Decision making in animal breeding programs and their consequences for animal production

Tomadas de decisão em programas de melhoramento animal e suas consequências para produção animal

C. McManus¹, J. Cobuci¹, J. Braccini Neto¹, S. Paiva³

¹Universidade Federal do Rio Grande do Sul, Departamento de Zootecnia, Porto Alegre, RS, Brasil.
²Universidade de Brasília, Campus Darcy Ribeiro, DF, Brasil.
³EMBRAPA Recursos Genéticos e Biotecnologia, Brasília, DF, Brasil.

Corresponding authors: concepta.mcmanus@ufrgs.br, jaime.cobuci@ufrgs.br, jose.braccini@ufrgs.br, samuel@cnenargen.embrapa.br

Abstract

Animal breeding technologies have advanced radically over the last 40 years and changed the way in which animals are farmed worldwide. While advances have been made, these methods have not always lived up to their promise or have led to the appearance of other unpredicted results. This has been caused by various factors such as ignorance of the correlated effects of selection or superestimation of the value of the technology. Also, a dependence on technological advances often ignores important factors such as genotype x environment interaction, avoidance of inbreeding or maintenance of variation. This paper looks at some of these advances and their impact on farming practices.

Keywords: effective herd size, inbreeding, molecular genetics, quantitative genetics.

Resumo

As tecnologias de melhoramento animal têm avançado radicalmente nos últimos 40 anos e mudaram a maneira com que os animais são criados no mundo inteiro. Enquanto avanços têm sido realizados, os métodos nem sempre corresponderam a sua promessa ou levaram ao aparecimento de resultados inesperados. Isto se deve a vários fatores tais como ignorância dos efeitos correlacionados da seleção ou superestimação do valor da tecnologia. Além disso, uma dependência nos avanços tecnológicos frequentemente ignora fatores importantes como a interação genótipo-ambiente, impedimento da endogamia ou manutenção da variação. Este artigo estuda alguns desses avanços e seu impacto nas práticas de criação dos animais.

Palavras-chave: endogamia, genética molecular, genética quantitativa, tamanho efetivo de rebanho.

Introduction

The twentieth century has become a turning point for the way animals are bred and farmed. The human population explosion gave rise to widespread competition with other species for agricultural land, and many species and breeds became extinct or are now threatened with extinction primarily as a consequence of these activities (Flint and Woolliams, 2008). The industrial culture created during this time also influenced the environment in which animals are raised with increased intensity of production and the consequences of these include changes in production systems, breeds used and eventually climate change. Modern animal breeding is based on integrating many sciences and technologies, including genetics (both quantitative and molecular), statistics and computing science, information technology, as well as the physiology and endocrinology underlying growth, disease resistance, reproduction and fertility. The majority of advancements have been largely made using quantitative genetics approaches. Recently this switched to molecular genetics and genomics, but once again we see the pendulum swing back to quantitative genetics as molecular techniques have become highly automated (Caetano, 2009), producing large quantities of data that need to be analysed.

The use of new technologies without proper knowledge of system have led to major problems in some areas. There is concern about how rapid genetic change can be made without being harmful or perceived to be so (Maki-Tanila, 2007). While technologies have potential to change production systems in many areas the impact of these has many times fallen short of expectations. To be sustainable, animal breeding needs to take account of food safety and public health, animal health and welfare, biodiversity, economic efficiency and care for the environment (Flint and Woolliams, 2008).

Improved understanding of the physiology and growth will be critical to future success of breeding programs. Breeding also has an important role to play in improved efficiency in feed conversion, methane production and use of nitrogen and phosphate. All these priorities will have to be taken into consideration when
creating breeding objectives for specific farming environments (Falconer and McKay, 1996). These objectives can only be achieved by improved recording of information on performance and disease (Flint and Woolliams, 2008) as well as rational use of available and new technologies. Advances in the fields of transcriptomics, epigenomics, proteomics and metabolomics, imaging and behaviour are necessary for us to better understand the link between phenotype and genotype (Houle et al., 2010).

Breeding programs have become quite successful because of the high accuracy of breeding value estimation, the moderate to high heritabilities of most production traits and the use of large and fast databases containing production records of many animals and their genetic relationships. However, apart from desired effects of genetic selection focused on high economic production efficiency, negative side effects have become apparent. Animals in a population that have been genetically selected for high production efficiency seem to be more at risk for behavioural, physiological and immunological problems (Rauw et al., 1998). The aim of this paper is to look at advances in animal breeding, the potential use of the technologies developed and the impact of these at the farm level.

**Use of technologies and their implications for production systems**

Classical genetics and other efficiency measures have been used in agriculture focused on improving the productive output of farm animals in terms of growth, yield and efficiency (Burfenring et al., 2006). Recent studies have shown that timed artificial insemination (TAI) has economic advantages over natural service (Lima et al., 2010), even without taking into account genetic gain with improved quality of AI bulls. This sped up the rate of genetic change of livestock populations by increasing the selection pressure and the reliability of sire breeding values, estimated from the performance of a large number of relatives. ‘Improved’ germplasm is available worldwide, displacing locally adapted populations and inducing loss of genetic variation. This genetic improvement in some important traits may have caused other problems, such as lowered resistance to diseases.

Inbreeding has always been avoided by breeders (Taberlet et al., 2008). Avoidance originally included the exchange of parents among herds, culling of parents when daughters became sexually mature or breeding groups with mating with alternate males. With AI, most semen comes from related bulls. The individual farmer does not have access to or does not consider this information. Inbreeding can then occur, compounded by the fact that semen doses are available for a long time after a bull is dead and most pedigrees do not go back more than three generations.

Faria et al. (2009) studied registered Nelore, Gyr and Guzerat cattle in Brazil. Total inbreeding increased in all the breeds reaching values of 2.13, 2.28 and 1.75% respectively. Effective population size decreased from 85 to 68 in Nelore, from 70 to 45 in Gyr and remained nearly constant around 104 in Guzerat over a 20 year period. The quantities assessing the number of contributing ancestors decreased with time in all the breeds, and in the last analysed period the most important ancestor accounted for 14, 3.1 and 4.1% in Nelore, Gyr and Guzerat, respectively. Results indicate that the studied breeds are suffering from a loss of genetic variability which can result in negative effects on breeding and conservation purposes. Other studies (Peixoto et al., 2006; Panetto et al., 2010) also show important negative effects of the use of AI.

Despite this, high levels of genetic variation at the nuclear DNA level still appear to exist in populations under high selection pressure, such as Holstein in the USA with observed heterozygosity above 0.6 (Maudet et al., 2002; Vallejo et al., 2003). As the microsatellites chosen were selected from a larger set with the specific aim of maximising the level of polymorphism and/or heterozygosity, these estimates may be overestimated due to bias produced by nonrandom sampling of markers used (Rogers and Jorde, 1996). Usually models for estimating genetic values involve simple linear models, not considering interactions between factors. They do not therefore take into account dominance and epistasis effects, thus overestimating the genetic value of heterozygotes which are consequently more likely to be selected for reproduction (Cappuccio et al., 2003).

Sufficient within-breed genetic diversity needs to be maintained to preserve populations (McManus et al., 2010) and guarantee the long-term sustainable exploitation of livestock, especially in the light of predicted climate changes with increased mean temperatures and decreased growing days (Romanini et al., 2008; Scholtz et al. 2010). This may lead to the need for introgression of genes for certain resistance traits or breed substitution. In harsh environments such as the Pantanal in Brazil, it had been shown that while Nellore cattle have a calving interval of almost two years the naturalized breeds such as Pantaneiro or Curraleiro calve once a year (McManus et al., 2002).

The dairy breeding objectives for ruminants assume that an increase in individual milk yield will be followed by an increase in the economic margin per animal. This is acceptable only if selection for milk yield maintains or increases feed efficiency and milk quality. There is evidence that selection for milk yield increases both feed intake and mobilisation of body reserves to support milk production (Marie-Etancelin et al., 2002; Veerkamp, 2002) without an increase in body weight. Gross efficiency is improved with increases in genetic merit for milk yield, and probably also residual feed intake. On the other hand, selection for milk yield also results in poorer female fertility in dairy cattle, probably as a result of more negative energy balance (Veerkamp et al., 2003). Given the increasing interest in functional traits and the balance to be chosen between production
and functional traits, estimation of economic weights and their robustness for given management systems should be promoted to define the breeding objectives in these species.

Although positive trends for milk production have been seen, several studies show negative results for protein and fat percentages. Breeding for increased milk production has been found to have negative side effects on health and fertility (Pryce et al., 2004; de Jong, 2007). Washburn et al. (2002) found an increase in days to first service, days open in Holstein and Jersey cows in the Southern US while other studies found similar trends with conception rates, calving interval and pregnancy rates (Rajala-Schultz and Frazer, 2003). These are thought to be a combination of both management and physiological factors (Lucy, 2001). Samoré et al. (2008) found that larger values of Somatic Cell Score were genetically associated with increased production. Few Holsteins cows in the US currently survive beyond their fifth parity and their average lifetime parity number has fallen over the past 20 years from 3.4 to only 2.8 (Tsuruta et al., 2005). Rauw et al. (1998) presented over 100 references on undesirable (or) related effects of selection for high production efficiency, with respect to metabolic, reproduction and health traits, in broilers, pigs and dairy cattle. Further discussion can be found in Wathes et al. (2008).

It should also be remembered the success of a breeding program depends on derivation of economic selection objectives which are rarely estimated or selected for (McManus et al., 2010). Estimated breeding value (EBV) also depends on the base of animals used in its prediction. Interbull uses Multiple Across Country Evaluation (MACE) to calculate International Genetic Evaluations but attempts to unite different programs within Brazil have not met with success, making it difficult to compare animals in different selection programs. Speculation within breeding programs may also be harmful. Just because an animal has been produced by a specific technique may overinflate its true economic value.

**Current perspectives for breeding and conservation**

Social interactions between individuals, such as cooperation and competition, are key factors in evolution by natural selection. Biologists have studied theories to attempt to understand the consequences of social interactions for response to natural selection. Current genetic improvement programmes in animal husbandry largely ignore these. Results have shown that including social effects into breeding programmes may reduce negative social interactions in farm animals increase positive social interactions, by breeding animals with better social skills (Rodenberg et al., 2010).

Adaptive traits may be rapidly lost by poorly designed crossbreeding leading to dilution of local genetics by exotic germplasm (McManus et al., 2010). Crossbreeding with a breed with higher production levels is widespread and can affect the specific adaption traits of a native or naturalised breed within a few generations. Recovery from such loss can be difficult, requiring many generations of backcrossing. According to Paiva et al. (2005), Santa Inês sheep in the Northeast and Center-west regions of Brazil can be classified in two sub-populations, with significantly different genetic standards. According to these authors, crosses between the original Santa Inês and rams of the Suffolk breed were carried out in the Northeast to improve conformation of the breed and then successive selections for lack of wool, leading to a predominance and preference by farmers for black and brown Santa Inês, due to preconceptions on their production value and the “fad” for black or brown animals. This crossbred was also considered pure “new” Santa Inês, a larger animal with improved carcass quality. How these selection actions will affect future responses of the breed to heat tolerance and disease resistance has yet to be seen. The white Santa Inês were separated from the other groups and shown to be better adapted to heat stress (McManus et al., 2009b) with lower heart and breathing rates as well as lower rectal temperature. Important factors such as scrapie susceptibility, never before reported in naturalized sheep in Brazil, have now been documented in Santa Inês sheep (Sotomaior et al., 2008; Ianella et al., 2009). The latter authors also showed a high level of susceptibility in Dorper which are extensively used in crossbreeding in Brazil which may affect future trade negotiations with Brazil.

Fecal egg count (FEC) has been used as an indicator of resistance in sheep (McManus et al., 2009a). Breeds with European blood (pure or crossbred) showed higher infection levels than hair breeds, Santa Inês (SI) and Morada Nova (MN). These breeds may be naturally more resistant to parasite infections. SI sheep had a lower PCV than Ile de France x SI, both measures were within normal ranges (McManus et al., 2009a). MN and Bergamasca had lower FEC for Strongylida, while lowest values for Strongyloides were found in SI and its cross with Ile. The lowest FEC was found in Ile sheep.

The results of studies carried out with animals produced by the crossing of resistant with susceptible breeds have demonstrated that the degree of resistance of the hybrids can vary as a function of the breeds evaluated, the age of the animals and whether the evaluations were from natural or artificial infections (Amarante et al., 2009). Depending on the production system used, crossbreds are not necessarily better than purebreds (Rocha et al., 2009). The impact of changes in adaptation may not be limited to the farm population. Increased use of drugs to control emerging diseases on wildlife health was studied by Blanco and Lemus (2010) who found high concentrations of multiple veterinary drugs, primarily fluoroquinolones, in most failed eggs and nestlings of threatened avian scavengers feeding upon medicated livestock carcasses. These deaths were
associated with multiple internal organ damage. Livestock pathogens caused disease in these birds, especially septicaemia by swine pathogens and infectious bursal disease.

**Current perspectives for reproductive technologies**

There are a number of assisted reproductive technologies, many of which are at various stages of development and have not necessarily been widely adopted, but which are considered to be technological solutions to problems associated with the declining reproductive efficiency of farm animals as a result of advances made in increasing production (Barillet, 2007). These include Assisted reproductive technologies (ART) include Artificial Insemination (AI) and Cryopreservation, Multiple (Super) Ovulation and Embryo Transfer (MOET), In Vitro Fertilization, Sex Determination of Sperm and Embryos, Cloning (Nuclear Transfer) and Transgenics. Other techniques include in vitro maturation (IVM), in vitro fertilization (IVF), and ovum pick-up (OPU). Thus, advances made in the ARTs are viewed as potential solutions to maintain and improve the genetic superiority of dairy animals. It is difficult to predict with any confidence the actual nature of the technology that will eventually emerge. Provided most of the technological problems are eventually overcome, the question remains as to whether it could or will become an economically feasible technology (Butler and Wolf, 2010).

The largest improvements that have occurred with AI include the ability to cryopreserve semen and embryos and to make this technology available and accessible to increasing numbers of farmers. More than 60% of dairy cows are bred by AI each year in the US but only about 5% of inseminations in the beef industry (Barillet, 2007). Multiple (or super) ovulation is used by less than 20% of dairy producers and 5% use IVF. These illustrate the gap between not only sectors of the industry but between propaganda and reality.

Knowledge about genetics of domestic animals is cumulative, and in spite of the high incertitude inherent to long term predictions, this knowledge is useful sooner or later (Blasco, 2008). Molecular genetics has lead to a much better understanding of the mechanisms regulating the expression of genes, and research in molecular genetics leads to uncontrovertible progress in our knowledge about nature. The question is whether the high amount of facilities that are invested in genetic engineering in particular and in molecular genetics in general are justified by the results, considering the expectations that were built up in them and considering the risk associated to the incertitude.

Use of cloning in animal genetic improvement may increase the rates of selection progress in certain cases, particularly in situations where artificial insemination is not possible, such as in pastoral systems with ruminants (Montaldo, 2006). High costs of cloning are limits its use in on-farm breeding. Van Vleck (1999) also noted that clonal groups, though more uniform than full sibs, still maintain differences caused by the environment, which is usually more than 50% of total variation.

Trangenic sheep and goats with high levels of serum growth hormone have been obtained, but an increment of its rate of growth was not observed, and only in some lines average daily gain increased with the supplement of the diet with high levels of protein. The highest effects were observed in the reduction of body fat. A large number of different serious pathologies and a severe reduction in reproductive capacity were described in these animals (Murray et al., 1999).

Frequently the used promoters have not allowed an efficient control of the expression of the transgene. It is necessary to develop more complex constructions that activate or repress the expression of the transgene more precisely. Adams et al. (2002) found inconsistent results regarding the effect of a growth hormone construct in sheep on growth and meat quality. Recently, a transformation was obtained by insertion of a plant gene in pigs. Saeki et al. (2004) generated transgenic pigs that carried the fatty acid desaturation gene for a fatty acid desaturase from spinach. This opens up the possibility of modifying the fatty acid composition of products from domestic animals. Another promising application of transgenesis is the synthesis of biomedical products of high commercial interest (Teulé et al., 2009). Use of genetic engineering for animal and plant improvement is in its infancy, therefore many questions regarding efficiency, safety and societal benefits in particular situations remain.

The techniques for obtaining transgenic animals in species of agricultural interest are still inefficient. Approaches to overcome this problem are based on cloning strategies. Using these techniques it is feasible to reduce to less than 50% the number of embryo receptor females, which is one of the most important economic limiting factors in domestic species (Montaldo, 2006). In theory, rapid dissemination of the genetics of selected animals by nuclear transfer could result in the generation of mini-herds in two to three years. Nevertheless, inefficiencies in the techniques (mainly the micromanipulation of oocytes and culture of donor cells and cloned embryos) make this almost impossible to attain. It is also important to note that the genetic merit of the ‘cloned’ animals will remain stable, while improvements will be introduced in commercial herds using traditional breeding programs (Karatzas, 2003).

Cloning is commercially available. Since in theory unlimited numbers of identical animals could be produced with cloning, an overpopulation of the same genetic makeup could result in inbreeding and loss of genetic variation, which is not desirable. This same concern was expressed when AI was implemented
commercially. With careful management and planning of breeding schemes these problems should not occur. While many of the problems associated with cloning raise significant barriers to its success, a number of other technologies that are currently under development could be extremely useful in helping to overcome such problems, such as Preimplantation Genetic Diagnosis, Gamete Storage, Sequencing and Functional Genomics Studies, Proteomics, and Bioinformatics. One question may be “where will it all end”?

**Current perspectives genomic technologies**

The area of genetic parameter estimation has advanced over the last 40 years, allowing more appropriate models to be fitted to larger datasets due to advances in statistical and computing methods. Over the next 10 years even more complex models fitted using molecular information are expected to be used. Identification, characterization and use molecular markers for use with genetic resources and for animal breeding began at the end of the 80s using RFLPs (Restriction Fragment Length Polymorphism) through SSR (Simple Sequence Repeats) and microsatellites (Caetano, 2009). The latest technological innovations include methods to identify and genotype SNP (Single Nucleotide Polymorphism) markers in large scale. High density DNA chips are used to genotype up to hundreds of thousands of SNPs in a single assay. Medium density technologies allow for the automated genotyping of tens to hundreds of markers in large numbers of samples at high speed. These technologies mean that animals can be genetically evaluated and selected on their Genomic Estimated Breeding Value (GEBV; Zhang et al., 2010). Genomic breeding values are predicted to be the sum of the effect of SNPs across the entire genome (Hayes and Goddard, 2010). These technologies also open opportunities for development of diagnostic tests for paternity testing, individual identification, traceability, etc.

The aim is to use genetic markers not only to predict the ‘best’ mating strategy for breeding, but also to individualise the management of animals (e.g. customised feeding strategies). Companies have begun to develop genotyping tests to identify those animals with the greatest potential for tenderness, fat content and weight gain. Some large scale farmers manage diets according to genetic tendencies using these markers, thereby tailoring the development of the animal and its meat to the demands of its market destination, saving feed costs (Elstein et al., 2005), which may provide a better system to grade meat quality than the subjective system used at present. This also has problems when transferred to other countries. For example are the responses and markers the same in *Bos taurus* as in *Bos indicus* cattle? In contrast to EBVs and to the emerging use of genetic markers in livestock breeding, genetic modification and cloning have not yet impacted on this section of commercial agricultural practice (Gibbs et al., 2009).

The statistical methods for genomic evaluation and selection are being developed, and in the United States (US), genomic data have been used to enhance predicted transmitting abilities (PTA) for production, conformation, and fitness of dairy cattle since January 2009 (Weigel et al., 2010). VanRaden et al. (2009) estimated the changes in reliability (REL) due to inclusion of genomic data which were greatest for Holstein breed (23-50%), but somewhat less for Jersey (3-36%) and Brown Swiss (8-18%) depending on the traits measured. By reducing the generation interval, this approach is expected to double the rate of genetic improvement per year in many livestock systems (Goddard and Hayes, 2009).

Genetic marker technology, a technique assaying the DNA of specific animals for ‘markers’ of genes associated with particular qualities (such as meat tenderness), relies more on direct relationships between breeders and private companies, who market their technology packages directly to farmers (Holloway and Morris, 2008). Material samples of the animal (hair, blood, etc) can be collected and mailed to a testing centre, and the results delivered to the breeder electronically. Unfortunataely most farmers have no idea what to do with this information without contracting specialist advice which is still in short supply in some countries and may bring high costs for the farmers. Another problem is the reduction in number of academic animal breeding programs worldwide. This has resulted in a deficit of human resources in the area. Not only are quantitative geneticists lacking, those who are qualifying are being contracted by plant and biomedical companies, with few remaining in academia. The need to rebuild infrastructure for developing scientists and expertise in the animal breeding area is critical and must be addressed through new strategies and models (Green et al., 2009).

Importation of techniques and processes from other countries or systems should also be looked at in the light of the where they are being applied. Eight microsatellite markers were suggested by the The Brazilian Ministry of Agriculture (normative 74/2004) for parental identification in sheep and goat breeds. Souza et al. (2006) tested this panel against other 23 markers suggested in a study of 5 Santa Inês herds and found that some of the markers suggested by MAPA could be substituted by others that are more informative for Brazilian breeds.

In general, every advance of molecular genetics has been received with high expectations in the field of animal production, but the consequent application, if any, has been much more modest. There is a notoriously high production of theoretical or computer simulation papers about the possibilities of marker-assisted selection but the current applications are scarce. Marker Assisted Selection (MAS) is not generally used by poultry or pig genetic companies, and even in dairy cattle its use is rare. Moreover, there are no selection experiments actually testing the efficiency of MAS (for example, comparing a line selected using MAS with a line selected by current
methods). Theoretical or simulated results only give a relatively small advantage (about 10%) to programs using MAS, depending on the conditions of the simulation.

A key goal of biology is to understand phenotypic characteristics, such as health, disease and evolutionary fitness (Houle et al., 2010). Phenotypic variation is produced through interactions between genotype and environment, and such a 'genotype–phenotype' map is inaccessible without the detailed phenotypic data that allow these interactions to be studied. An implicit premise of genomics is that inheritance is best studied by accumulating a list of all the genetic variants that influence a phenotype, rather than studying the phenotype in detail. The results of the recent flood of genome-wide association (GWA) studies suggest that for many traits this reasoning is backwards. The details of genetic causation are turning out to be so complex that they validate the continued use of phenotype-centred approaches to study inheritance. GWA studies have revealed well-supported associations, but these generally explain only a small proportion of the phenotypic variance.

Conclusion

The genome projects have led to gains in basic research at least as great as the proponents during the 1980s foretold, although the promise is largely unfulfilled. Important novel phenomena have been discovered, including many that could not have been found in the 3-5% of the genome that was thought to be interesting in 1987. The generation of genomic data has given rise to new disciplines that use the availability of genome sequence as a starting point. Phenotype is as important or more so than genotype as progress can be accelerated in the parts of biology that have benefited only indirectly from genomics (Houle et al., 2010). Domestic animals are currently losing genetic diversity either through intensive selection for production traits or breed substitution. Sufficient attention has not been paid to the preservation of overall genetic variation and multiple traits leading to low effective population size despite total number of individuals. Autochthonous breeds in marginal areas are being substituted by more competitive industrial breeds, without considering environmental genotype interactions and impacts of such changes on production systems.

In a review of selection experiments, Hill (2011) states that straightforward selection on phenotype in the environment of application usually does as well as some more complicated and expensive breeding programme that may incur more rapid inbreeding or longer generation interval. Advances in technology are important but their use must be taken in context of cost-benefit and practical applications need to be taken into account so that when all the hype has died down a more pragmatic look can be taken at these technologies and their true use in production systems can be evaluated. Examples are used to illustrate specific points but it is important to note that many other examples are available in other livestock species.

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