Genetic improvement in Colombian cattle, a reality or an intention? A review

Mejoramiento genético de bovinos en Colombia, ¿una realidad o una intención? Revisión

Melhoramento genetico de gado bovino na Colômbia, uma realidade o uma aspiração? Revisão

Alejandro Amaya*[1]; José-Miguel Cotes-Torres[2]

[1-] *Universidad de Ciencias Aplicadas y Ambientales U.D.C.A, Programa de Zootecnia.*
[2] *Universidad Nacional de Colombia - Sede Medellín, Facultad Ciencias Agrarias.*

To cite this article:
Amaya A, Cotes-Torres JM. Genetic improvement in Colombian cattle, a reality or an intention? A review. Rev Colomb Cienc Pecu. *Year, Vol, number, and pages pending.* DOI: https://doi.org/10.17533/udea.rccp.v38n2a1

Abstract

Background: Genetic improvement programs in domestic species require a set of steps involving the definition of breeding objectives, information systems, variance component estimation, genetic evaluations, selection indexes, and the estimation of genetic progress and variability. **Objective:** To

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* **Corresponding author.** Calle 222 # 55 – 37, Bogotá, Colombia. adamaya@udca.edu.co

Received: *March 21, 2024.* ***Accepted:*** *June 20, 2024*

identify strengths and weaknesses in the design and implementation of genetic improvement programs in Colombian cattle through scientific and academic contributions derived from research. **Conclusion:** The greatest challenges in the design and implementation of genetic improvement programs in Colombian cattle are currently related to the absence of consensus breeding objectives among farmers and associations. Additionally, there is a need in the short term to improve both the quality and quantity of information available in databases. Finally, conducting economic analyses that consider genetic parameters is essential for optimizing the response to genetic selection, considering the different productive systems and environmental conditions that Colombia offers.

Keywords: *Animal breeding; bovines; breeding values; cattle; genetic improvement; genetic progress; genetic variability; phenotype; profit; quantitative genetics; selection.*

Resumen

Antecedentes: Los programas de mejoramiento genético en especies domésticas requieren de un conjunto de pasos que involucran la definición de objetivos de cría, sistemas de información, estimación de componentes de varianza, evaluaciones genéticas, índices de selección y la estimación del progreso genético y la variabilidad genética. **Objetivo:** identificar falencias y fortalezas en el diseño e implementación de programas de mejoramiento genético bovino en Colombia mediante los aportes científicos y académicos derivados de la investigación en genética bovina en el país. **Conclusión:** Los mayores desafíos en el diseño e implementación de programas de mejoramiento genético bovino en Colombia actualmente están relacionados con la ausencia de objetivos de cría consensuados por los productores y asociaciones. Asimismo, es necesario en el corto plazo una mejora tanto de la calidad como de la cantidad de información disponible en las bases de datos. Finalmente, suplir la ausencia de análisis económicos que se vinculen y sean considerados en los análisis genéticos para optimizar la respuesta a la selección genética considerando contextos productivos y la diferente oferta ambiental que posee Colombia.

Palabras clave: *Bovinos; cría de animales; fenotipo; ganado; genética cuantitativa; mejoramiento genético; progreso genético; selección; utilidad económica; valores genéticos; variabilidad genética.*

Resumo

Antecedentes: Para desenvolver um programa de melhoramento genético animal, é preciso definir objetivos de melhoramento, possuir sistemas de informação ótimos, realizar estimativas dos componentes de variância e a análise genética correspondente, além de estimar índices de seleção, progresso genético esperado e variabilidade genética**. Objetivo**: identificar debilidades e fortalezas no desenho e implementação de programas de melhoramento genético para gado bovino na Colômbia, fazendo uma revisão dos avanços científicos e acadêmicos obtidos através da pesquisa nesta disciplina no país. **Conclusão**: O principal problema encontrado foi a ausência de objetivos de melhoramento feitos em conjunto entre produtores e pesquisadores. Além disso, é preciso, no curto prazo, melhorar tanto a qualidade como a quantidade da informação disponível nos bancos de dados. Finalmente, é necessário realizar análises econômicas que considerem o componente genético, com o objetivo de otimizar a resposta à seleção genética, levando em conta as diferenças dos sistemas produtivos e da oferta ambiental que a Colômbia possui.

Palavras-chave: *Criação de animais; fenótipo; gado; genética quantitativa; melhoramento genético; progresso genético; seleção; utilidade económica; valores genéticos; variabilidade genética.*

Introduction

Improving animal productivity in production systems can be achieved through the implementation of genetic, nutritional, health and reproductive strategies. In genetic improvement, the use of mixed models has been, so far, the most widely used tool to indirectly estimate breeding values in order to increase the average zootechnical performance of the herd (Henderson, 1975). In domestic animals, poultry have possibly been the most successful case in the implementation of genetic improvement programs. Zuidhof *et al*. (2014) reported phenotypic gains due to genetic selection exceeding 350% for slaughter weight in poultry. The response to selection in cattle has not been as large as in poultry. However, the genetic gains are not negligible. For example, the American Angus Association reported a genetic difference in weaning weight of 85 kg when comparing animals born in 1972 and 2023. In Holstein cattle in the United States, García-Ruíz *et al*. (2016) calculated a genetic gain of over 1500 liters of milk per lactation. In cattle systems based on grazing, a genetic increase of 13.6 liters/cow/year was reported in pure and crossed Holstein cattle in New Zealand, between the years 2000 and 2020 (López-Villalobos et al., 2021). This genetic progress could be higher in the medium term due to the use of genomic information in selection programs, which reduces the generation interval and increases the accuracy of the estimated genetic merit, leading to an increase in genetic gain (Schaeffer, 2006).

Examples of genetic progress due to the use of selection strategies are numerous and varied in the literature; however, all successful cases have something in common, a procedure composed of five steps: 1) definition of breeding objectives, 2) phenotypic and genotypic information systems, 3) estimation of variance components, 4) genetic evaluation and selection indexes, 5) economic evaluation and genetic variability (Garrick y Golden, 2009). This framework allows breeders and scientists to understand, at first glance, that the implementation a breeding program is a demanding task, both technically and logistically.

In Colombia, research efforts have primarily focused on second, third and fourth steps. In this context, there is a lack of studies addressing the first and fifth steps (in some cases, none) for the implementation of genetic improvement programs. The improvement of these aspects would improve not only primary production, but also the processing industry at the meat and dairy level. Additionally, the strengthening of these aspects could facilitate the incorporation of innovative genetic selection tools, such as the use of genomic information for the early identification of the best individuals and the improvement of polygenic traits of complex measurement (feed efficiency, carcass quality, resistance diseases, among others), which are currently not possible to select or evaluate in Colombian populations given the absence of large-scale phenotypic measurements.

On the other hand, although an important part of the national herd is crossed animals, this review did not include the analysis of genetic aspects in crossed populations due to the lack of scientific evidence over time. However, reports found for crossed populations in Colombia were discussed andf included at the end of the text. Similarly, the evaluation of genetic improvement programs in Colombian dual-purpose systems is complex given that the scientific production that has evaluated phenotypes or productivity indicators from a dual-purpose perspective is practically null. There was only one study reported by Galeano and Manrique (2010), who evaluated genetic aspects of an index that evaluates females through considering traits as milk production, weaning weight of offspring and calving interval.

Then, the objective of this review was to identify weaknesses and strengths in the genetic management of specialized dairy and beef breeds used in Colombia. Furthermore, to motivate the academic community and farmers to constantly optimize the efficiency of livestock systems through the application of genetic improvement. This work will also allow readers to recognize areas of genetic science that have not been explored thus far. Additionally, efforts could be directed towards strengthening the design and implementation of robust genetic improvement programs aimed at optimizing the sustainability and economic development of local cattle production systems.

Definition of breeding objectives

A breeding objective is the combination of economically important traits for a production system, and it is the first step in the implementation of a genetic improvement program (Wolfova *et al.,* 2005). Its purpose is to increase the profit of the production cycle and must be redefined as production or market conditions change (Byrne *et al.,* 2016). As far as our literature review went, there are no studies of this type for cattle in Colombia. The absence of this knowledge in Colombia could have some practical and scientific reasons described below.

In Colombia, the traits evaluated in selection programs have been largely limited to traits such as age at first calving, calving interval (Amaya *et al.,* 2020a; Rocha *et al*., 2012; Ramírez *et al.,* 2021), weights at different ages, weight gains (Ramírez *et al*., 2020; Amaya *et al.,* 2020a) and milk production (Restrepo *et al*., 2008; Solarte & Zambrano, 2012; Echeverri *et al.,* 2014; Rincón *et al.,* 2015; Amaya *et al*., 2019a). However, in animal production, the characteristics that most affect profitability could be classified into four categories: 1) adaptation and reproduction, 2) quantity and quality of the final product, 3) animal welfare, and 4) environmental footprint. Ignoring these types of variables could generate negative effects in the short term, mainly due to the current demands of governments and final consumers.

Other traits such as anatomical conformation, longevity, heat stress, and eco-physiology have been explored in Colombian cattle (Betancur-Zambrano *et al*., 2012; De León *et al*., 2021), but those studies have a small number of records (Ramírez *et al*., 2021; Amaya *et al.,* 2021; De León *et al.,* 2021). Thus, in these cases is common to find numerical computational problems for the estimation of bi-trait and multi-trait models because the algorithms have difficulty finding convergence.

Another important trait is the feed efficiency, which has not been evaluated but is economically vital for animal production because represents the highest variable cost within the industry. The reported heritabilities have been medium and high (0.35-0.55, Schenkel *et al.,* 2004). However, measurement presents the following challenges: 1) it is difficult to measure in a large number of animals, 2) it is necessary to know the correlations with other traits of the breeding objective, and 3) it is very expensive because it requires individual control. One strategy that could partially overcome these limitations is genomic selection, however, its implementation in Colombia is challenging due to the high economic resources required and the need for a good quality of phenotypic databases. Pryce *et al*. (2014) suggested combining genomic platforms from different populations. For foreign breeds, this alternative could work due to the genetic connectivity generated by the massive use of imported bulls in artificial insemination, but in Creole breeds, it would not be available.

These scenarios reflect the immediate need in the definition of breeding objectives. For this, the local productive needs, market conditions and the high heterogeneity of production systems in tropical conditions must be considered. This last, represents an additional challenge when compared to countries with temperate climates, where production conditions and systems are usually more homogeneous.

Information system and selection criteria

Selection criteria are defined as those traits that allow breeding objectives to be improved. An ideal selection criterion must meet three requirements: easy to measure, medium or high heritability, and a high genetic correlation with the breeding objective (Ponzoni y Newman, 1989). The most favourable scenario is when the selection criteria also acts as a breeding objective.

At this point, breeders' associations have a fundamental role in collect phenotypic records and then to develop information systems that guarantee the success of the breeding programs. However, there are two mainly limitations: a) it is common for Colombian farmers not to keep records or report them to the association, and b) someone of the Colombian farmers think that the costs of affiliation and registration are high or unnecessary, which means that a significant amount of data does not reach by the association. These conditions severely limit access to reliable and large databases. Nonetheless, there are published research works derived from the joint work between the academic community and breeders' associations which is limited in most of the cases to estimate genetic parameters.

In the country, cattle production can be classified into: (1) specialized milk production systems, (2) breeding and fattening production systems, and (3) dual-purpose systems. For milk production, most reports are distributed in Holstein, Jersey and Simmental breeds (Solarte *et al.,* 2012; Rincón *et al*., 2015; Zambrano *et al.,* 2015; Amaya *et al*., 2019). Regarding meat production, there is a greater number of reports in Blanco Orejinegro, Romosinuano, Brahman and Simmental breeds (Martínez *et al*., 2018; Amaya *et al*., 2020a; Ramírez *et al*., 2020; López *et al*., 2021). The reproductive traits primarily considered have been age at first calving, calving intervals and open days (Table 1).

Estimates for milk production were mostly in the first three lactations. The number of cows in onestudies ranged from 620 to 7723, shows heritabilities between 0.02 and 0.28 (Amaya *et al.,* 2019; Múnera *et al.,* 2014; Rincón *et al.,* 2015). While accurate estimates exist, most have errors that hinder to make appropriate selection decisions, affecting genetic progress. For the traits associated with product quality, the estimates were less precise, both in milk and meat, with heritability estimation errors of up to 0.32 for protein and fat, and with accuracies of breeding values less than 0.5 for loin eye area and back fat (Rincón *et al.,* 2015; Asocebú, 2022).

The collection of data associated with quality is often conditioned by external funding, which limits the develop of a robust and permanent information system. For example, between 2014 and 2016, official dairy control at the national level was a joint initiative of the Unión Nacional de Asociaciones Ganaderas (UNAGA), the Ministerio de Agricultura and FEDEGAN. This work was valuable and allowed breeders to have an initial information system to evaluate criteria such as the percentage of protein and fat in milk. However, these efforts have not been sustained since that date, at least not at the scale necessary for the development of reliable genetic evaluation

Table 1. Selection criteria and heritability estimates for cattle breeds in Colombia. Only studies involving a minimum of one thousand animals were considered.

Source	Breed	Selection criteria	Animals	Records	Heritability
Amaya *et al*. (2020)	Simmental	AFC	3063	3063	0.20
		CI	1098	1098	0.04
Betancur *et al*. (2012)	Holstein	MY	1198	2372	0.21
		MF	1198	2372	0.14
		MP	1198	2372	0.14
Caivio *et al*. (2021)	Blanco Orejinegro	CI	3308	3308	0.11
Cerón *et al*. (2001)	Holstein	MY	25608	69464	0.20
Cerón *et al*. (2004)	Holstein	AFC	25569	25569	0.13
De León *et al*. (2021)	Blanco Orejinegro	AFC	1927	1927	0.06
De León *et al*. (2021)	Sanmartinero	AFC	1927	1927	0.20
López *et al*. (2021)	Romosinuano	BW	4079	4079	0.17
		W8M	4079	4079	0.13
		W16M	4079	4079	0.06
Martínez *et al*. (2018)	Brahman	BW	105784	105784	0.47
		W4M	14743	14743	0.30
		W7M	105771	105771	0.24
		W12M	12404	12404	0.38
		W18M	10215	10215	0.36
Múnera *et al*. (2014)	Holstein	MF	1210	9479	0.14-0.38
		MP	1210	9479	0.12-0.32
Ramírez *et al*. (2020)	Blanco Orejinegro	BW	7304	7304	0.10
		W4M	1281	1281	0.23
		W8M	4791	4791	0.10
		W16M	3339	3339	0.38

		W24M	1364	1364	0.39
Rincón *et al.* (2015)	Holstein	MY	7723	7723	0.16
		MF	5866	5866	0.30
		MP	5709	5709	0.32
		SCC	5769	5769	0.01
Rocha *et al.* (2012)	Blanco	AFC	1256	1256	0.15
	Orejinegro	CI	3803	3803	0.13
Vergara *et al.* (2016)	Romosinuano	AFC	1079	1079	0.04

AFC: Age at first calving; CI: Calving interval; MY: Milk yield; MF: Milk fat; MP: Milk protein; BW: Birth weight; W4M: Weight at 4 months of age; W7M: Weight at 7 months of age; W8M: Weight at 8 months of age; W12M: Weight at 12 months of age; W16M: Weight at 16 months of age; W18M: Weight at 18 months of age; W24M: Weight at 24 months of age; SCC: Somatic cell score.

The traits associated with the quality of the carcass had a similar scenario. The Brahman breed has the highest participation as a pure breed in Colombia for meat production. In 2010, the first genetic estimates of carcass quality were published, with a phenotypic basis of approximately one thousand measurements (Jiménez *et al*., 2010). The genetic evaluation made by Asocebú in 2022 included 10332 records for the loin eye area and the thickness of the dorsal fat. However, the accuracies of most selection candidates are below (<0.5). In this case, constant work on updating information systems is a short-term need. The current development of technologies such as sensors, cameras, microphones, among others, could partially overcome these obstacles and accelerate data collection for the strengthening of information systems and genetic evaluations for these traits.

Traits associated with reproduction have been less explored, and the phenotypes have primarily focused on the calving interval and age at first calving (Rocha *et al.,* 2012; Vergara *et al*., 2016; Amaya *et al*., 2020a; Ramírez *et al*., 2021). Although these two traits may have a direct relationship with reproductive performance, zootechnical practices in Colombian production systems may deviate slightly from that focus. Age at first calving could indirectly evaluate puberty age or the speed at which a female matures sexually. However, in Colombian livestock farming, age at first calving depends more on the growth rate because farmers prioritize weight over age for the first service.

On the other hand, the calving interval trait has two disadvantages in its recording. The first is the preferential treatment given to some females, which could confuse the genetic effect with environmental advantages, although effects as the farm or year are included in the model. The second problem is the inclusion of females in embryo transfer programs and the use of seasonal mating, technologies that are becoming increasingly common. In these scenarios, the phenotype for the calving interval does not represent the real biological value (Aby *et al.,* 2012), complicating the estimation of genetic potential. Therefore, the reproductive component in Colombian cattle populations should be reconsidered, focusing efforts on traits less sensitive to management practices or production conditions.

Variance components and genetic parameters

The estimation of heritability, genetic correlation, and repeatability allows researchers to quantify the effects of genetic and environmental factors on the phenotypic performance of economically important traits. The statistical procedures are based on the degree of relationship between animals, frequently using family structures of half-siblings or full siblings. The estimation of these parameters in Colombia has been based on the use of the animal model, under restricted maximum likelihood methodology. Although there are other methodologies such as Bayesian inference for variance components estimation, its application in Colombia is scarce, and as far as our search went, there are no scientific reports of its official use for decision-making in national selection programs.

For dairy cattle populations, estimation has been done for accumulated milk production, protein and fat, somatic cell count, and total milk yield (Amaya *et al*., 2019; Rincón *et al.,* 2015; Múnera *et al*., 2014). These studies have been focused on Holstein, Simmental, and Jersey dairy cattle breeds. The reported heritabilities for these traits have ranged from 0.01 for somatic cell count to 0.46 for fat and protein production. Average heritabilities (0.2-0.4) have been more common for milk yield per lactation or per day (Table 1).

In beef cattle, weights at different ages, daily weight gains, loin eye area, backfat, and hip fat have been evaluated (Jiménez *et al*., 2010; Martínez *et al*., 2018; Ramírez *et al*., 2020; Ossa *et al*., 2021a). Most of the reported heritabilities for weights at different ages (from birth to 24 months) ranged from 0.09 to 0.38 (Ossa *et al*., 2021a; Martínez *et al*., 2018), with lower heritability values found for weights before weaning. The highest values were reported for weights at 12 to 24 months of age. Regarding traits associated with quality, the average heritability values were higher, ranging between 0.29 and 0.37; however, the reported errors for these estimations were higher (Jiménez *et al*., 2010) due to a smaller number of records.

Other estimations have been reported for calving interval, age at first calving, adaptation coefficient, rectal temperature, and respiration rate (Amaya *et al.,* 2020a; De León *et al*., 2021). The heritabilities for these types of traits ranged between 0.0 and 0.15 (Rocha *et al.,* 2012; Caivio-Nasner *et al*., 2021). The lack of these estimations in Colombia could be due to the information systems implemented on farms, where farmers have greater interest in variables directly associated with the final product (meat and milk). Although most variables associated with reproduction are easily measurable and of high economic importance (Amaya *et al*., 2020; Amaya *et al*., 2022), their use in genetic selection programs has not been successful, primarily due to the low number of individuals with phenotypic information, leading to numerical problems in computational algorithms such as non-convergence (Ramírez *et al*., 2021).

Other problems include connectivity in pedigrees, accuracy of phenotype measurement, and fixed effects in genetic models. The number of records used for milk production estimations varied from 620 to 25608 cows (Cerón *et al*., 2001; Amaya *et al*., 2019). Regarding the number of animals included in the relationship matrix, populations ranged from 801 to 27986 animals (Rincón *et al*., 2015; Amaya *et al*., 2020a). However, very few publications describe the number and size of families in the pedigree, making it difficult to contextualize the effect that family structure has on the estimation of genetic parameters.

Understanding this genealogical structure is crucial because pedigree connectivity influences the prediction errors of variance, which are affected by genetic relationships between and within management units (farms, contemporary groups). Although this is not a strong limitation for specialized dairy production systems due to the widespread use of imported bulls in artificial insemination programs, in beef cattle, this connectivity could be low, affecting the quality of genetic evaluation. Although genetic connectivity studies have been reported in Colombia (Taborda *et al*., 2015), their use is not widespread in the estimation of variance components and the genetic merit of animals.

The reports of genetic correlations were more diverse. For example, one correlation of interest is the age at first calving and calving interval. In Simmental breed, this correlation was positive (0.25; Amaya *et al*., 2020a), which is favourable at the zootechnical level. However, in the Blanco Orejinegro breed, the simultaneous selection of these two variables is more complex, as the reported correlation was negative (-0.43; Rocha *et al*., 2012). While this could be addressed through the identification of animals whose breeding values are favourable for both traits, genetic progress would be slow, and the change in correlation could occur, but in the long term, hindering genetic gains and balanced selection. For this reason, prior identification of breeding objectives is vital to define the correlations of interest to be considered in the selection program.

The traits associated with milk production and quality showed greater consistency among the consulted studies. Solarte *et al*. (2012), Rincón *et al*. (2015), and Amaya *et al*. (2019) reported correlations ranging from 0.64 to 0.97 for accumulated milk productions at different stages of lactation and correlations ranging from -0.27 to -0.40 for volume and protein and fat content. These results generally align with worldwide reports, where higher milk production proportionally results in lower total solids content in milk. No reports of positive correlations between quantity and quality of milk were identified, neither in dual-purpose cattle nor in specialized dairy farming.

In Creole cattle, correlations between weights at different ages and daily weight gain have been reported, with values ranging from 0.04 to 0.96 (Ramírez *et al*., 2020). Reported correlations between growth rate and carcass quality have been positive, ranging from 0.91 to 0.95. In Brahman cattle, estimations included variables such as loin eye area, backfat, and daily weight gain (Jiménez *et al*., 2010). In Colombia, improving traits associated with product quality could be interesting for emerging markets willing to pay for added value in the final product. The current use of these correlations should be approached with caution due to limitations in the number of records and the difficulty of capturing all non-genetic effects in the models, however, efforts in measuring these traits should be increased by farmers and associations.

Regarding repeatabilities, the number of reports was lower than that found for heritabilities. The variables analysed included birth and weaning weights of female offspring, calving interval, milk production, and services per conception (Donicer *et al*., 2009; Rocha *et al*., 2012; Solarte *et al*., 2012; Ossa *et al*., 2021b). The highest reported value for this genetic parameter was for milk production in Holstein cattle, with a value of 0.31 (Solarte *et al*., 2012). On the other hand, the lowest value was for calving interval in a Romosinuano cattle population, with a value of 0.02 (Ossa *et al*., 2021b). In other traits, such as services per conception, values of 0.08 were reported in Holstein cattle (Solarte *et al*., 2012), while birth and weaning weights of offspring reported higher values of 0.11 and 0.19, respectively (Donicer *et al*., 2009). These reports would indicate a limitation in selecting young animals considering the phenotypic performance of their initial measurements.

The estimation of variance components in Colombian populations has also included the use of genomic information, mainly through the single-step genomic best linear unbiased prediction (ssGBLUP) methodology, generating a relationship matrix that combines pedigree and molecular information. The reports in Colombia are scarce and the evidence generated is that the genomic information did not produce important changes in the estimation of heritability, at least for traits associated with beef production such as weighing at different ages, milk production, age at first calving. and calving interval (Amaya et al., 2019; Amaya et al., 2020a; Ramírez et al., 2020).

The number of animals with genomic information in those evaluations ranged from 718 to 1224, with a genotyping density of 30106 and 50932 molecular markers, respectively. These results may be partially explained by the conditions of the genotyped animals, which usually do not have a significant number of offspring with phenotypic records, reducing the benefit of using genomic information for genetic estimates. Another factor to consider is that usually most animals genotyped in Colombian populations are females with few progenies with phenotypes, which further limits the opportunity to obtain a pedigree with a greater number and magnitude of genetic relationships.

Genetic evaluation and selection indexes

In quantitative genetics, the use of statistical methods allows scientists to obtain not only an estimation of the genetic variances but also the empirical best linear unbiased predictor, which is a quantity associated to the breeding values of each parent. The breeding value of a parent can be defined as the capacity due genetic factors to modify an overall mean under a specific population, meaning its assessment varies over time and space.

Genetic evaluations can be classified as uniracial if the target population belongs to a single genetic group, and multiracial if the population belongs to various genetic groups or crossbred animals (Elzo, 2007). Regardless of whether the evaluation is uniracial or multiracial, selection decisions should preferably be based on a combination of several economically important traits, which may be phenotypically and genetically related (Mrode, 2014). Subsequently, breeding values are used to construct a selection index that considers the economic weight of each trait. These indexes are the best methodology for increasing genetic progress of multiple traits simultaneously within a population.

In Colombia, most genetic evaluations have been developed using uniracial methodology. However, more than 90% of the cattle destined for meat and milk production in the country could have a multiracial genetic composition (Elzo, 2011). Elzo *et al*. (1997) suggested a strategy to implement a national genetic evaluation program in cattle. However, since then, scientific and technical publications on multiracial evaluations have been scarce and isolated in the country. The conclusion in all the consulted studies was the same. Multiracial evaluations are a more objective method of selection given our production context; however, the amount of phenotypic information available is extremely low, resulting in biases in the selection processes. In Colombian cattle production systems, data collection, even if not widespread, is a more prevalent practice among farmers who manage uniracial populations than among those who use crossbred animals. This condition further limits the implementation of multiracial evaluations in the medium and long term.

Regarding uniracial genetic evaluations, the breeds with the largest participation in Colombian livestock are foreign, primarily Brahman, Holstein, Jersey, Normando, and Simmental. On the other hand, Colombian Creole cattle breeds (Blanco Orejinegro, Romosinuano, Hartón del Valle, Costeño Con Cuernos, Casanareño, Sanmartinero, Chino Santandereano) are the populations that have the highest number of studies in the field of genetics to date. This is consistent with AGROSAVIA and some Colombian universities having the direct responsibility to research, conserve, and disseminate these genetic resources.

The traits included in genetic evaluations appear to be universal across breeds. Among the most studied for meat production are daily weight gain and weights at different ages, such as birth weight, weight at 120, 240, 365, 480, and 720 days of age (Amaya *et al*., 2020a; Martínez *et al*., 2018; Ramírez *et al*., 2020; Ossa *et al*., 2021a; Ramírez *et al*., 2021). Few studies have evaluated carcass quality traits such as backfat thickness, loin eye area, and hip fat thickness (Jiménez *et al*., 2010). For milk production, there were more reports, evaluating variables such as milk yield, fat and protein production, linear classification, and somatic cell count (Cerón *et al*., 2001; Echeverri *et al*., 2014; Múnera *et al*., 2014; Amaya *et al*., 2019; Rincón *et al*., 2015; Solarte *et al*., 2012). The most explored reproductive traits were age at first calving, calving interval, and services per conception (Amaya *et al*., 2020a; Caivio-Nasner *et al*., 2021; Ramírez *et al*., 2021; Restrepo *et al*., 2008).

Although there is a wide range of populations and traits evaluated, it is important to highlight the most significant limitations that seem to be common to all the studies consulted. The utility of genetic evaluations depends on the accuracy with which breeding values are estimated. However, based on the experience of researchers, the precisions are often low (<0.5) in most evaluations. The precision of breeding values depends on several factors, such as the heritability of the trait (which mainly depends, among other factors, on the genetic diversity and homogeneity of the productive systems where it is evaluated), the accuracy of the parents of the evaluated animal (which depends primarily on the number of offspring), the availability of phenotypic, genealogical, and genomic records of the animal (i.e., complete information per animal), non-genetic effects considered in the models (quantification of the productive system and environmental variables), and the genetic correlations with other traits included in the evaluation.

In relation to the number of available records, according to the literature review, this could be the factor that contributes the most to low accuracies. Only two studies had more than twenty thousand records. Although this number of records is not negligible, its effect is diluted in the models when considering non-genetic aspects such as year, birth season, farm, sex, parity number, among others. Another important aspect is the climatic and management heterogeneity of local herds, which further complicates capturing sources of variation to adjust phenotypic values and improve the precision of breeding values. A last aspect, of equal importance, is the genetic connectivity required in genetic evaluations, which is usually low in Colombian herds and is also not evaluated a priori for the development of genetic evaluations, further limiting estimations and corrections for non-genetic effects (Kennedy y Trus, 1993).

In recent years, efforts have been made in Colombia to incorporate the concept of genomic selection. The breeds in the country with the most scientific evidence at the moment are Brahman, Simmental, Holstein, Blanco Orejinegro and Romosinuano (Bejarano et al., 2018; Martínez et al., 2018; Amaya et al., 2019; Zambrano et al., 2019). The number of animals with genomic information in the Brahman breed did not exceed 1700 animals and in the other breeds 1000 animals. Even reports on the Holstein breed do not exceed 150 animals. Although the accuracies of the breeding values for animals with genomic information could improve, the change is minimal or absent for the rest of the population included in the genetic evaluation. This context limits the use of genomic information in genetic improvement programs on a national scale.

Although there are numerous statistical methodologies to incorporate genomic information in genetic evaluations, all of them require a robust reference population with phenotypic and genomic information. Goddard and Hayes (2009) showed the relationship between the number of animals required in the reference population and the accuracy of breeding values for animals without phenotype in a genomic program. Considering traits with medium heritabilities (0.3), we would need at least 4500 animals in the reference population so that the precision of the estimation of genetic values in animals without phenotype is approximately 0.5. In this context and given the theoretical requirements of genomic selection, the benefits in Colombian populations could occur, but in the long term and through a strong practice of farm record-keeping. Although researchers and farmers have proposed the inclusion of foreign genotyped populations, its use must be analyzed in detail and caution, given that genomic estimates, like quantitative estimates, will depend on the genetic structure of each population and environments conditions in which animals perform.

Environmental effects also require attention within genetic evaluations, especially when the response of a genotype may be different according to the environment. Studies in Colombia that evaluated this effect are scarce (Cerón et al., 2004; Arboleda Zapata et al., 2010; Toro-Ospina et al., 2023). Cerón et al. (2004) and Toro-Ospina et al. (2023) evaluated the genotype-environment interaction of Holstein cattle in Colombia and Brazil. Although the evaluation of this effect between countries is important for decision-making in the use of imported semen, the evaluation of the environment and genotypes could be more important within Colombia given the high heterogeneity in the systems, not only at the climatic level but zootechnical management. The only report found that evaluated the interaction of genotypes and environments within the country was the one carried out by Arboleda Zapata et al. (2010), however, its use for decision-making at a national scale is very limited given that the data came from a single livestock company.

Once all the aspects described above are considered, the models used to estimate breeding values can be unitrait or multi-trait, but the most recommended methodology is a multi-trait evaluation. One of the main advantages of this approach is increasing the accuracy of breeding values, which is particularly beneficial for traits with low heritability (Mrode, 2014). However, genetic evaluations published in Colombia tend to be unitrait, mainly due to the low number of records and incomplete pedigrees (sometimes with inconsistencies), leading to numerical issues in multi-trait model algorithms.

Once breeding values are obtained, a common practice is to combine all the breeding values into a single value, a methodology known as selection index, which is theoretically the most efficient method (Hazel y Lush, 1942). The application of this methodology requires fulfilling two assumptions: estimating breeding values using multi-trait models and estimating economic values. However, most published genetic evaluations come from single-trait models, and what is more concerning, they do not include economic analyses for the traits and its expected genetic progress.

Several selection indexes have been reported in the literature for cattle populations in Colombia (Restrepo *et al*., 2008; Betancur-Zambrano *et al*., 2012; Agudelo-Gómez *et al*., 2016; Amaya *et al*., 2020b; Amaya *et al*., 2021; Ramírez *et al*., 2021; Amaya *et al*., 2022). Methodologies for estimating the weights have been primarily regressions, principal component analysis, and relative importance considering the phenotypic variance of the traits. Economic approaches for their estimation have also been used, however, there are only two articles of this type to date (Amaya *et al*., 2020b; Amaya *et al.,* 2022).

The use of these indexes is limited because they do not consider all the traits that the farmers wish to improve. The indexes included between three and eight productive traits (Agudelo-Gómez *et al*., 2016; Amaya *et al.,* 2022), but they are often very focused on a group of variables. For example, for populations whose zootechnical objective is meat production, it was identified that weighting at different ages accounted for 71-75% in the construction of the indexes (Ramírez *et al.,* 2021; Agudelo-Gómez *et al.,* 2016). For populations with a milk production objective, volume and quality of the milk accounted for 50-66% of the traits included in the indexes, with the remaining variables being associated with reproductive performance (Betancur-Zambrano *et al.,* 2012; Amaya *et al.,* 2021).

Traits associated with adaptation, longevity, and product quality stand out in production systems due to their economic importance, but their weighting and inclusion in indexes are virtually non-existent in Colombia. It is important to design more robust information systems that allow for the evaluation of these traits and their inclusion in indexes. An additional limitation is that given the heterogeneity of production systems in Colombia, the proposed weightings would not apply to all farmers, so it is necessary to characterize the production systems and offer recommendations based on the productive context of each type of systems.

In Colombia, some breeders' associations have incorporated indexes into the catalogues of imported bulls based on the country's productive and economic realities. These indexes include milk production traits, anatomical conformation, mastitis resistance, and reproductive efficiency. However, the breeding values used for the index are still those obtained for European populations, and there is no scientific evidence regarding the methodologies used for estimating the economic weights. While the proposed indexes for some populations in Colombia could be useful in genetic improvement programs and serve as a guide for some farmers, technical limitations such as the precision of breeding values, the inclusion of a greater number of traits, and their economic analysis are aspects that need to be investigated.

Economic evaluation and genetic variability

The real objective of selection is to change the population in a certain desired direction, rather than maintaining a group of traits within an optimal range (Simianer *et al*., 2023). These changes must be evaluated economically, considering that the farmers' real interest is the increase in economic utility, not the phenotypic change of traits.

According to this literature review, there are few scientific papers that include economic aspects for the construction of selection indexes, but no studies related to the economic evaluation of genetic progress were found. While the academic community has estimated genetic and phenotypic trends (Vergara *et al.*, 2016; Ramírez *et al*., 2020; Ossa *et al.,* 2021a), the results are inconclusive due to limitations in the precision of estimated breeding values and also did not include economic analysis. Although phenotypic changes in traits of zootechnical interest have been reported, it is unknown whether these changes have resulted in an increase or a decrease in profit for farmers. Research in this field is an immediate need to evaluate the selection processes that have been carried out in the different cattle populations of Colombia. An interesting example to use as a reference is the structure of the breeding scheme in New Zealand. The selection of dairy cattle relies on a selection index that considers nine traits associated with milk production, milk quality, resistance to mastitis, reproductive efficiency, and adult live weight. Genetic progress is estimated in dollars and considers the simultaneous change in all traits. For the period from 2013 to 2023, the genetic gain measured by the annual changes in the index reported an economic average gain of 14.93, 17.82, and 7.98 New Zealand Dollars for the Jersey, Holstein, and Ayrshire populations, respectively (DairyNZ, 2023). This index reflects the potential of breeders to produce offspring whose productive performance is as profitable as possible. It is necessary to have a mechanism in Colombia to evaluate the economic improvement of systems due to the use of genetic selection tools.

Finally, breeding programs must ensure the maintenance or minimal reduction of genetic variability. One of the most widespread criteria for assessing genetic diversity in a population has been the estimation of inbreeding rate. According to FAO (2013), the acceptable rate of inbreeding increase per generation depends on the population status and characteristics of each species. Recommendations range from values less than 1% in populations at risk of extinction to a maximum of 2% in commercial breeds. Assessments of genetic variability have been more widespread in Colombian Creole cattle populations (Martínez *et al*., 2008; Martínez *et al*., 2023). In specialized breeds, reports exist for Simmental, Normande, and Holstein breeds (Rodríguez *et al*., 2017; Amaya *et al*., 2020c; Betancur-Zambrano *et al*., 2022).

For Colombian Creole breeds, the results have varied depending on the population evaluated. Bejarano *et al*. (2018) reported high correlations between genetic markers (SNP) at 70 to 100 Kb in a conservation nucleus of AGROSAVIA for Blanco Orejinegro cattle. Ocampo et al. (2020) estimated an effective population size of 124 animals and an increase of 0.4% in inbreeding rate per generation, meeting the FAO recommendation (<1%). Caivio-Nasner *et al.* (2021b) also estimated an effective population size of 123 for this breed.

Valderrama *et al*. (2021) evaluated the genetic structure of three populations of Blanco Orejinegro cattle, differentiated by their zootechnical purpose (germplasm bank, genetic improvement program, commercial farmers). As expected, the effective population size for animals categorized as part of the commercial farmers was high (400), but much lower for the improvement program and germplasm bank (<150). While comparing variability estimates can be complex due to differences in databases and methodologies (genealogical, genomic, or both), there is a trend in the results indicating acceptable variability in these genetic resources, except for the Sanmartinero breed, which had the lowest reported effective population size of only 27 animals (Martínez *et al.,* 2008).

The maintenance of variability in Creole resources may be attributed to controlled mating programs, where there is a rotation of males among families of each breed in designs known as rotational mating schemes, minimizing the loss of variability despite being closed populations. For foreign breeds, mating decisions should be simpler due to a wider availability of genetic material worldwide. However, breeders often focus on the massive and indiscriminate use of a small group of sires in the artificial insemination programs, leading to a loss of genetic variability in the population.

In the Colombian Cebu population, inbreeding levels of up to 15.5% have been reported (Martínez *et al*., 2008). In taurine breeds, studies based on genealogical information have been extended to the Simmental and Normande populations. Reports on Simmental cattle indicate that 51.8% of the population has a non-zero value for inbreeding (Amaya *et al.,* 2020c). For the Normande breed, despite analysing a pedigree of 77311, the effective population size estimated ranged between approximately 118 and 139 animals (Rodríguez *et al*., 2017). This same scenario, although not evidenced in scientific publications, could be occurring in other foreign breeds in the country such as Holstein, Jersey, Ayrshire, where the massive use of a low number of sires leads to a higher probability of matings that generate inbreeding. An additional problem, mainly in foreign breeds, is the lack of genealogical records in most commercial herds, further limiting the estimation of parameters of genetic structure and diversity. While cattle breeders' associations require the genealogy of each animal for registration, most breeders are not affiliated with these associations, increasing the complexity in collecting information to evaluate genetic variability and progress.

Crossbreeding

Although crossing systems are not within the structure of a genetic improvement program for a pure population, their use in animal breeding allows greater profit given the effect of heterosis. Technically, crossings must be carried out between individuals from populations that were subjected to genetic selection, as currently occurs on a massive scale in poultry and pig farming. In Colombia, the benefit of crossbreeding has been explored through mating animals of different breeds, but without any selection criteria based on the genetic merit of the individuals. This condition significantly limits the objective quantification of heterosis in studies carried out in Colombia. However, the most representative research will be presented and discussed in this review.

Studies in Colombia methodologically designed to evaluate non-additive genetic effects in crossing schemes have just been done by Elzo et al. (2001) and Martínez et al. (2012). In the first study, an incomplete diallelic scheme was designed that considered the Zebú and Sanmartinero breeds, including animals born between 1971 and 1996, evaluating birth weight, weaning weight and weight gains. However, the results were obtained in experimental farms, which differs significantly from the management practices of commercial farmers. In this same study, the authors recommended expanding these analyses in commercial herds, but to date, studies were not found on a national or commercial scale. In the second study, Martínez et al. (2012) used 37 bulls from 9 breeds (Braunvieh, Limousin, Normando, Simmental, BON, Romosinuano, Gray Brahman, Red Brahman and Guzerat) in 352 Brahman cows. This study was carried out in the Cesar region during the years 2008 and 2009. The traits evaluated were weighings, loin eye area and back fat thickness at different ages. Although the main objective of the study was the estimation of non-additive genetic effects, the study concluded that although it was carried out in commercial herds, the number of animals included per genetic group was low (between 22 and 100 animals), therefore the errors in all parameters were high, recommending an estimation based on larger populations for more efficient decision making. However, as for the study by Elzo et al. (2001), no reports have been generated to date with a significantly higher number of animals and on a commercial scale.

Other studies carried out in Colombia, with less impact on the evaluation of crossbred animals, have been carried out from historical databases of animals whose parental breeds were Angus, Zebu, BON, Romosinuano, Holstein and Senepol (Madrigal et al., 1998; Arango et al., 2000; Martínez et al., 2011; Quijano et al., 2000). The number of animals in these studies varied between 10 (milk production per lactation) and 15256 (birth weight). However, the databases were from one or a maximum of four farms, limiting the inference about the genetic parameters of crossed animals and their benefits in commercial-scale crossing schemes. Furthermore, the evaluations have been more focused on productive comparison than on the estimation of non-additive genetic effects.

Elzo (2006) describes that the multiracial databases available in countries that carry out productive monitoring are characterized by: 1) having an extremely unbalanced structure, 2) a large number of parental breeds represented (many of them with very little information), and 3) a large percentage of production and pedigree records with incomplete information. The collection of this information has been the product of articulated work between associations of pure cattle breeders and associations of breeders of commercial producers. Although in Colombia there are associations of pure cattle breeders, there is no official association for commercial breeders that carries out productive control of crossed animals.

Pure cattle associations currently lead programs related to genealogical registration and to a lesser extent the productive control of animals. However, logistics still depend a lot on the intention and reports given by affiliated farmers, who are a minority compared to those commercial farms that are not affiliated. In this context, the role of associations in data analysis for genetic decision-making at the national level would require greater articulation between government entities, livestock breeders' associations, and commercial farmers. Meanwhile, the isolated efforts of farmers, researchers, private and public entities will hardly allow the optimization of cattle production systems through the use of genetic improvement technology.

Conclusion

The design and development of a genetic improvement program require breeding objectives, information systems, variance components, genetic evaluations, selection indexes, and genetic variability. In light of this literature review, the major challenges currently could be related to 1) discussing the definition of breeding objectives with farmers and breeders' associations, 2) improving both the quality and quantity of information available in current databases, and 3) addressing the lack of economic analyses in genetic evaluations. In this context, decision-making to implement and direct genetic improvement programs becomes a challenge, which can only be overcome through coordinated and ongoing work among farmers, cattle breeders' associations, and researchers. Finally, it is important to consider the heterogeneity of production systems for some breeds, which must be somehow incorporated into the genetic selection procedures of Colombian cattle, as in other regions (Europe or North America), this issue either does not exist or does not significantly influence the outcome of genetic evaluations.

Declarations

Acknowledgments

The authors would like to express their gratitude to all those who have contributed in one way or another to the development of research in the field of animal breeding and genetics in Colombia. The research carried out by all of them has made this publication possible. Although we have achieved key results for optimizing genetic selection of cattle in Colombia, we still have many challenges to explore and improve as an academic and productive community.

Funding

This study was funded by Universidad de Ciencias Aplicadas y Ambientales U.D.C.A (Colombia) and Universidad Nacional de Colombia, Sede Medellín (Colombia)

Conflicts of interest

The manuscript was prepared and reviewed by the authors, who declare that there is no conflict of interest.

Author contributions

Alejandro Amaya: Information search, writing, and review of the article. José-Miguel Cotes-Torres: Writing and review of the article.

Use of artificial intelligence (AI)

No AI or AI-assisted technologies were used during the preparation of this work.

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