishing and operating breeding programmes in low-input systems

The recording scheme of a community-based breeding programme needs to be cost-effective and should not be too elaborate for local conditions (Wurzinger *et al.*, 2011). Performance testing at central stations and visual appraisal in herds are commonly used in recording schemes for meat and fibre production. A milk-recording scheme is more challenging, as it requires repeated measurements. Timely feedback is needed in order to maintain livestock keepers’ interest in the recording scheme (Wurzinger *et al.*, 2011; Iñiguez *et al.*, 2013).

As most livestock keepers are interested in improving many different traits, the use of an economic selection index (see Subsection 3) to determine which animals should be used for breeding is generally recommended (e.g. Gizaw *et al.*, 2010). In the case of breeding schemes based on dispersed nuclei, livestock keepers will need to be more involved in the implementation of the animal identification and recording activities, and they will also need to agree on arrangements for sharing males to establish genetic linkages between herds/flocks.

TABLE 4C10

Characteristics of conventional and community-based livestock breeding programmes

Characteristic	Conventional breeding programme	Community-based breeding programme
Geographical limit	Regional – inter-regional	Communities
Market orientation	Commercial	Subsistence – commercial
Agent of programme	Breeding company – breeder organization	Livestock keeper – breeder
Breeding objective	Defined by company – breeder organization	Defined by breeder – livestock keeper
Breeding structure	Large scale, pyramidal	Small scale, one or two tiers
Genetic resources	International	Local
Infrastructure	Available	Limited
Management	Intensive – high input	Extensive – low input
Risk taker	Company – livestock keeper organization	Livestock keeper
Decision on share of benefits	Variable	Livestock keeper

Source: Mueller *et al.*, 2015.

TABLE 4C11

Selected community-based breeding programmes

Country	Species	Main product	Period	Location	Total animal population	Breeding system	Key references
Argentina	Goats	Mohair	1987 – ongoing	Dispersed	62 000	Open nucleus	Mueller, 1995; Lanari <i>et al.</i> , 2009; Mueller, 2013b
Bolivia (Plurinational State of)	Llamas	Fibre	2008 – 2012	Villages	2 500	Open nucleus	Wurzinger <i>et al.</i> , 2008
Ethiopia	Sheep	Meat	2009 – ongoing	Communal	10 000	All flock	Haile <i>et al.</i> , 2011; Duguma <i>et al.</i> , 2011; Mirkena <i>et al.</i> , 2012
Iran (Islamic Republic of)	Goats	Cashmere	2009 – ongoing	Nomad	2 800	Open nucleus	Mueller, 2013
Kenya	Goats	Dairy	1997 – ongoing	Dispersed groups	20 000	Open nucleus	Ojango <i>et al.</i> , 2010
Mexico	Goats	Dairy	2007 – ongoing	Village	200	All flock	Wurzinger <i>et al.</i> , 2013b
Mexico	Goats	Dairy	2000 – ongoing	Villages	1 500	Open nucleus	Valencia-Posadas <i>et al.</i> , 2012
Peru	Sheep	Wool	1996 – ongoing	Communal	160 000	Open nucleus	Mueller <i>et al.</i> , 2002; Mueller, 2013
Uganda	Chickens	Eggs	2003 – ongoing	Dispersed groups	>120 000	Multilevel cross-breeding	Roothaert <i>et al.</i> , 2011
Viet Nam	Pigs	Meat	2000 – ongoing	Villages	700	Open nucleus	Valle Zárate and Markemann, 2010; Roessler <i>et al.</i> , 2012

Sources: Mueller *et al.*, 2015; Valencia-Posadas *et al.*, 2012.

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Box 4C5

GENECOC – the breeding programme for meat goats and sheep in Brazil

In 2003, the Brazilian Agricultural Research Corporation (EMBRAPA) launched the Breeding Program for Meat Goats and Sheep – GENECOC*. Up to that time, there had been no structured breeding programmes for goats and sheep in Brazil and there was a lack of recorded information on the performance of these species.

GENECOC is a genetic advisory service that aims to encourage and assist programme participants with record keeping in their flocks and the generation of reliable information that can be used in selection decisions. GENECOC targets all kinds of animals and breeders, focusing particularly on locally adapted breeds and low-input systems. Breeding strategies are matched to local production systems. However, the main feature of the scheme is the use of web-based software to record, organize, store and manage the information generated. The system includes tools for selecting animals for total genetic merit through the use of (breed specific) selection indexes and identifying the set of matings that maximizes the genetic gain of the flock, while controlling inbreeding.

One important action undertaken under the programme targets the Morada Nova sheep, a locally adapted breed that was once at risk of extinction. Participatory methodologies are used

in the implementation of a community-based programme, including in the definition of breeding objectives, performance testing in young rams and the organization of monthly planning meetings.

Today, in addition to its activities in Brazil, GENECOC also participates in projects in other countries, including Ethiopia and the United States of America.

The principal impacts of the programme have been in adding value to locally adapted sheep and goat breeds and optimizing their use while respecting environmental concerns. Experience has shown that it is important to identify and involve key stakeholders, to use a well-organized and well-trusted data-collection system backed-up by government funding and, when designing breeding objectives and selection criteria, to consider not only traits related to market trends, but also traits that livestock keepers judge to be important. Future plans include expanding activities to include additional sheep and goat breeds and expanding the system for multiplying improved animals to cover additional local production systems.

Provided by Raimundo Nonato Braga Lôbo.

For further information see Lôbo *et al.* (2010); Lôbo *et al.* (2011) and Shiotsuki *et al.* (2014).

*<http://srvgen.cnpc.embrapa.br/pagina/english/principal.php>

Morada Nova sheep in Northeast region of Brazil

Photo credit: Olivardo Facó.

Weighing Morada Nova lambs

Photo credit: Olivardo Facó.

Box 4C6

Establishing a cross-breeding scheme for dairy goats in the United Republic of Tanzania

Toggenburg goats were introduced into Babati, United Republic of Tanzania, as the result of a Farm Africa project in 1990. The project originally brought in four pure-bred Toggenburg does and one Toggenburg buck and established a women's group that operated a goat-in-trust* scheme. Because of the poor performance of the women's group, a sister project was initiated, under which commercial groups (groups of goat keepers raising animals for commercial as well as subsistence purposes) were established through a goat-in-trust scheme.

In 1997, the commercial goat raisers formed the Toggenburg Breed Association (TOBRA) as a commercial dairy goat production association. In 1998, TOBRA was registered by the Ministry of Home Affairs. At the time it had only 12 members. In 2001, TOBRA established eight dairy goat production groups. By the end of 2007,** the number of groups had expanded to 52, involving 188 farmers, with an average of eight goats each. People were initially very reluctant to join the groups, but following sensitization efforts they began to join voluntarily. Association members raise pure Toggenburgs, 75 percent Toggenburg crosses and 50 percent Toggenburg crosses. The cross-bred animals are carefully evaluated by analysing their pedigrees and productive and reproductive performances.

TOBRA started with 249 000 shillings*** in the form of registration fees and other contributions. As of 2007, it had more than 12 000 000 shillings. It has employed a treasurer and manages the costs of its meetings and agricultural shows at district, region, zonal and national levels.

The main objectives in forming the association were:

- to increase milk productivity from goats through cross-breeding Toggenburg and indigenous goats, taking advantage of the high milk production of the former and the disease resistance of the latter;
- to produce pure Toggenburgs so that genetics could be exchanged with farmers from Kenya and Uganda; and
- to improve the income of the members through selling milk and live animals (pure-breeds and crosses).

*A scheme in which the loan of a goat is paid back in the form of another goat that can be passed on to another participant.

**This is the most recent date for which published figures are available. Since then the farmers have continued their goat breeding and production activities under the supervision of the local extension services.

*** Equivalent to approximately US\$400 at the time.

Provided by Yacobo Msanga, National Coordinator for the Management of Animal Genetic Resources, the United Republic of Tanzania.

For further information see Msanga and Bee (2006) and Bee *et al.* (2006).

Participatory approaches to setting breeding goals and identifying traits to be recorded have been recommended as a means of promoting the involvement of livestock keepers in the operation of community-based programmes (Gizaw *et al.*, 2010; Wurzinger *et al.*, 2011). Potential methods include individual interviews with livestock keepers, workshops with groups of livestock keepers and exercises involving the use of choice cards or the ranking of live animals (e.g. Duguma *et al.*, 2010; Haile *et al.*, 2011). More generally, a participatory approach that engages the various actors involved will help ensure their commitment and ownership,

prerequisites for the long-term sustainability of a breeding programme.

Controlling inbreeding can be a major issue in breeding schemes in low-input systems, especially in closed central nucleus schemes and in community-based schemes operating on a limited scale. Gizaw *et al.* (2009) recommend that for an acceptable rate of inbreeding, sheep breeding schemes should include at least 600 ewes and 15 rams. Rotation of males between livestock keepers' herds/flocks or between the nucleus and livestock keepers' herds/flocks can help to limit inbreeding. The use of sire-reference schemes (i.e. schemes in which each cooperating livestock keeper agrees

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Box 4C7

Community-driven breeding programmes for locally adapted pig breeds in Viet Nam

Demand for pork in Viet Nam has increased substantially since the 1990s, driven by economic development and urbanization. Although large-scale private enterprises have benefited from subsidies introduced with the aim of expanding exports, smallholder farmers still represent the backbone of the Vietnamese pig sector, especially in the northern part of the country. To cope with increasing competition and quality requirements, market-oriented smallholders increasingly raise modern pig lines and hybrids, often in unsystematic cross-breeding schemes. This has reduced the population sizes of autochthonous breeds and pushed them into remote areas.

Under a pilot project implemented by German and Vietnamese research institutions in collaboration with the provincial veterinary department and private partners (funded by the German Research Foundation, DFG), a community-driven pig-breeding and marketing programme was established in the mountainous Son La province in northwestern Viet Nam. The farmers' pig-breeding cooperative involves ten villages, representing communities with different resource endowments, production objectives and consequently different requirements from their pig genetic resources.

Initially, pure-bred indigenous Mong Cai and Ban gilts were distributed among 179 cooperative members and a revolving fund was established with the aim of

enabling the smallholders to be independent in terms of supplying replacement animals and improving genetic stocks. Prolific Mong Cai gilts were distributed mainly to semi-intensive producers and robust Ban sows to less market-oriented smallholders.

Although some of the collective actions planned under the project were successfully implemented – for instance, improving the access of rural small-scale pig producers to veterinary services and establishing multipronged market outlets – the attempt to establish a community-based stratified cross-breeding scheme proved to be difficult. The organizational structures of a cross-breeding scheme must be accompanied by a well-balanced business plan that accounts for the greater burden placed upon nucleus breeders. In this example, although farmers preferred to use pure-bred dam lines, and Mong Cai breeders could therefore obtain a good price for sows, this was

Mog Cai sow and fatteners**Ban sow and litter**

Photo credit: Kerstin Schöll.



Photo credit: Kerstin Schöll.

(Cont.)

Box 4C7 (Cont.)

Community-driven breeding programmes for locally adapted pig breeds in Viet Nam

not sufficient to compensate them for the low prices obtained for pure-bred Mong Cai finishers. The market for the latter completely collapsed because of rapid shifts in customer preferences towards leaner pork. In the future, farmers will probably turn to breeding centres or commercial farms to obtain pure-bred Mong Cai sow replacements. In contrast, marketing of pure-bred Ban products via a short supply chain, avoiding a large number of intermediaries, proved to be successful in linking remote resource-poor Ban keepers to highly remunerative specialty markets in the Red River Delta. Because of the prices that can be realized

in these niche markets, farmers will probably continue pure-breeding the Ban breed and this will create a pool of sow replacements for farmers that exclusively practice cross-breeding.

In conclusion, this case illustrates how a self-sustained community-driven pig breeding and marketing programme can only sustainably contribute to rural development and breed conservation if it can be flexibly adapted to market conditions.

Note: This box updates Box 89 of the first SoW-AnGR (FAO, 2007a).
Provided by Philipp Muth and Anne Valle Zárate.

to use sires or semen from a group of high-quality so-called "reference" sires – Simm *et al.*, 2001) in the implementation of dispersed-nucleus schemes may reduce inbreeding in the short term but increase it in the long term at herd level. Systems for regularly providing males from other herds/flocks are particularly important in situations where introducing animals (or semen or embryos) from outside is not feasible.

When calculating the economic efficiency of a given breeding programme, it is important to take into account both the tangible and the intangible benefits that accrue to various different groups of stakeholders (livestock keepers, retailers, government, etc.). Advice on how to evaluate investment decisions in breeding programmes is provided in FAO's guideline publication *Breeding strategies for sustainable management of animal genetic resources* (FAO, 2010). Computer simulation of the breeding programme can be used to predict changes in targeted traits and their sensitivity to changes in various factors affecting genetic response (e.g. Gebre *et al.*, 2014).

Finally, in addition to genetic considerations, factors related to market chains usually have a major influence on the success of breeding programmes in low-input environments. The absence of effective marketing chains will present a significant

challenge. This is true for both output and input markets (Haile *et al.*, 2011). Although a multi-trait breeding objective is likely to be optimal, such breeding programmes are usually designed so as to increase production to some degree. In theory, the increased production may be used simply to improve food security and nutrition within a subsistence system, but more commonly the programme is designed so as to generate excess product that can be marketed. Genetic improvement requires investment of human and financial capital, and these inputs will be wasted if no market channel is available. Improvements to productivity achieved by breeding programmes in low-input systems are rarely due only, or even primarily, to genetic improvement. Successful genetic improvement programmes are usually complemented by enhanced veterinary care and nutrition, so reliable access to these resources is also important. Organization of livestock keepers into associations or cooperatives to coordinate activities and increase access to input and output markets is usually beneficial. In the longer term, establishing a marketing system for superior breeding stock will also be beneficial, as it will provide breeders with another source of income and incentive for genetic improvement.

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5.3 Genomics and future developments

As discussed in Subsection 2, techniques that enable the use of genomic information in animal breeding have advanced greatly in recent years, particularly in the case of cattle, pigs and poultry. While these techniques offer major potential benefits, particularly in terms of allowing the selection of animals at earlier ages and reducing generation intervals, there are several concerns regarding their use in low-input production systems. Effective use of these techniques requires more than just vague information on the phenotypes and genotypes of the breeds concerned. A reliable data-recording scheme is absolutely necessary in order to provide the basis for associating genotypes to phenotypes. Such schemes are lacking in most low-input situations. There are nevertheless steps that can begin to be taken towards the use of these new technologies in developing countries. Efforts to identify genes or genomic regions associated with adaptation or variation in production traits in harsh environments need to be stepped up in developing countries and in low-input smallholder and pastoralist production systems (Rothschild and Plastow, 2014). Once relevant genes have been characterized, livestock populations can potentially be improved through genetic introgression or gene-assisted breeding programmes. With regard to genomic selection more specifically, implementation requires the establishment of training and validation populations, in which both phenotypes and genotypes are recorded, so that the prediction model can be established. Indigenous populations with low linkage disequilibrium generally do not meet these requirements (Akanno *et al.*, 2014). The use of widely used international transboundary breeds as reference populations for genomic selection in locally adapted breeds seems to have little or no value, except perhaps in cross-bred populations, but this has not been studied. Any attempt to implement genomic improvement programmes needs to take into account the need for adequate infrastructure, technical skills, policies and communication

strategies, and the need for a long-term perspective in planning and implementation (Rothschild and Plastow, 2014).

6 Conclusions and research priorities

The main advances in breeding programmes and related technologies over recent years have been in the application of genomic information, particularly in high-input production systems. Genotyping costs have dropped precipitously and for some species nearly all of the important selection candidates are genotyped, as have been the major ancestors from which genetic material is available. Genomic selection increases the accuracy of EBVs, particularly for those animals for which no phenotypic data are yet available. The impact on the commercial dairy breeding industry has been revolutionary. Progeny testing now plays a minor role. Breeding goals have seen various adjustments. In particular, greater emphasis is now being placed on profit, rather than output, and therefore on health, survival and other traits that influence production costs.

The genomic revolution has yet to affect developing countries to a significant degree. Accurate genomic selection depends on the availability of phenotypic data, which are usually lacking in the low-input production systems typically found in developing countries. Nevertheless, the situation in these countries has not remained static. Formal breeding programmes, usually community-based, have become more common and are improving the productivity of animals and livelihoods of their keepers. However, significant work is still required. Animal identification and pedigree and performance recording need to be expanded. This is necessary even to take advantage of traditional approaches to breeding, let alone genomic selection.

Little if any direct progress has occurred since the first SoW-AnGR was prepared in terms of determining the underlying genetics of phenotypic adaptation to the environment. However, the

tools with which to do this are in place. Genomic analysis should allow breeders to determine actual genetic by environment interactions, although a tremendous amount of work remains to be done in order to obtain the phenotypic information needed to accurately predict such interactions.

Future research will need to address the need for new modes of production that can help meet the expected growth in global demand for animal protein in ways that are economically, environmentally and socially sustainable and address the need to adapt livestock production to changing environmental conditions. In other words, efficiency of production will be an increasingly important consideration. This will include a wide range of efficiencies and involve not only increasing product yield per unit of input, but also addressing negative effects such as environmental damage (see Box 4C8 for an example). Improvement in the use of feed resources, reproductive efficacy and prolificacy, and animal health will be key topics for research, both in developed and in developing countries.

The following list of research priorities draws on the Strategic Research Agenda of the Sustainable Farm Animal Breeding and Reproduction Technology Platform, an extensive review of research priorities in livestock breeding in Europe (FABRE TP, 2011).

Selection to balance functionality and production

- improving knowledge of the genetics of:
 - disease resistance, resilience and immune response;
 - host–pathogen interactions;
 - gut functionality and its relationship with gut microbiota in different environments;
 - emission of methane and production of other greenhouse gases;
 - variation in digestion of specific amino acids and phosphorus – along with improving knowledge of nutrient (e.g. amino acid) requirements under different production conditions; and
 - uniformity;

- developing economically viable means of including traits of increasing consumer concern in breeding goals, including traits with uncertain economic value;
- developing strategies for improving disease resistance without compromising production;
- developing phenotype definitions for novel traits;
- establishing standard phenotypic trait ontologies encompassing production traits, disease traits and other welfare traits and environmental sensitivity;
- developing tools to estimate and exploit non-additive genetic variation;
- developing social-interaction models including, male–female interactions, to facilitate the improvement of reproductive, health and welfare traits;

Genomics and other “-omics”

- characterizing the genome sequences (and variation therein, including epigenetic transmissible variants) of species, populations and individuals;
- developing methods for optimal incorporation of genomic information in breeding-value estimation;
- developing proteomic and immunological metabolomic technologies for high-throughput analyses;
- developing schemes incorporating large-scale genotyping at embryo level;
- metagenomic sequencing of gastro-intestinal microbial communities;

Bioinformatics and biostatistics

- developing statistical programming tools relevant to new traits and new phenotypes;
- supporting continued annotation and maintenance of public genome databases;
- developing scalable bioinformatics tools to handle high-throughput data (e.g. genomic selection procedures or inference of genome-wide diversity parameters);

PART 4

Box 4C8

Genetic selection for reduced methane production – a future tool for climate change mitigation

The expanding world human population will require greater food production within the constraints of increasing societal pressure to minimize impact on the environment. Animal breeding has in the past achieved substantial reductions in environmental load per unit of product, despite no explicit inclusion of environmental load in breeding goals. Higher gains can be expected if breeding goals focus more specifically on environmental objectives. One important objective is to reduce the amount of enteric methane – a greenhouse gas with a warming potential 25 times that of carbon dioxide – produced by ruminants. However, a successful breeding strategy requires measurements on a large population of animals. To facilitate genetic selection for reduced methane production, it would therefore be highly desirable to combine individual national datasets to produce a multicountry database. However, data are collected using different protocols, and combining them requires intensive consultation among contributing scientists across a range of disciplines. More importantly, however, scientists planning to undertake future studies on methane production have not yet agreed protocols for how to proceed with the collection of data.

The networks of METHAGENE (www.methagene.eu) and ASGGN (www.asggn.org) have joined

forces with the International Committee for Animal Recording (www.icar.org) to develop consensus on protocols for the collection of methane production data, with the aim of facilitating the harmonization and combination of existing and future data obtained from different countries and with different collection methods. The project will also facilitate discussions among experts aiming to identify possible predictor traits for methane production (e.g. biomarkers in milk) that could be easily exploited. Methane production is currently not directly included in any national cattle breeding objective anywhere in the world. This is not only because of a lack of sufficient data with which to make selection decisions, but also because of a lack of consensus on how to optimally include methane production in a breeding objective. The project will develop standards for expressing methane production, taking into account the advantages and disadvantages of expressing methane per unit (digestible) feed and per unit of consumable product (i.e. milk and/or meat) and also the need to consider the time horizon of emissions via a life-cycle assessment and to ensure that selection for low emissions does not compromise production efficiency.

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- developing means of exploiting distributed computing technologies (GRID, Cloud) for more effective data storage, sharing, integration and analysis;
- improving the use of genomic sequences for predicting genetic values and detection of *de novo* mutations;
- developing transcriptomic tools (arrays and RNA-seq);

Breeding strategies in low-input production systems

- improving methods for planning and implementing breeding strategies in production systems where there is little or no organizational infrastructure, including means of determining where breeding programmes are feasible and appropriate and how they can be adapted to local circumstances;
- exploiting the use of telecommunications and informatics technologies to improve data collection;

- improving strategies for the establishment of stable cross-breeding systems; and
- developing simulation tools to predict the consequences of introducing exotic breeds into local populations (as part of genetic impact assessment).

Improving research cooperation

Research in the field of animal breeding could be strengthened by promoting greater cooperation among the various stakeholders involved. Relevant measures include:

- promoting even greater collaboration between the breeding industry, academia and the public sector;
- exploring the feasibility of capturing and using production data from commercial producers (e.g. encouraging the use of commercial populations for high-resolution genetic analyses); and
- developing data-sharing policies that allow the value extracted from complex datasets to be maximized without compromising legitimate commercial interests.

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Section B: Characterization, inventory and monitoring

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Part 5 NEEDS AND CHALLENGES

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