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Animal Breeding Methods and Sustainability

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Article Outline

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Glossary

Breed A population of animals with common morphological characteristics that is recognized as a breed by the administration, by a breeders association, or by other groups of people.

Best linear unbiased prediction (BLUP) It is the most common statistical method used in breeding evaluation.

Quantitative trait locus (QTL) A gene having influence in a quantitative trait.

Markers Fragments of the DNA molecule for which their position is known.

Response to selection Genetic progress.

Definition of the Subject

After domestication, animals were selected in different environments and for different traits leading to the modern breeds. Long before the appearance of the science called now as "Genetics," animal breeding had been practiced by humans following intuitive criteria, less efficient than the scientific ones, but criteria that had provided success along many generations of selection [1]. The lack of a theory explaining inheritance slowed down animal breeding for many years, but with the rediscovery of Mendel's rules at the beginning of the twentieth century and the development of quantitative genetics in the 1920s and 1930s animal breeding had the tools needed for its development. Animal breeding methods were developed in the 1930s and 1940s, and the first animal breeding companies and cooperatives started in using scientific methods for animal selection [2]. The development of artificial insemination in cattle in the 1940s and frozen semen in the 1950s led to the modern schemes of progeny test, in which bulls are proved with a high number of daughters, and semen of the best bulls is available worldwide. Large companies of animal breeding were created in the 1960s for poultry and pigs, and nowadays they dominate the market of reproducers, particularly in the avian case. In 1953 the structure of the DNA was published, leading to a quick development of all molecular genetics techniques. Today, DNA information is widely used as a complementary tool to the statistical methods based on data from records, to estimate the genetic values of the candidates to selection [3]. Although the commerce of genes is now extended worldwide, there is a recent interest in conserving breeds in danger of extinction due to this globalization. These breeds are a genes reserve for ensuring possible changes in the future market. Besides, some breeds can be helpful for developing sustainable systems in areas in which modern developed animals cannot be bred because of the lack of resources, climate, or other reasons [4].

Introduction

Long before the appearance of the science that is now called "Genetics," animal breeding had been practiced by humans following intuitive criteria, less efficient than the scientific ones, but criteria that had provided

success along many generations of selection. Darwin himself was impressed by the achievements of farmers, and artificial selection was a source of inspiration for his theory of evolution [5].

▶ We cannot suppose that all the breeds were suddenly produced as perfect and as useful as we see now them; indeed, in several cases, we know that this has not been their history. The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to make for himself useful breeds.
C. DARWIN
On the origin of species (1859, p. 30)

Animal breeding starts with domestication. Although there are several theories about the domestication process, it is generally admitted that selective breeding led to modern domestic animals, a hypothesis corroborated by the experiment of domestication of wild silver foxes started by Dimitri Belyaev in 1959 and still continued. After 40 years of selection for quiet temperament, silver foxes, which are aggressive to humans in the wild, became as friendly as dogs [6]. As a correlated response, some physical appearance also changed, and some bones of the skull were modified in the same direction as dogs when compared with wolves [7]. Modern molecular techniques permit to reconstruct the history of domestication [8]. After domestication, animals were selected in different environments and for different traits, leading to the modern breeds. References to animal breeding can be found in ancient Greek and Roman authors' works [9]; however, modern breeding practices start with the self-taught work of Robert Bakewell (1725–1795), who produced new breeds and had a high reputation as breeder [1]. He focused his work in the performances of his cattle and sheep, hiring rams, recording the offspring and keeping the sons of the best males. He fixed few and clear breeding objectives mating the best females with the best males. However, he disregarded the damaging effects of inbreeding and due to this, he had fertility troubles with his new breeds, but he is still considered as the first farmer practicing modern animal breeding.

The lack of a theory explaining inheritance slowed down animal breeding for many years. The theory of blending inheritance, sustaining that offspring was intermediate between parents, could not explain the persistence of genetic variability. Some hybrid breeders had noticed that crossing hybrids they can recover discrete traits that were present in the parental population [10], but Gregor Mendel (1822–1884) was the first in calculating the frequencies in which the observed traits were transmitted, allowing him to propose the first rules of genetic inheritance [11]. Although Mendel was conscious of the importance of his research, his work, published in a context of hybrid plant production, was largely ignored until it was rediscovered at the beginning of the twentieth century, and it was widely used to explain the inheritance of discrete observable traits. Mendel's rules worked well for discrete traits like yellow or green color, but many traits like milk production or body weight showed a continuous variation and seemed to follow different inheritance rules. The biometrician school, founded by Karl Pearson (1857–1936), was using and developing statistical methods, and rejected Mendel's rules, considering them as a special case of inheritance for some discrete characters [12]. Mendel was aware about the fact that the simple rules he discovered could not be applied to continuous variation, but he suggested that in these cases many inheritance factors might act simultaneously producing all intermediate indistinguishable classes. After some exam of this possibility, it was disregarded by the biometricians, and a bitter dispute about the mechanisms of inheritance started until Fisher (1890–1962), in a seminal paper [13], used statistical methods to reconcile Mendel's laws on inheritance with the continuous variation observed by biometricians. (For a history of early development of genetics and this dispute, see [12].)

The work of Fisher in this and subsequent papers started both modern statistics and modern quantitative genetics, but the methods of this new science had still to be applied to animal breeding. This task was accomplished by Lush (1896–1982), who harmonized breeding practices with the knowledge provided by the new discipline. Lush defined concepts like heritability, and proposed methods of selection including the information of relatives, weighed according to the genetic contribution predicted by Mendel's rules and quantitative genetics. The several editions of his book "Animal breeding plans" contributed to spread the new knowledge among scientists, technicians, and breeders [14]. Modern indexes of selection for several traits were

developed for plants by Fairfield Smith [15] closely following some indications given by Fisher, and Hazel [16] applied them to animal breeding allowing on one side to use family information and on the other side to weigh all traits of economic interest according to the predicted benefits that the offspring would give.

The development of artificial insemination permitted having offspring of the same sires in many farms (see [17] for a history of its development). As environmental effects were different depending on the farm circumstances, data had to be corrected in order to evaluate the animals properly. Corrections for environmental effects like parity, season, length of lactation, etc., had been made before, but then the problem was more complex. Several methods were developed to pre-correct the data before genetic analysis was made, but it was Henderson (1911–1989), who proposed a method for integrating the genetic values and the environmental ones in the same statistical model. This allowed the prediction of genetic values at the same time that corrections for environmental values were made [18]. The development of computers allowed using all relatives in the evaluation, and some computing difficulties derived from the use of all relatives were solved by Henderson himself [19]. Nowadays his method called best linear unbiased prediction (BLUP) is the standard method in animal breeding evaluation. BLUP needs the variance components (genetic and environmental) for predicting the genetic values. To estimate them is a difficult task, because data come from different farms and different environments and they should be corrected as before. Paterson and Thompson [20] showed how to correct for the environmental effects and how to estimate the genetic variance components at the same time. Their method is called REML (Residual or Restricted Maximum Likelihood) and it is a standard for variance component estimation.

Animal breeding was dominated by REML and BLUP – and they are still the most common methods – until the development of modern computers allowed the use of Bayesian methods. These methods use probabilities for inferences, which give them several advantages and permit to express the uncertainty about the unknowns in a natural way. For example, it is easier to understand that the probability of a breed having a higher growth rate than another is 93% than to understand that when estimating the difference in

growth rate between breeds, in an infinite number of repetitions of the experiment, new samples will be higher than the actual sample in a 7% of the cases (which is the definition of a *P*-value of 7%). A review of Bayesian methods compared with classical statistical methods in animal breeding can be found in [21]. Bayesian methods were introduced by Daniel Gianola in the 1980s [22], but they lead to complicated integrals that could not be solved even by approximate methods. The rediscovery of a numerical method called Monte Carlo Markov Chains permitted to overcome this problem and to use Bayesian methods, leading to a high development and extension of them in animal breeding (see [23] for a detailed exposition of the methods).

With the arrival of DNA analysis techniques, a new field was open for research. Transgenesis looked as a promising area, but its real usefulness in animal breeding has been discussed [24]. Molecular markers, however, have been widely used in animal breeding as a complementary tool in genetic programs. They have been also used for capturing major genes; unfortunately, most traits are not controlled by major genes and molecular markers have had a limited success in this area [25]. Recently, simple molecular markers consisting in a single nucleotide substitution in the DNA chain (SNP) have been made easy and cheap to detect. This permits to use several thousand markers in each individual, thus all genes controlling a trait can potentially be associated to SNPs [26]. A main problem of this procedure is that these associations between SNPs and genes are lost after few generations of selection [27], but new associations can be reestimated. Nowadays genomics is being examined as a promising tool for many genetic programs, particularly in species like dairy cattle in which there is a continuous recording, the trait is expressed only in females, and generation intervals are large. In this case, genomics can be used for a better evaluation of young bulls that still have no offspring. Other uses of genomics will appear in the forthcoming years and it will be probably established as a useful complementary tool to current genetic programs.

Animal Breeding and Sustainability

Animal breeding consists essentially in selecting animals kept in close reproduction systems, often

accompanied with crosses between these groups of animals [2]. Historically, the groups of animals kept in close reproduction were breeds, although modern intensive meat production of prolific species is now based in selection of synthetic lines. These lines are called "synthetic" because they do not correspond to traditional breeds, but have been generated by crossing animals from different breeds or crossing commercial "hybrids" (which are not hybrids in a genetic sense, as it will be seen later). This procedure allows obtaining a large genetic variability available for selection on productive traits. The relevance of breeds for sustainability lies in that some breeds can be particularly well adapted to local conditions, although this does not mean that local breeds are always better for local conditions than foreign breeds. A foreign breed can be better adapted or can be economically more interesting than a local breed. This is common mainly in species like poultry, pigs, or rabbits, which are usually kept in better environmental conditions than beef, sheep, or goats, but it also happens in ruminants. For example, Nelore cattle, a foreign breed in Brazil, has had a high success and now it is extensively implanted there [28].

Definition of Breed

There is no consensus about the definition of what a breed is. Many definitions of breed have been compared [29–31], and the only common requirement to all of them is the genetic homogeneity, which applies essentially to external traits. It can be said that *a breed is a group of animals with some common external characteristics defined by some people who consider this group of animals to be a breed.* A breed requires some people who decide the external characteristics used to define the breed; often they also attribute some "average performances" to the breed. The problem with this definition is that it depends too much on external characteristics that may be very useful for dog or ornamental animals, but not necessarily for animals producing meat or milk in an efficient way. Some breeds were historically selected for improving some traits and they have been established as the most productive ones in intensive production systems; Leghorn hens for white eggs, Friesian cows for dairy cattle and Landrace and Large white in pig production are now widely

established. However, the word "Leghorn" or "Landrace" only define the external appearance of the breeds; there are many types of Landrace in the world, depending on the traits for which they have been selected, and the few multinational companies that control the eggs market use specific highly productive Leghorn lines, therefore the concept of "breed" is often of little utility. Other words used in animal breeding that can lead to confusion are "pure breed" and "hybrid." In plants, a hybrid is the cross of two pure lines. A pure line is homozygous for all its genes, and all individuals have the same genotype, all hybrids have also the same genetic composition, and the cross of two plant hybrids produces very different plants due to the segregation of all the alleles (Fig. 1).

There are no "pure lines" in animals in the same sense as in plants. Pure lines in plants have been produced by self-fertilization or by fertilization of close relatives, something that is not possible in animals. Some attempts of creating highly inbred lines in pigs and poultry were done in the 1940s and 1950s, without positive results, because inbreeding produces infertility and abnormalities to a degree that prevents its use in animal breeding [2]. "Pure lines" in animals are only groups of animals in closed reproduction that will not be homozygous for all their genes, therefore animal "hybrids" will be crosses between lines or breeds with no genetic homogeneity. Moreover, it is a frequent practice in animal breeding to open the lines to some animals from other commercial lines in order to reduce inbreeding. This practice is also useful to capture genes that would be in lower frequency in the recipient line
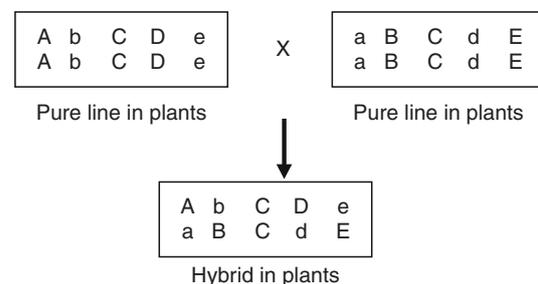
Animal Breeding Methods and Sustainability. Figure 1 Pure lines and hybrids in plants. Couples of letters indicate genes; capital letters indicate one allele of a gene and small letters another allele of the same gene

and that may be in higher frequency in the imported animals [32]. As "animal hybrids" are only crossed animals, they can be used to produce new "animal pure lines" with high genetic variability available for selection; for example, several rabbit breeds used for commercial purposes were originated by crossing commercial "hybrids" [33].

Breeds were created by humans after domestication by selecting traits they particularly liked. New breeds can be created nowadays. Apart from pets, many companies of pigs, rabbits, and poultry now use synthetic breeds without giving special importance to external characteristics, with the exception of the functional ones.

Breed Conservation

Some breeds, local or not, can perform better than some intensively selected lines in systems in which food is less rich in protein or energy, or less balanced than in intensive systems. Some breeds can also perform better in some areas in which climate or breeding conditions are very different from the ones of current intensive production systems. There are more reasons for conserving breeds [34]: keeping genes that may be useful in the future, supporting sustainable animal production systems for food security, maintaining genetic variability for further use, conserving cultural heritage, etc. However, when a breed is useful, it does not normally need special aids for conservation, since it produces some profit and then it is kept for obtaining benefits. Help is needed especially for breeds that are not profitable, but there are reasons for inferring that they have genes that may be useful in the future. A question then would be whether the object of conservation should be breeds or genes, that is, whether it can be created as synthetic breeds having the genes of interest instead of spending funds in several programs for conserving several breeds. Although focusing the problem in keeping genes seems to be simpler, this can produce some problems. A first problem is that creating synthetic breeds may lead to undesirable gene interactions, difficult to manage for both the survival of the breed and the transmission of the interesting genes. Another problem would be the difficulties in integrating new synthetic breeds in areas in which farmers would not be prepared or accustomed to manage [35].

One of the main objectives of breed conservation, keeping genes for the future, has been discussed [35]. This objective is too vague unless the concrete purpose for using these genes in the future is envisaged. When a breed is a tool for making meat, milk, or eggs, conservation should be focused on whether this tool works now or whether there are expectations for using this tool in the future. This is an important point, because the extinction of a breed is completely different from the extinction of species. Breeds extinction, which can be created, transformed, or recovered, should not be compared with losing unrecoverable species created by natural evolution and forming part of a peculiar ecosystem.

The more concrete objective of maintaining genetic variability can be attractive for two reasons. First, genetic variability is needed for selection. Second, genetic variability implies a gene reserve that may also be useful when a rapid change in selection objectives is needed, for example, the current fertility problem of Holstein, partially caused by the increasing levels of inbreeding, can be managed by crossing Holstein with more fertile breeds [36, 37]. We should, however, notice that the genes of interest in animal breeding control economically relevant traits, thus keeping genetic variability is not an objective if the trait is near its optimum (100% of survival, for example). Genetic variability can be divided in between breeds variability and variability within breeds. It is important to know how much of the total existing genetic variability can be found between and within breeds, because if most of the genetic variability is contained within breeds, there is no genetic reason for conserving many breeds. For example, measuring the number of SNPs per kb in chicken, the International Chicken Genome Sequencing Consortium [38] detected "surprisingly little difference in diversity in comparisons between red jungle fowl and domestic lines, between different domestic lines, and within domestic lines." For productive traits, it is generally admitted that about 50% of genetic variability is between breeds and 50% within breeds [39, 40]. Some methods of measuring genetic variability, like estimating genetic distances between breeds by molecular markers, have among other problems that they do not consider within breed genetic variability. The core of the argument for maintaining between breeds genetic variability is that

some breeds have genes that other breeds do not have or have in low frequency, and these genes may be useful in the future. It is a type of "insurance argument": insurance against changes in market or environmental conditions, and safeguard against potential emerging disasters as emergent diseases [4]. There is nothing wrong in keeping every breed in danger when having an unlimited amount of financial resources, but when resources are scarce, for example, in developing countries, a precise analysis of the foreseen benefits is needed.

Breeds and Sustainable Systems

By animal breeding sustainable systems, it is generally understood that farming systems are capable of maintaining their productivity indefinitely without damaging the environment [41]. This definition does not prevent having intensive systems with highly productive animals integrated in an industrial food chain, but sustainability is often associated to some kind of traditional farming at small scale in which waste is recycled, local breeds and local sources of food used and a rather high amount of hand labor is needed. Local breeds have a key role in this second type of sustainable systems, particularly when the environmental conditions are harsh or the food resources are not particularly good. This second type of sustainable systems is in general much less efficient for producing meat or animal products than intensive systems. There are, however, some reasons for establishing them:

1. *There are harsh environments in which no other systems will work properly.* A common example is cattle in swamp tropical areas. This applies essentially to cattle, sheep, and goats, and not necessarily to pigs, rabbits, or poultry, which have been kept in much better conditions traditionally.

2. *Using these systems in poor areas avoids land abandoning and migration of people to urban areas, avoiding desertification.* If life in these areas is hard for humans, this type of sustainable system should be considered as a temporary solution, because people living there deserve a better life.

3. *Sustainable systems are more environmentally friendly and produce a better animal welfare.* Although this reason is frequently invoked, this

may or may not happen, and each case should be critically examined. Intensive industrial egg production can use enriched cages and manure process ensuring both welfare and sustainability. Moreover, animals in intensive systems arrive to commercial slaughter weight much earlier, thus they can produce less CO_2 and pollutants *per unit of product* than animals bred in extensive production systems, including pollution producing for transport, machinery, etc. A report ordered by the British government to the University of Cranfield [42] shows how this happens in poultry meat production, being organic chickens more contaminant *per kg of meat produced*, although results are more variable in pig production (for most pollutants, organic pigs contaminate less per kg of product). The same can be said about welfare: free-range hens are not necessarily happier than hens in enriched cages [43]. Looking for better animal welfare is not a particular task of industrial systems; it affects non-intensive systems as well.

4. *Some of these systems provide farmers an independence from big multinational companies.* This may be true, but is not necessarily good. Feeding people is a priority of poor countries, and the cheapest way may be to buy the genes to multinational companies. Genetics is very cheap; the genetic cost of 1 kg of pork, chicken, or rabbit meat is less than a 1% of the total cost of the meat as it will be seen in next section, and the same can be said about the genetics of 1 l of milk. Few companies provide the cheapest animal protein in the world (eggs and poultry meat and, up to a certain extent, pork meat), and genetics of dairy cattle is now managed in what is a world nucleus in practice. Poor countries need efficient genetic material for meat production even if this does not ensure genetic independence from multinational companies; this happens in industrial products and in other sectors (cars, industrial products, energy, etc.), and there is no reason for not accepting this in animal breeding.

5. *Some breeds are better adapted to local environment.* As said before, some breeds can be particularly well adapted to local conditions, although this does not mean that local breeds are better for local conditions than foreign breeds. There are spectacular examples of foreign breeds particularly well

adapted, as Nelore cattle in Brazil. Besides, adaptation is a bigger problem in some species than in others. Poultry, pigs, and rabbits have been raised in better environments than sheep or goats, thus intensive commercial breeds have less adaptation problems than in other species. Local food sources are often of lower quality than the usual food provided for highly productive breeds, and it has been said that local breeds can take a better profit of it. This is highly speculative, since the available information for these local breeds is normally scarce or null. Moreover, highly productive breeds of pigs, poultry, or rabbits can be bred with success in developing countries, even by small farmers [44]. Table 1 shows that small farms in rural conditions can obtain a similar profit as better farms using the same genetic material of a big multinational company (PIC). Local breeds of cattle, sheep, and goats may be better adapted in some harsh environments, although it is important to check whether this is true and when it is true.

6. *Local breeds produce better quality products.* The question is too general to give a simple answer. It is rather obvious that an Iberian pig (local breed) produces a much better cured ham than a Large White pig. Production of high quality products is one among several reasons for keeping breeds that are less efficient in producing meat or meat products. It is nevertheless convenient to check whether this better quality is detectable by the consumer. Some products like fresh cheese are not easy to differentiate, and local breeds sometime only show an external appearance of the animals different from the main breeds used for cheese production. It is also important, as St. Clair Taylor has stressed many times [45], that comparisons between breeds are performed at the same stage of maturity. As breeds have often different adult size and growth rate, if they are slaughtered at the same commercial weight, they can be compared at different stage of maturity, thus differences between them can be due to the fact that one breed is younger, in physiological terms, than the other. For example, a breed can have a better meat quality than another only because at the same commercial weight it is slaughtered at a more mature stage.

Animal Breeding Methods and Schemes

### Breeding Companies: Organization and Diffusion of Genetic Progress

Animal breeding can be practiced at small scale by farmers or small farmers associations, but this affects only the local breeds and its efficiency is low [21]. Nowadays animal breeding is generally in the hands of multinational companies or large cooperatives, although there are still medium sized ones performing animal breeding at a smaller scale. There are two types of schemes, based on recording data on farm or concentrating on all animal improvement in a small nucleus and diffusing later the genetic progress. The first scheme applies mainly to dairy cattle, and the second one to pigs, poultry, and rabbits.

The standard example of the first scheme is dairy cattle. A 20% of the cows of a cooperative are inseminated with semen of young bulls that are going to be tested. The daughters are then inseminated with semen from other bulls in order to have lactation. Milk, protein, fat and cell count of the milk, and sometimes longevity, are recorded for each of the daughters, and these data are used to decide which 10% of the bulls being tested will pass to the catalogue of the cooperative (Fig. 2), to be used by the farmers to inseminate their cows in order to replace their stock. Each bull being tested provides semen for 1,000 cows in order to be sure that most of them will have at least 100 daughters, in order to achieve a high precision in the estimation of their breeding value [46].

Animal Breeding Methods and Sustainability. Table 1 Sow reproductive performance of PIC pigs in Philippines [44]

|	Ave total born per litter	Ave born alive per litter	Ave weaned pigs per litter	Ave birth weight (kg)	Ave 30 day weight (kg)
Large farm sector	10.7	10.2	9.2	1.4	7.7
Small farm sector	11.9	11.4	11.1	1.5	8.8

Source: From Gibson et al. [44]
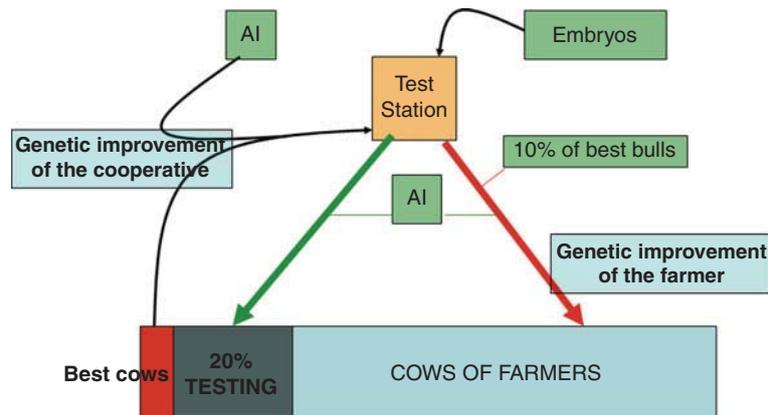
Animal Breeding Methods and Sustainability. Figure 2
Schemes of genetic evaluation and gene diffusion for dairy cattle

This implies that an association created for bulls testing should have at least 100,000 cows in order to include a couple of bulls per year in their catalogue. Nowadays there are many practices: big cooperatives test their bulls; some associations test few bulls that are available in their catalogue after having 60 or 70 daughters, and import semen and embryos making them available to the members; some companies test bulls and then commercialize the semen; etc. In a global society in which frozen semen can be bought worldwide and records are collected in different countries, a global genetic evaluation has been established by an association called Interbull that publish their world evaluation for all sires of different countries.

Selection is made from the records, but since a bull being tested will inseminate 1,000 cows, a previous strong selection is made when deciding which bulls will go to the test station to be proved. To do this, the best cows of the association are inseminated with the best semen available to produce the bulls to be proven. Nowadays it is also possible to buy embryos from the best cows evaluated in the world and the best semen available. Genomics is used here to help in the evaluation of these bulls that will arrive to the station. A particularity of the system is that individual farmers can make their own genetic improvement. Catalogues contain an accurate prediction of the genetic value of bulls for many traits, thus a farmer having particular problems with protein content of the milk, functional conformation, or other trait, can buy semen from bulls particularly well evaluated for these traits, improving

the genetic level of his farm in the aspects he particularly needs.

The other scheme commonly used in animal breeding is the nucleus-multiplier scheme [47, 48]. Here all improvement is concentrated in a farm, from which it is spread to commercial farms through multiplication steps. This is the typical scheme for pigs, poultry, and rabbits (Fig. 3). Usually two lines are selected in closed reproduction, and males of one of the lines and females from the other are sent to farms called "multiplication units," in which both are crossed to produce the crossed female sent to the farmers. Typically, these lines are selected for prolificacy and they may be selected for other traits. A third line is selected to produce the males that the farmers will use (called "terminal sires"); in this case, the line is not selected for prolificacy because this is a trait attributed to the dam, in which males seem to have little influence. Commonly, there is only one nucleus of selection in each company, and multipliers are spread in several countries. Multipliers act usually under a contract with the company; they buy parental stock for multiplication and they are in charge of providing facilities for breeding and commercializing the product: This system has allowed a rapid development of the business. There are some variations of the scheme; terminal sires are sometimes the product of a cross between two lines C and D, and sometimes there is a multiplication step more, in which other multipliers receive females A × B to be crossed by a male from other line E to produce females (A × B) × E for the commercial farmers.
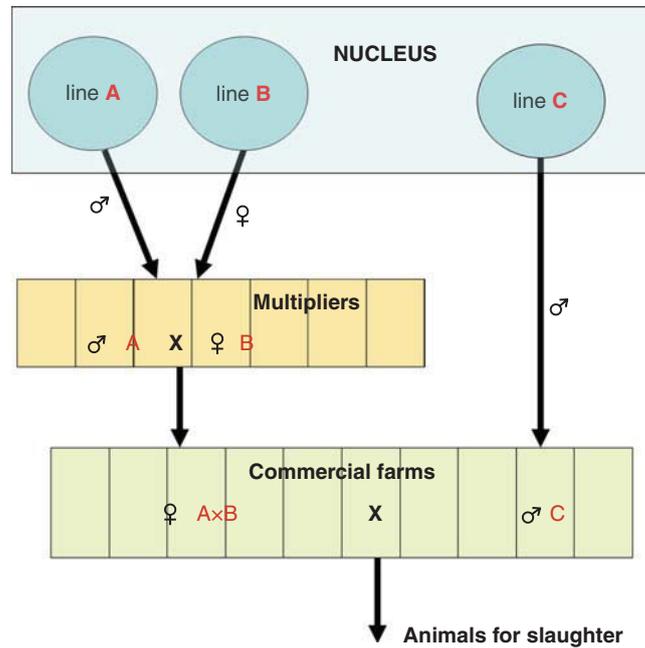
Animal Breeding Methods and Sustainability. Figure 3
Scheme of selection and gene diffusion in pigs, poultry, and rabbits

Multiplication permits to reduce the cost of selection, for example, in pigs, a female coming from one of the lines of the nucleus and entering a multiplier can cost 600 € from which 500 € is the cost of the genetics and the rest is the cost of producing a pig. This female will produce about 15 crossbred females for production farms during her life, the rest of them being culled for various reasons (leg problems, diseases, etc.). This means that the 500 € of the genetic cost should be divided by the 15 females, giving 33 € of genetic cost for the farmer. If each female produces an average of 50 pigs for slaughter during his life, the cost of genetics for slaughtered pig is about 67 cents per pig, less than 1 cent for kg. These figures are extreme in poultry production, in which each female of the nucleus can produce nearly 100 females for the multiplication step, and each female of a multiplier can provide about the same quantity for commercial farms.

Statistical Methods of Selection

Statistical methods used in animal breeding are essentially based in the infinitesimal model [49].

In this model, traits are determined by many genes independently distributed, having each one a small effect on the trait. A first consequence of the model is that genetically good animals can produce by chance some genetically poor sons, since by chance a son can inherit most of the alleles producing poor performances, whereas other sons can be genetically better than the parents if they get good versions of the alleles. As an average, all possible offspring of a parent will define how good this parent for breeding is. This is known as "breeding value" or additive value of the parent. The genetic value of an animal is not exactly this because genes can interact between them or among them producing better or worse individuals than the sum of their individual effects. These interactions are known as "dominance" when they appear between the two alleles of one gene or "epitasis" when they appear between alleles of different genes. Interactions can also occur between genotypes and environment, when the best genotypes in an environment (e.g., in the farm where the animals are selected) are not the best in other environments (e.g., in commercial farms). The development of artificial insemination in cattle and the prominent situation in the market of large

companies selling parent stock along the world has made the interactions between genotype and environment an important area of research in modern animal breeding [50].

Another consequence of the infinitesimal model is that it permits to invoke a theorem of statistics known as the *central limit theorem*, which permits considering the traits genetically distributed according to multivariate normal distributions. The multivariate normality has many advantages, for example, zero correlation implies independence between variables (which does not occur in other distributions), variables are determined by few parameters, and all relationships between variables are linear. Statistical methods in animal breeding are based thus in linear regression techniques. The most common models applied in animal breeding are called "mixed models" because they estimate simultaneously the breeding values, considered as random effects, and the environmental values, considered as fixed effects.

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

where $\mathbf{y}$ is a vector with the data, $\mathbf{b}$ is a vector containing the environmental effects (season, herd, parity, etc.), $\mathbf{u}$ is a vector with the breeding values, and $\mathbf{e}$ is a vector with the residuals. $\mathbf{X}$ and $\mathbf{Z}$ are known design matrixes containing 1s and 0s indicating the presence or absence of the effects. Fixed effects remain when repeating the experiment, and random effects change each repetition. Due to this, random effects are not usually estimated in classical statistical theory, but geneticists are interested in the value of these random effects, because they are the breeding values that, *as an average*, will be transmitted to the offspring; thus the best animals can be selected by taking offspring only from the ones with better predicted breeding values. The covariance structure of the breeding values is known due to our knowledge of Mendel's rules for gene transmission. For example, half brothers share *as an average* half of the genetic information of their father. This allows calculating the genetic covariance matrix between random effects $\mathbf{G}$ after knowing which part of the observed variance is due to the genes and which part to the environment. The most common method to estimate these variance components, correcting at the same time for the environmental effects, and using the same model as for

estimating breeding values, is called REML (Restricted or residual Maximum Likelihood) [20].

The data need not be normally distributed; in these cases, the model gives the best linear solution. Directly solving this model for many individuals, for example, several thousands or millions of data in dairy cattle, would not be possible, but an equivalent system of equations allows finding the solutions easily [18]. This system is known as Mixed Model equations, and the solution is known as the best linear unbiased prediction (BLUP) of the random genetic values.

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X'y} \\ \mathbf{Z'y} \end{bmatrix}$$

There is a technical difficulty in solving the mixed model equations, because inverting a large matrix as $\mathbf{G}$ is difficult. However, there is an easy way for directly calculating $\mathbf{G}^{-1}$, allowing a general use of these equations in animal breeding programs [19]. The model can be complicated adding repeated data, effects corresponding to single genes, and many other possibilities. It can also be used for many traits simultaneously. When several traits are used, the random effects are correlated not only due to the relationships between individuals, but also due to the genetic correlations between traits, originated when some genes have influence not in one trait but in several ones. Multitrait genetic variances and covariances can be estimated by REML as before, but Bayesian techniques, using a numerical procedure known as Markov Chain Monte Carlo (MCMC), have been particularly useful in complex situations, for example, when some traits have repeated data and other traits not and consequently the design matrixes X, Z are not the same for both traits. Bayesian methods also permit to transform multivariate problems in series of unvaried estimations. Bayesian techniques with MCMC have been rapidly developed in the field of animal breeding, mainly for complex models, for example, when traits have different distributions, for censored data, for robust models, etc. (see [21] for a scope of their use and a comparison with classical methods and [23] for detailed description of Bayesian procedures).

In the case of using many traits, the objective is maximizing the economical benefit, which is obtained weighing each trait by economic weights. These weights can be calculated with more or less sophisticated

A

models [51, 52], but in essence they represent the amount of benefits, measured in economical units, obtained by improving one unity of the trait, for example, the number of euros of benefit for producing 1 kg of milk.

The Use of Molecular Genetics in Animal Breeding

Molecular genetics has influenced modern genetic programs. Two different aspects, will be commented here, transgenic animals and molecular markers, including in the late genomic selection. A critical review and discussion about the uses of transgenesis and cloning in animal breeding, with references to markers, can be found in [24]. Genomic selection is very recent and its possibilities and development are still under discussion.

Transgenesis The first transgenic mice growing twice than normal created an enormous expectation about what could be done with transgenic animals [53], particularly in the field of animal production. However, few transgenic animals are now available, and the economical advantage of transgenic animals is small [24]. Although apparently it is economically viable to produce transgenic products useful for human health, the application of transgenic animals in medicine will not be considered here.

To apply transgenesis in animal production, genes with major effects are needed, but unfortunately, most economically interesting traits are determined by many genes of small effects. Sometimes there are genes with major effects for some traits, for example, for fat deposition in pigs, but classical selection has fixed yet the favorable alleles in commercial populations, thus they are not particularly useful now. When a trait of an economic interest has a major gene segregating in the population of study, this gene can be easily captured by selection. This can be shown by computer simulation [54, 55] but a simple example can help in understanding this. In Fig. 4, it can be seen the phenotypical distribution of a trait is controlled by a single gene. When selecting the best 50% of the animals, copies of the allele "A" are selected with preference. Therefore, in few generations of selection the gene will be in high frequencies or will get fixed. If the frequency of the favorable allele is low, the process takes more
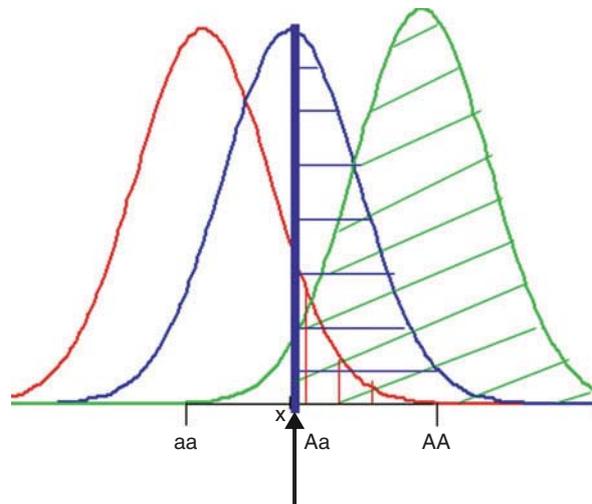
Animal Breeding Methods and Sustainability. Figure 4
Phenotypic distribution of a trait determined by a major gene with a high additive effect. Selection of the best 50% individuals

generations, but in general, it hardly will compensate to use transgenesis to capture it. Marker-assisted selection can be used for augmenting more rapidly the frequency of such genes of major effects, as it will be commented in next section.

Some major genes that are present in a breed or a line but not in other can be easily introduced by introgression without requiring transgenesis. The breed with the gene of interest G is crossed with the breed objective O, and then backcross is made by crossing O with the animals of the G × O cross that carry the gene of interest. After several backcrosses, the gene is introgressed. An example of gene introgression is often performed with the Boorola gene in sheep that augments litter size, due to the high prolificacy of the carriers that permit an easy identification. When the carriers do not clearly show the gene of interest, genetic markers can be used to help the introgression [56].

The process of transgenesis is extremely inefficient. Genes are placed at random, thus the gene can be inserted in an inappropriate tissue or it can happen that genes around the inserted gene modify the expression of it. Transgenes are not always expressed and they are not always transmitted to descents. Moreover, many animals are needed for obtaining a viable embryo expressing the genes transferred. For example,

36,500 embryos were needed to obtain 18 transgenic calves expressing the trait, and the cost of each transgenic cow was higher than 500,000 dollars [57]. Lentivirus vectors can produce transgenic animals more efficiently in some species and at a lower cost, but they still suffer the former problems [58].

Transgenic animals should be tested to prove that they are commercially viable [24]. They should be tested for the trait that is the object of transgenesis, because it should be proved that the transgene is expressed in the animal and in the offspring for several generations. They should be also tested for commercial traits, since a transgenic line might be good for a trait but might have a poor productivity for other economic traits. The overall productivity should be evaluated. Transgenic animals may have poor fitness, sensitivity to diseases for which non-transgenic animals are resistant and poor performances in other traits that might affect longevity; it is also frequent that transgenic animals have reproductive problems.

Once the major gene has been transferred in an animal, a whole population or line having this gene has to be constituted. In the nucleus-multiplier scheme, inbreeding depression will increase when creating the transgenic nucleus, since mating with relatives during several generations are needed to spread the gene [59]. The process of evaluation of transgenic animals, and the diffusion of the transgene in a line, increases the genetic lag between the transgenic line and the commercial lines, due to the genetic improvement made during this time by its competitors. Diffusion of a transgenic animal in dairy cattle, in which a world nucleus of selection is much higher than in prolific species, and generation interval is large due to progeny testing (6 years), has also been studied. It has been calculated that in a population of 10,000,000 cows, three generations later after the introduction of the transgenic founder (18 years later), the presence of the gene in the population would be between 1% and 4% [60]. The genetic lag produced, the fact that a transgenic animal may be genetically inferior for other traits not controlled by the gene transferred, the complications of the processes and the scarce number of gene candidates for being transferred, makes transgenesis little attractive, even if it would be a less expensive and more successful technique [24].

Genetic Markers and Genomic Selection   Genetic markers are parts of the DNA molecule that can be identified in individuals. They may be close to a gene of interest, so they can be used to select the favorable version of a gene affecting a quantitative trait. Genes controlling a quantitative trait are called QTL (quantitative trait loci), and occasionally they can have a large effect and can be selected with the help of a marker. However, generally quantitative traits are controlled by many genes with small effects, thus the effectiveness of markers has been rather limited [25]. The situation has dramatically changed since it has been possible to obtain a large number of markers at low cost and since they can be associated to many of the genes controlling traits even having small effects. There are several types of markers; the simplest one is the Single Nucleotide Polymorphism (SNP), which marks a place in the genome in which there is variability in a single nucleotide. Nowadays there are microchips allowing detection of about 50,000 SNPs in a genome; the number of SNPs that can be easily detected is increasing to 500,000 and soon it will be possible to genotype the whole genome of livestock species at reasonable prices. Prediction equations can be fitted, in which a set of SNPs will be used for predicting breeding values. Taking data from 1,000 to 4,000 animals (calling this *training population*), the model to be fitted can be

$$y = b_0 + b_1 x_1 + b_2 x_2 + b_3 x_3 + \cdots + b_{50,000} x_{50,000}$$

where $x_1, x_2, \ldots, x_{50,000}$ are the variables indicating the presence of one polymorphism (AA, Aa, aa) of each SNP (usually indicated by 1, 0, −1, or by 0, 1, 2), and $b_1, b_2, \ldots, b_{50,000}$ are the regression coefficients to be estimated. These equations cannot be solved by least squares given the high number of SNPS in relation to the data available for the prediction, and Bayesian techniques should be used. The use of prior information allows solving these big equation systems, and depending on how prior information is included, the Bayesian methods differ [61]. This method can also be used for several traits [27]. Many of these SNPs are noninformative, and there are some techniques to select only informative SNPs [61, 62]. There is now a promising research area for selecting informative SNPs for prediction, often using nonparametric statistics [62].

Genomic selection has been proposed for traits that are difficult or expensive to measure (e.g., adult weight [24], index of conversion [63], mortality [64]). It has also been proposed in dairy cattle, in which the traits of interest are expressed in dams but selection acts mainly in sires, and the generation interval is very long [65]. It may be useful for other traits like litter size, difficult to select due to their low heritability, but studies are needed to determine its usefulness in these cases, because very low heritabilities will give poor prediction equations since the records will then be determined mainly by the environment.

A main problem of genomics is that the association of SNPs with the genes responsible of the trait quickly disappears in few generations of selection, thus the prediction equations have to be reestimated and new training populations are needed. Figure 5 shows an example of the loss in accuracy of the prediction of genetic values. It can be observed that accuracy is practically halved in four generations of selection.

This limits the use of genomic selection in current programs, because in some species the generation interval is short (6–9 months in rabbits or hens,
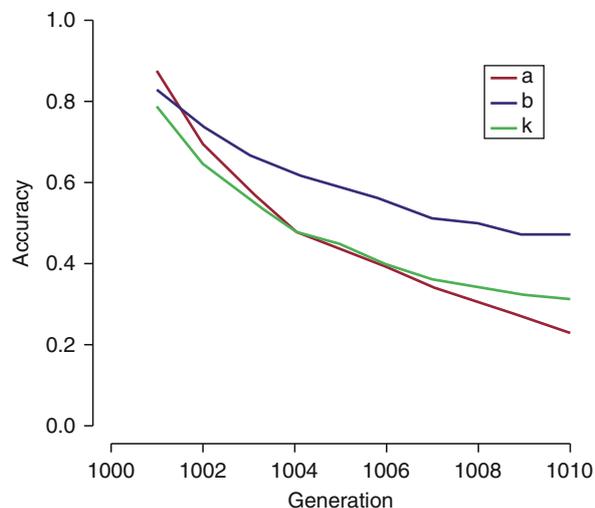
Animal Breeding Methods and Sustainability. Figure 5
Loss of accuracy of genomic selection on parameters a, b, and k of Gompertz growth curve. Selection acts on trait a, and the loss of accuracy of traits b and k are due to genetic correlations with trait a (From Blasco and Ibáñez-Escriche [27])

1 year in pigs), and a continuous reestimation can be difficult or expensive. Finding when and how genomics can be included in current genetic programs is one of the most important research areas nowadays.

Future Directions

The Future Evolution of Methods and Schemes

Prediction of breeding values from records seems to be well established with the methods briefly exposed in section "Statistical Methods of Selection" and it does not seem that dramatic changes will occur in the future at short or medium term. The revolution in methods for estimating breeding values is in the area of genomics. The possibility of having information from several thousands of markers at a reasonable price, now from several hundred thousands and in the near future from the whole genome, has brought the problem of how to manage all these data, and prediction methods are examined from other areas of knowledge as artificial intelligence, using nonparametric or semiparametric methods, Bayesian methods, etc.

Schemes of selection are also changing due to the globalization of the market of genes. Today the best cows of the world are not dedicated to produce milk but embryos that are sexed, frozen, and commercialized. Some of the deficiencies of current dairy cattle programs such as long generation intervals can be partially solved by using genomic selection and having a quicker and better evaluation of the bulls being tested. Larry Schaeffer suggested that genomic evaluation can substitute progeny test, dramatically shortening generation intervals [66], but it is doubtful that farmers will accept genomics evaluation as they accept now tests mainly based in offspring records [65]. It can also happen that private companies will compete with others or that breeders can organize brands in which semen is not identified, like in pigs, as Maurice Bichard suggests [67], but it looks unlikely, since farmers like to perform their own genetic improvement at farm level by buying semen from accurately tested sires. Poultry genetics is now in the hands of two large holdings, and the only change envisaged in their structure is related to possible troubles with laws about competence. Pig companies tend also to be bigger, but they will probably coexist with nucleuses of smaller companies well

established in local markets, and with large pig production companies producing parental stock for themselves. Both pigs and poultry companies will introduce genomics in their programs not only as a complementary tool for selection but also as a commercial strategy, using modern methodologies as an added value to their products. The interest in meat quality traits and quality of animal products will probably increase. Companies will also stress the sustainability of their productions and the good welfare of their animals, thus there will probably be an increasing interest in traits like robustness and disease resistance. The new emphasis in sustainability will give importance to breed conservation programs, which will receive more attention and will get substantial public funds. Nevertheless, no dramatic changes in objectives are envisaged in the near future. Changes in genetic objectives are slow and the product of the selection arrives with delay to the market, thus this prevents short-term selection policies.

The Limits to Genetic Progress

The theory of selection limits was developed by Alan Robertson (1920–1989) [68]. Classic quantitative genetics theory predicts the extinction of genetic variability by selection, and consequently the end of genetic progress. Frequencies of favorable genes increase with selection until they are close to 100%, and the genetic response is necessarily low, or genes are fixed by genetic drift, which occurs more likely when they are at high or low frequencies and when the selected population is small. Mutation can introduce new genetic variability, but useful mutations are rare and they were disregarded in the classical theory of limits of selection. A decline in genetic response is thus expected until genetic variability is exhausted, and some experiments arrived to a plateau after showing response to selection along 20 or 30 generations in drosophila [69] and mice [70]. However, there is little evidence of any loss of genetic variability in commercial populations [71, 72]. Heritability of milk production in dairy cattle is not decreasing with time but augmenting! [73] and this is not only due to a better control of environmental variance or methods of correction, but also to the continuously maintained response to selection in the last 50 years (Fig. 6).
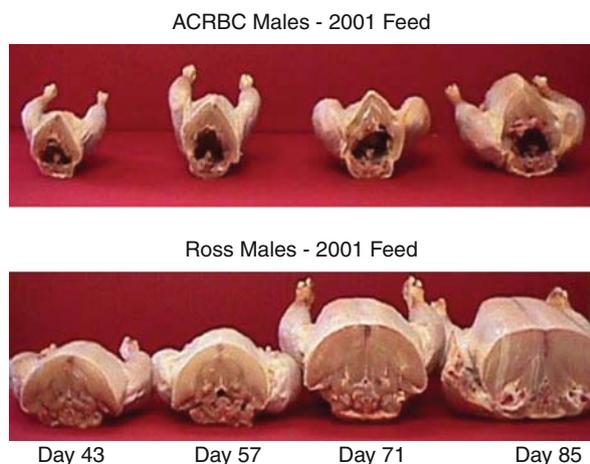
Long-term genetic responses have been observed in both plants and animals, and there are several examples of continuous genetic progress in all livestock species. A part of the success of the phenotypic trends observed in animals is due to improvements in nutrition, but when comparing chicken broilers fed with food as prepared in 1957 and as prepared in 2001, most of the observed differences are due to genetic improvement [74]. Figure 7 shows carcasses of poultry from an unselected line and a selected line of the same company, fed with modern food.

Broilers show a continuous growth, egg mass production continuously increases, pigs' lean growth selection has dramatically decreased the amount of fat of the carcasses, and in general all selection programs
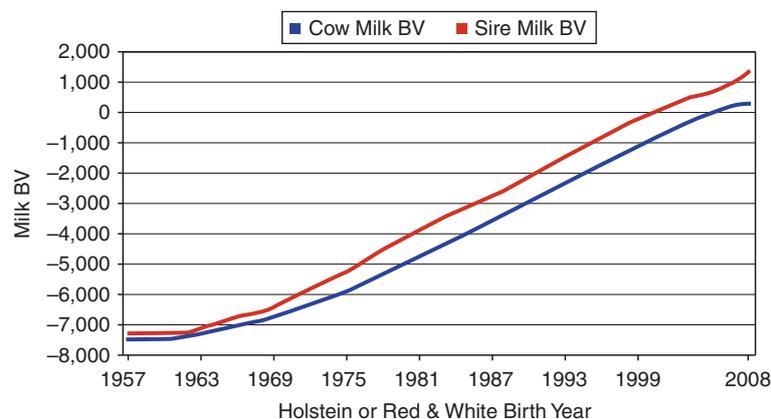
Animal Breeding Methods and Sustainability. Figure 6
Genetic values of sires and cows in USA in the last 50 years (From USDA http://aipl.arsusda.gov/eval/summary/trend.cfm)

ACRBC Males - 2001 Feed

Ross Males - 2001 Feed

Day 43   Day 57   Day 71   Day 85

Animal Breeding Methods and Sustainability. Figure 7
Carcasses of 1957 and 2001 of an unselected and a selected line of poultry fed with the same food [75]

continue having success [72]. The reasons for this apparent non-limits to selection are selection pressure on genes produced by mutation (which has a heritability of about 0.1% [72, 76]) or epistatic interactions, but even when epistatic interactions are important, additive variance typically accounts for over half, and often close to 100%, of the total genetic variance [77]. Bill Hill moved further the classical theory of limits of selection showing how new mutations with selective advantage can increase genetic variability [78]. An experiment corroborating the theory showed how totally homozygous lines produced artificially in drosophila melanogaster could recover genetic variability by selection [79].

Are there limits to the genetic progress? Some traits have biological limits but still genetic progress can be obtained acting on related traits, for example, it is not possible to produce more than one egg per day, but it is possible to increase the laying period, and most of the new response to artificial selection in egg mass comes from this [72]. Highly productive animals can increase the incidence of pathological problems like ascites in broiler chicken or fertility in dairy cattle, but selection on these unfavorable traits [80] or crossbreeding [36] can be performed to continue the progress. Selection including traits different from strictly productive ones should be considered to avoid undesirable consequences of the continuous genetic progress [81]. Apart from some obvious limits (e.g., traits measured

in percentage, like survival, cannot surpass 100%), it seems that genetic response can be directed to overcome the biological limits presented when selection acts only in one or few productive traits.

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Animal Breeding, Long-Term Challenges

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Article Outline

Glossary
Definition of the Subject
Introduction
Sustainability
Sustainable Animal Breeding