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Genomic Selection: Accelerating Genetic Gain with Precision in Livestock Breeding

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Abstract

Carcass characteristics and pork quality from finished pigs fed enzyme supplemented palm kernel cake-based diets as replacement for maize was evaluated. Thirty finisher pigs with average initial weight of between 21.5kg - 23.17kg were assigned to five dietary treatments in a Completely Randomized Design which lasted for twelve weeks. The first dietary treatment (T1), which was the control, contained 0%PKC and without enzyme supplementation. The second treatment (T2) contained 40%PKC + enzyme. The third treatment (T3) contained 40%PKC but without enzyme. The fourth treatment (T4) contained 60%PKC + enzyme while the fifth treatment (T5) contained 60%PKC but without enzyme. There were significant ($P<0.05$) differences in weight gain, average daily feed intake and feed conversion ratio. There were significant ($P<0.05$) differences between the mean carcass characteristics of the experimental animals as a result of their different diets containing different levels of PKC (with or without enzyme supplementation) inclusion. There were also significant ($P<0.05$) differences between the dressed weight percentages of the loin, the kidney and the heart. The dressed weight was higher ($P<0.05$) for treatment 3 than other treatments while the loin was higher ($P<0.05$) for treatments 3 and 2. There were also significant ($P<0.05$) differences in the mean of the kidney and the heart. The results of the serum chemistry showed that there were no significant ($P>0.05$) differences between the Serum levels of total protein, cholesterol and the Urea of the experimental animals. However, there were Significant ($P<0.05$) differences between the mean values of albumin and glucose. In conclusion, PKC inclusion of up to 60% did not have any deleterious effect on the serological and carcass characteristics as well as the general performance of finisher pigs. This study therefore provides useful information for farmers, nutritionists, researchers, research institutions and other stakeholders.

Keywords: Carcass characteristics, weaner pigs, meat quality, palm kernel cake

Introduction

The world population is growing faster than it has resisted to grow. Recent demographics projections indicate that the world can be accommodating almost 9 billion by year 2030. This fast increase imposes tremendous stress on the agricultural sector that needs to come up with a method to produce much more food with less and less natural resources. Early estimates state that the world food production will have to grow by almost 2 times per capita in the next fifty years to meet the increasing demand that basically means producing more food than the total amount that has been grown during the previous ten thousand and ten years combined (Food and Agriculture Organization, 2006). When 2000 is taken as the base year, when compared with projections in 2030, it is approximated that the global intake of meat can go up by approximately 68 percent whereas intake of milk may go up by about 57 percent (Steinfeld and Gerber, 2010) [22]. These targets will be availed by extensive technological and biological advancements increasing agricultural output, lowering the cost of production, and decreasing the adverse environmental impact (Capper, 2011) [5].

Traditional Breeding Methods

Hundreds of years of livestock breeders have managed to domesticate the genetic make-ups of

the animal populations; they take advantage of the natural variation available amongst the species, breeds and even individual animals. Classical breeding practices have been developed many years earlier than the molecular mechanisms behind quantitative traits have been realized. They made advances by taking only those animals that have the desired traits and breeding them to produce the future generations and thus enhance their breeding value. This was enhanced by close documentation of the performance of an animal as well as pedigree data. Although these approaches have achieved considerable genetic payoffs, their utility reduces when used with expensive, slow or immeasurable traits or with a low heritability trait. Regrettably, numerous characteristics that are important to livestock production in the modern context, including reproduction rates, resistance to diseases, feed consumption as well as survivorship, are included in these categories. Since these features cannot be increased quickly and consistently using traditional methods of selection, genetic-based approaches have become indispensable to further genetic development.

Marker-Assisted Selection to Genomic Selection:

Since the beginning of the 1990s, livestock breeders started using gene-marker technologies in marker-assisted selection (MAS). In this way, detrimental alleles (e.g., the gene encoding halothane in pigs or substances accompanied by off-flavours in brown-shelled chicken eggs) could be identified, eliminated and specific favourable traits (e.g., the polled hornless state in cattle) could be selected. Even though MAS was a significant advancement, it was limited in a number of ways. It was highly dependent on the prior knowledge of associated specific genes or/and markers, traits of which were expected to be related to a trait, and the precise approximation of the strength with which those performance markers would relate within a particular population. This led to MAS being typically limited to selection schemes based on families and able to explain only a small part of the overall genetic variation of animals. With the advent of cheap, high-density whole-genome SNP partitions of key livestock species, this situation changed radically. Breeders now have the ability to track the inheritance of almost all the segments of the chromosome instead of only a few of the known loci with enough genetic markers throughout the entire genome. This shift in breeding technique will be the basic alteration of the MAS towards genomic selection: it is no longer necessary that similarities in performance be explained in terms of pedigree relationship since dense SNP data can be used to indicate directly shared regions of the genome.

Genomic Selection

Innovations in high-throughput genomic and sequencing of DNA have identified enormous amounts of single nucleotide polymorphisms (SNPs) in the cattle and other food-producing species (see Table 1). A variety of commercial SNP-genotyping arrays (highly densely mapping the entire bovine genome) has today enabled capturing of the majority of genetic variation in economically significant traits. This innovation is the basis of the idea of genomic selection, initially, which is a practice that relies on whole-genome data to predict the genetic quality of animals (Meuwissen *et al.*, 2001) [17]. Under this system genomic estimated breeding values (GEBVs) are calculated by approximating SNP impacts by forecasting by means of prediction models created on a reference group that comprises of genotyped and phenotyped animals with explicit phenotype of a trait of

interest. Another significant grounds that led to the genomic revolution in livestock was the Human Genome Project, which improved the progress of the highly advanced DNA sequencing methods and large-scale genotyping platforms. The subsequent fall in sequencing costs made possible allowed the assembly of complete genome sequencing of many animal species of domestic interest, which formed the basis of genomic selection initiatives in the modern context.

Table 1: Summary of first sequenced genomes for animal species

Species	Genome Size (Gb)	Year
Chicken	1.05	2004
Dog	2.4	2003
Cattle	2.91	2009
Horse	2.47	2009
Pig	2.2	2008
Sheep	2.78	2008
Cat	1.64	2006
Rabbit	2.67	2009
Turkey	1.08	2009
Goat	2.72	2010
Camel	2.2	2011
Honeybee	0.24	2011
Buffalo	2.5	2021

Principle of Genomic Selection:

Genomic selection, firstly envisaged by Meuwissen and colleagues (2001) [17] is based on the premise that breeding values can be estimated based on the value of an extremely large number of genetic markers regardless of whether the specific location of the genes affecting a trait is known. At the point that tens of thousands of carefully chosen SNP markers are scattered throughout the genome, it is very likely that at least one of these will be situated near any gene or functional area of DNA that is of interest to performance. The combination of these markers (when they are in general linkage disequilibrium with closely located causal mutations) is revolutionary, impacting much of the genetic variation, on the phenotype level, associated with their single markers. This enables breeders to estimate genetic merit much more accurately compared to relying on the traditional methods.

Methodology

Genomic selection starts with the formation of a large, strongly characterized group of animals, also known as a reference or training population, all of which have extremely dependable phenotypic data on the traits of interest. A whole-genome SNP array is then performed in order to genotype these animals. This is the combined genotype and phenotype information that is utilized to construct the statistical models that approximate the contribution of each SNP to the trait that is of interest (Fig. 1). Based on this modelling step, researchers come up with an equation of prediction that could be applied to calculate the genomic estimated breeding value (GEBV). After validation of the predictive equation, the SNP genotypes of new candidates can be used to determine the predictions without the applicant having to undergo a direct phenotypic measure. These genomic predictions rely highly on the magnitude of the reference population and the heritability of the trait. Indicatively, at the example of poultry, Gonzalez-Recio *et al.* (2009) [9] have indicated that the accuracy of genomic predictions with regard to breeding values of feed conversion ratio is almost four-fold better than

when using parent-average estimations.

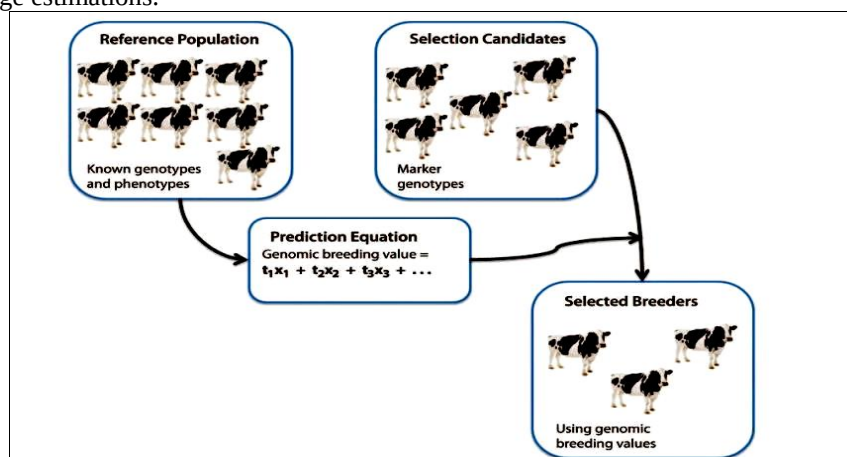


Fig 1: An overview of Genomic selection in livestock

Methods to develop Prediction Equation

- 1. Least Squares (LS):** The procedure involves testing of individual genes (or markers) to establish an indication of whether effects on the trait are significant. Authority: markers significance being significant are only retained and their effects are estimated all at once by least-squares method even as the effects of less significant markers are set at zero.
- 2. Best Linear Unbiased Prediction (BLUP):** In contrast to LS, BLUP does not assume allelic effects to be fixed but about to be random. With random-effect, since they do not use the degrees of freedom in the same manner, BLUP can estimate all marker effects simultaneously, which is much more efficient in situations where the number of SNPs (thousands) is involved.
- 3. Bayesian estimation (Bayes):** Bayesian methods are the same as BLUP except that they assume that there is a variance of every marker. The variances are estimated with the help of previous probability distributions, which allows the model to reduce the SNP effects of several SNPs strongly and large of the SNP approach of the markers with stronger evidence.

Accuracy of genomic selection in these three methods: LS (0.36) < BLUP (0.74) < Bayes (0.84) (Meuwissen *et al.*, 2001) [17].

How GS improve Genetic Gain?

There are four important elements that determine the rate of genetic increase of the population in case of artificial selection. The classical formula of Falconer (1989) writes it off as:

$$\Delta G = (i h \sigma_a) / L$$

Where,

i = the selection intensity

h = the accuracy of selection

σ_a = the additive genetic standard deviation of the trait

L = the generation interval

Genomic selection enhances genetic gain directly since it affects these factors directly, especially accuracy and generation interval.

Generation Interval

Conventional Progeny-Testing Systems are tedious and breeders are expected to wait until the offsprings performance data is available before parents are chosen. Since this process is meant to produce high accurate EBVs, the siremale (SM) pathway will result in a very long generation period. As Fig. 2 demonstrates, the traditional progeny-testing schedule causes the generation duration of about 63 months which is much slower than the genetic advancements.

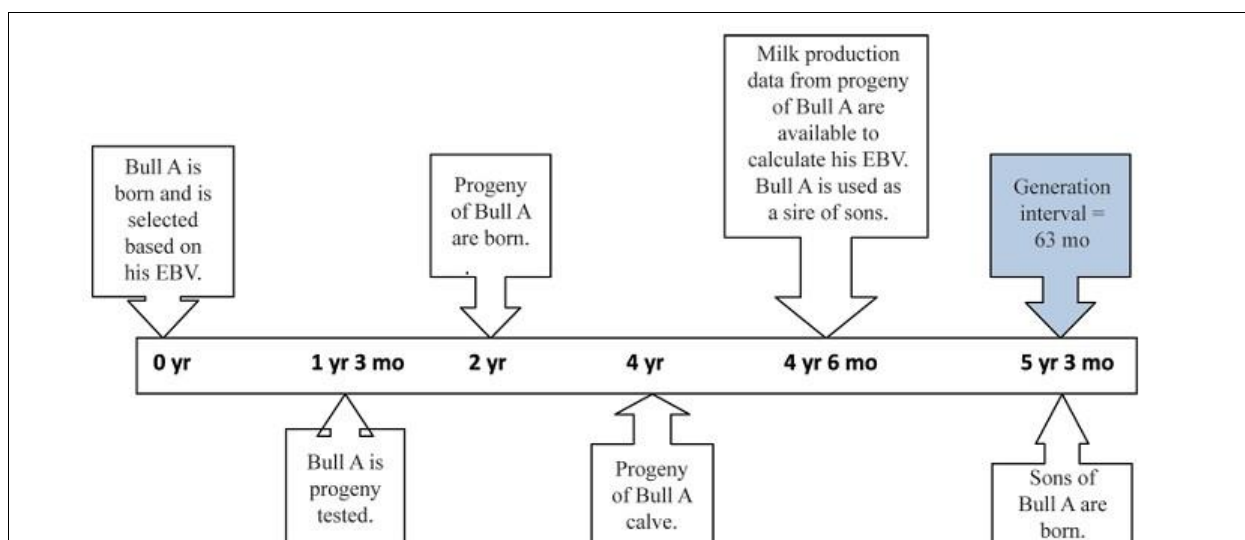
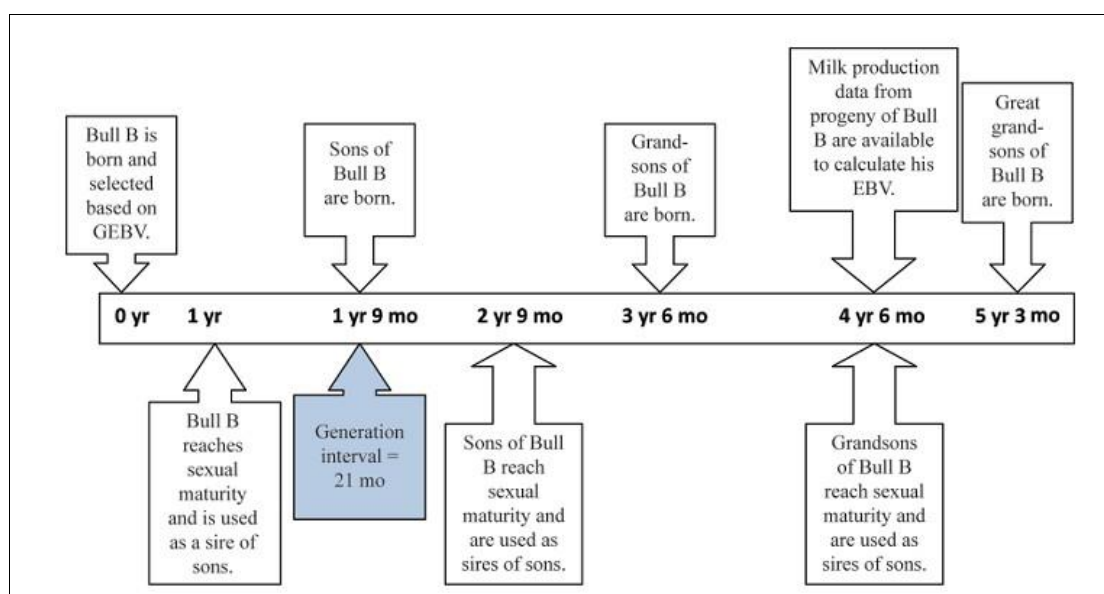


Fig 2: Timeline for traditional selection through progeny selection

Genomic selection will allow artificial insemination (AI) organizations to make precocious and correct decision making based on GEBVs that are obtained when the bulls are very young. Consequently, young males are able to join the sire-of-sons pathway immediately they become sexually active, instead of having to wait until they pass such protracted progeny tests. Conventionally, a bull could not be utilized as a sire of sons until at least 4.5 years. At about one year of age, however, bulls ranked high on the basis of genomic information can be utilized with the aid of DNA-testing. This stated dramatic decrease of the waiting time decreases the generation interval in the sire-male (SM) pathway and Schaeffer (2006) speculated that this kind of shortening might even increase the rate of improvement in generation twofold (Fig. 3). Genetic bulls are young males with GEBVs but yet

they do not have daughter performance records. In the recent years, AI firms have moved towards using such genomic bulls to varying degrees, with some having virtually no further need to purchase any additional genomic bulls after that point. Some have a hybrid approach, with a combination of the use of genomic bulls and older progeny-tested sires. The genomic bulls are not as reliable as the traditional bulls although they have higher genetic merit and therefore to control this the companies use a bigger pool of genomic sires.

Figure 3 shows the breeding schedule of an intensive AI program which emphasises the utilisation of one year old genomic bulls. Within this mode of operation, the duration required to generate the SM pathway may be reduced to say about 21 months, which is novel in the rapid generation of genetics.

**Fig 3:** Timeline for genomic selection

Selection Intensity

Two things have significant effects on the intensity of selection (i) in a breeding program. The former is the total population size of individuals under consideration. Greater populations are necessary in order to attain a greater selection intensity since it enables breeders to select more animals and to pinpoint some of the rarer genetic outliers. The second is associated with the percentage of those who were selected to be the parents of the successive generation. Genomic selection makes it possible that DNA samples could be collected soon postpartum and the AI companies could genotype thousands of young bull calves only to select a few of the best in their breeding programs. It is also possible to test female applicants, which will enable AI firms and breeders to screen a large number of cows and heifers on a commercial farm and choose a few high-quality animals which could be reproduced via MOET or IVF.

Genetic Variation

The additive genetic standard deviation, (σ_A) is a measure of genetic variation that is available in a population in respect to a trait. As inbreeding becomes more common, the effective population size of the population declines thus leading to the consequences that the genetic variation on which selection may act is reduced; producing a slower genetic improvement rate. Relative to the other elements of the genetic gain equation, there are few possibilities of

enhancing the genetic variation contained within a population, and those opportunities to enhance it are important.

Advantages

1. The application of genomic selection is at a very tender age.
2. It is not limited to the sex of the animal.
3. It is applicable to any trait which has been documented in reference population.
4. It works in enhancement of traits that are otherwise hard to achieve.
5. It will give greater accuracy in selecting decisions.
6. It reduces the production period.
7. It allows an increase in the intensity of selection.
8. It accounts a significantly bigger proportion of genetic variation in comparison with MAS.
9. It can be applied to all the populations and is independent of a particular family lineage.

Present Status of GS in Livestock

Genomic Selection in Dairy Cattle

In dairy cows, genomic prediction is at least as predictive as 0.8 in regards to production factors, and at least 0.7 in regards to fertility, longevity, somatic cell count, and a number of other factors (e.g. Wiggans *et al.*, 2011; Lund *et al.*, 2011) [23, 16]. Such high accuracies are an expression of large populations of reference to each dairy breed, the vast majority

of which contain progeny-tested bulls, which has a highly reliable phenotype since they rely on average daughter performance. Predictions made using genomes may be applicable to close relatives of animals within the reference populations which even enhances accuracy. The next significant aspect of the dairy genomic prediction is its high degree of international collaboration. There are three major consortiums that have been established: the Eurogenomics (Netherlands, Germany, France, the Nordic countries, Spain and Poland), the North American Consortium (USA, Canada, Italy, and the Great Britain) and the rest of the world consortium. Globally, approximately 2 million genetically predicted dairy cows have been genotyped. Genotyping of 934,780 Holsteins, 120,439 Jerseys, 19,588 Brown Swiss and 4,767 Ayrshires has been done in the USA alone (Wiggins, personal communication). Big datasets have also been donated by other countries such as 360,000 animals in France (Boichard, personal communication). Genetic gain has increased as a result of implementation of genomic selection which has been proved to exist through genetic trend analysis that has been done in a number of countries. As an example, it has been noted that the genomic selection has been introduced and the rate of genetic gain increased by a factor of two in Canada (VanDoormal, personal communication). It is not without evidence that genomic selection has also raised the rate of inbreeding on an annual basis (Schenkel, 2012) ^[21] however, future efforts should be done in a way that they maximise genetic gain whilst controlling the rates of inbreeding.

Genomic Selection in Sheep and Goat

The effectiveness of genomic selection has been experimented on small ruminants in both meat sheep in Australia (Daetwyler *et al.*, 2010, 2012a, 2012b) ^[5, 6, 7], in meat sheep in New Zealand (Auvray *et al.*, 2014) ^[1], in dairy sheep in France and in dairy goats in France (Carillier *et al.*, 2013) ^[4] and the UK (Mucha *et al.*, 2015) ^[18]. One of the main conditions of genomic selection is that the reference population must be large enough and with a rich phenotype that can represent the population at large. New Zealand contains the highest reference population in terms of 13,420 breed purebred (mostly Romney) and crossbred sheep. Other reference populations include smaller ones; 1,900 Western Pyrenees dairy sheep (Legarra *et al.*, 2014) ^[2], 2,400,270 goats in the UK and France, 4,800 Lacaune dairy sheep (Larroque *et al.*, 2014) ^[4], and up to 8,000 multi-breed Australian meat sheep (Daetwyler *et al.*, 2010, 2012a, 2012b) ^[5, 6, 7]. However, within-country purebred are even smaller with approximately 5,300 New Zealand Romney, 4,000 Australian Merino and 4,800 French Lacaune, where most other breeds have only a few hundred to few thousand animals. In spite of the smaller reference sizes, there have been improvements in the accuracy of GEBV. In case of Australian sheep, it was observed that carcass and meat quality traits had an increase of 0.05-0.10 (Daetwyler *et al.*, 2012a, 2012b) ^[5, 6, 7]. The profit of New Zealand varied between 0.05 and 0.27 (average = 0.13) in meat, fleece, and litter size characteristics (Auvray *et al.*, 2014) ^[1]. The increase in the accuracy of the milk production traits was 0.10-0.20 in French Lacaune dairy sheep (Baloché *et al.*, 2014) ^[14]. Milk yield, fat and protein content made gains of 0.06 and 0.14 in dairy goats in France and the UK, respectively (Carillier *et al.*, 2013) ^[4]. Daetwyler *et al.* (2012b) ^[5, 6, 7] demonstrated that reference population size was closely associated with improvements in accuracy and that the probability of further

gains in accuracy with increases in reference population will show stronger associations with genomic heritability.

Genomic Selection in Pig

In around 2009 new SNP marker panels commercially became available and had extremely large numbers of anonymous markers. The pig SNP chip is widely used having 64,232 markers out of which approximately two-thirds usually passed quality control and can be used in the genomic analysis. This was a significant departure of methods in candidate-gene methods where markers were selected due to their already known participation in biological pathways impacting the trait of interest.

Genomic Selection in Poultry

The initial livestock to which its genome had been sequenced was the chicken (Hillier *et al.*, 2004) ^[11] and this finding was followed by the discovery of several million SNPs. Early SNP chips in commercial chicken were 3,000 markers (3K) on a single chip (Muir *et al.*, 2008) ^[19], later found to be too dense. Later privately developed high-density chips led to two highly impactful medium-density arrays a 60K chip constructed under an agreement funded by the USDA and used by Cobb and Hendrix (released under their research license) and a 42K chip constructed in-house by the EW group. The earliest high-density 600K public SNP chip was recently launched (with backing by the BBSRC and the Roslin Institute) and contains variants of both broiler and layers lines (Kranis *et al.*, 2013) ^[13]. Since high-density SNP chips are still rather expensive, low-density SNP chips with genotype imputation have frequently been used in early poultry breeding programs, which enables selection candidates to be imputed on arrays as small as 400 SNPs (Habier *et al.*, 2009) ^[12], very significantly lowering costs without losing much genomic prediction power (Habier *et al.*, 2009) ^[12].

Challenges

Limited Infrastructure and diverse indigenous breeds require tailored approaches in developing countries.

Achieving acceptable accuracy in breeding value predictions require large training populations, which may lead to an increased annual rate of inbreeding.

The need of continuous phenotyping: Some simulation experiments have shown that accuracy using the same markers decline rapidly across subsequent generations and new training populations are required.

Preselecting bulls in dairy cattle using genomic information can lead to biased predictions with lower accuracy, leading to a decrease in genetic progress and distorting international dairy bulls' comparisons

SNP estimates calculated from a Holstein-Friesian reference population did not produce accurate GEBV in Jersey bulls, and the correlations ranged from -0.1 to 0.3 when the SNP effects from one breed were used to calculate GEBV in another breed & vice versa.

Implementing GS in current breeding schemes.

Future Directions & Conclusion

The ability to study the genome, transcriptome, epigenome and metagenome of any species is introducing new possibilities of livestock improvement. Their subspecies and pathogens are also being sequenced making breeders better equipped with the information required to build and optimize genomic selection methods as more economically important agricultural species are sequenced. In combination with MOET, genomic selection can dramatically decrease the

generation intervals, and superior embryos can be chosen to undergo the subsequent generation. It is also feasible to train prediction equation using commercial animals that are usually crossbred and grown under more adverse conditions of the environment and not just on purebred stud animals.

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