Genetic improvement of cattle in Colombia, an ideal or a reality?

Mejoramiento genético de ganado en Colombia, ¿un ideal o una realidad?

Melhoramento genético do gado bovino na Colômbia, um ideal ou uma realidade?

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Abstract

Background: Genetic improvement programs in domestic species require a series 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 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 lack of consensus on 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 on databases. Finally, conducting economic analyses that consider genetic parameters is essential for optimizing the response to genetic selection, taking into account the different production 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 una serie 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 y la variabilidad genética. **Objetivo:** Identificar fortalezas y debilidades 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 entre los productores y asociaciones. Asimismo, es necesario, a corto plazo, mejorar tanto la calidad como la cantidad de información disponible en las bases de datos. Finalmente, es fundamental suplir la falta de evaluaciones económicas que integren y se incluyan en los análisis genéticos para optimizar la respuesta a la selección genética, considerando los distintos contextos productivos y la diversidad de condiciones ambientales 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 necessário definir objetivos de melhoramento, possuir sistemas de informação eficientes, 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 fragilidades e fortalezas no desenho e implementação de programas de melhoramento genético para gado bovino na Colômbia, por meio de uma revisão dos avanços científicos e acadêmicos obtidos na pesquisa sobre essa área no país. **Conclusão:** O principal desafio encontrado foi a ausência de objetivos de melhoramento definidos coletivamente entre produtores e pesquisadores. Além disso, é necessário, no curto prazo, aprimorar tanto a qualidade quanto a quantidade das informações disponíveis nos bancos de dados. Finalmente, torna-se essencial realizar análises econômicas que considerem o componente genético, a fim de otimizar a resposta à seleção genética, levando em conta as diferenças entre os sistemas produtivos e a diversidade ambiental que a Colômbia possui.

Palavras-chave: *criação de animais; fenótipo; gado; genética quantitativa; melhoramento genético; progresso genético; seleção; rentabilidade econômica; 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 to enhance the average zootechnical performance of the herd (Henderson, 1975).

In domestic animals, poultry is possibly the most successful case of implementing genetic improvement programs. Zuidhof et al. (2014) reported phenotypic gains exceeding 350% in slaughter weight due to genetic selection in poultry. The response to selection in cattle has not been as pronounced as in poultry. However, the genetic gains are still significant. For example, the American Angus Association (2024) reported an 85 kg genetic difference in weaning weight between animals born in 1972 and 2023. In Holstein cattle in the United States, García-Ruiz et al. (2016) estimated a genetic gain over 1,500 liters of milk per lactation. In grazing-based cattle systems, a genetic increase of 13.6 liters/cow/year was reported in pure and crossbred Holstein cattle in New Zealand between 2000 and 2020 (López-Villalobos et al., 2021). This genetic progress could further increase in the medium term due to the use of genomic information in selection programs, which reduces the generation interval and enhances the accuracy of the estimated genetic merit, leading to an accelerated genetic gain (Schaeffer, 2006).

Examples of genetic progress resulting from selection strategies are numerous and varied in the literature. However, all successful cases have a common procedure comprising five steps: (1) definition of breeding objectives, (2) phenotypic and genotypic information systems, (3) estimation of variance components, (4)

genetic evaluation and selection indexes, and (5) economic evaluation and genetic variability (Garrick and Golden, 2009). This framework allows breeders and scientists to grasp, at first glance, that implementing a breeding program is a demanding task, both technically and logistically.

In Colombia, research efforts have primarily focused on the second, third, and fourth steps. Consequently, there is a lack of studies addressing the first and fifth steps (in some cases, none) for the implementation of genetic improvement programs. Enhancing these aspects would improve not only the primary production but also the processing industry at both meat and dairy levels. Additionally, strengthening these aspects could facilitate the incorporation of innovative genetic selection tools, such as genomic information for the early identification of superior individuals and the improvement of polygenic traits that are complex to measure (feed efficiency, carcass quality, disease resistance, among others). Currently, these traits cannot be effectively selected or evaluated in Colombian populations due to the absence of large-scale phenotypic data.

On the other hand, although a significant portion of the national herd consists of crossbred animals, this review does not include the analysis of genetic aspects in these populations due to a lack of long-term scientific evidence over time. However, reports on crossbred populations in Colombia are discussed and included at the end of this review. Similarly, evaluating genetic improvement programs in Colombian dual-purpose systems is challenging given that scientific studies assessing phenotypes or productivity indicators from a dual-purpose perspective are almost nonexistent. Only one study, conducted by Galeano and Manrique (2010), evaluated genetic aspects through an index that assesses females based on milk production, weaning weight of offspring, and calving interval.

Therefore, the objective of this review was to identify the weaknesses and strengths in the genetic management of specialized dairy and beef breeds used in Colombia. Furthermore, this review aims to encourage the academic community and farmers to continuously optimize the efficiency of livestock systems through genetic improvement applications. This work also seeks to help readers identify areas of genetic science that remain unexplored. Additionally, efforts should be directed towards strengthening the design and implementation of robust genetic improvement programs to enhance 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 implementing a genetic improvement program (Wolfova et al., 2005). Its purpose is to increase profitability within the production cycle and must be redefined as production and market conditions change (Byrne et al., 2016). Based on our literature review, there are no studies of this type focusing on cattle in Colombia. The absence of this knowledge in Colombia could be attributed to some practical and scientific reasons outlined below.

In Colombia, the traits evaluated in selection programs have mainly been limited to characteristics such as age at first calving and calving interval (Amaya et al., 2020a; Rocha et al., 2012; Ramírez et al., 2021), as well as weights at different ages, weight gains (Ramírez et al., 2020; Amaya et al., 2020a), and milk production (Restrepo et al., 2008; Solarte and Zambrano, 2012; Echeverri et al., 2014; Rincón et al., 2015; Amaya et al., 2019). However, in animal production, the characteristics that most affect profitability can 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 traits could generate negative effects in the short term, mainly due to increasing 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). However, these studies are based on a small number of records (Ramírez et al., 2021; Amaya et al., 2021; De León et al., 2021). As a result, it is common to encounter numerical computational problems when estimating bi-trait and multi-trait models, as the algorithms struggle to achieve convergence.

Another important trait is feed efficiency, which has not been evaluated but is economically vital for animal production as it represents the highest variable cost within the industry. Heritability estimates for this trait range from medium to high (0.35-0.55, Schenkel et al., 2004). However, its measurement presents the following challenges: (1) it is difficult to measure on a large scale, (2) it requires knowledge of its correlations with other traits included in the breeding objective, and (3) it is costly due to the need for individual monitoring. One potential strategy to address these challenges is genomic selection. However, its implementation in Colombia faces obstacles due to the significant financial resources required and the necessity of high-quality phenotypic databases. Pryce et al. (2014) suggested combining genomic platforms across different populations. For foreign breeds, this alternative may be feasible due to the genetic connectivity resulting from the massive use of imported bulls in artificial insemination. However, for Creole breeds, this approach would not be viable.

These challenges highlight the urgent need to establish breeding objectives. To achieve this, it is crucial to consider local production needs, market conditions, and the high heterogeneity of production systems in tropical environments. This last factor represents an additional challenge when compared to countries with temperate climates, where production conditions and systems tend to be more uniform.

Information system and selection criteria

Selection criteria refer to those traits that contribute to the improvement of breeding objectives. An ideal selection criterion must meet three requirements: (1) be easy to measure, (2) have medium or high heritability, and (3) exhibit a high genetic correlation with the breeding objective (Ponzoni and Newman, 1989). The most favorable scenario is when the selection criterion also serves as a breeding objective.

At this point, breeders' associations play a fundamental role in collecting phenotypic records and developing information systems that ensure the success of breeding programs. However, there are two main limitations: (a) it is common for Colombian farmers not to keep records or report them to the association, and (b) some Colombian farmers perceive the costs of affiliation and registration as high or unnecessary, resulting in a significant amount of data not reaching the association. These conditions severely limit access to large and reliable databases. Nonetheless, some published research has emerged from joint efforts between the academic community and breeders' associations, although in most cases, it is limited to estimating genetic parameters.

In Colombia, cattle production is categorized into three main systems: (1) specialized milk production, (2) breeding and fattening production, and (3) dual-purpose production. Regarding milk production, most reports focus on Holstein, Jersey, and Simmental breeds (Solarte and Zambrano, 2012; Rincón et al., 2015; Zambrano et al., 2015; Amaya et al., 2019). For meat production, there are more reports on Blanco Orejinegro, Romosinuano, Brahman, and Simmental breeds (Martínez et al., 2018; Amaya et al., 2020a; Ramírez et al., 2020; López et al., 2021). The main reproductive traits evaluated have been age at first calving, calving interval, and open days (Table 1).

Estimates for milk production have been primarily conducted on the first three lactations. The number of cows in these studies ranged from 620 to 7,723, with heritability estimates between 0.02 and 0.28 (Amaya et al., 2019; Múnera et al., 2014; Rincón et al., 2015). While there are accurate estimates, many studies present errors that hinder the ability to make appropriate selection decisions, ultimately affecting genetic progress. For traits related to product quality, the estimates were even less precise, both for milk and meat, with heritability errors of up to 0.32 for protein and fat, and with breeding value accuracies below 0.5 for loin eye area and back fat (Rincón et al., 2015; Asocebú, 2022).

The collection of quality-related data is often dependent on external funding, which limits the development of a robust and permanent information system. For example, between 2014 and 2016, the official dairy control program at the national level was a joint initiative involving the Unión Nacional de Asociaciones Ganaderas (UNAGA), the Ministerio de Agricultura, and FEDEGAN. This initiative provided valuable data, enabling breeders to establish an initial information system to evaluate criteria such as milk protein and fat percentage. However, these efforts have not been maintained since then, at least not at the scale necessary for developing reliable genetic evaluations.

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

Source	Breed	Selection criteria	Animals	Records	Heritability
Amaya et al. (2020a)	Simmental	AFC	3063	3063	0.20
		CI	1098	1098	0.04
Betancur-Zambrano et al. (2012)	Holstein	MY	1198	2372	0.21
		MF	1198	2372	0.14
		MP	1198	2372	0.14
Caivio-Nasner et al. (2021a)	Blanco Orejinegro Holstein	CI	3308	3308	0.11
Cerón-Muñoz et al. (2001)	Holstein	MY	25608	69464	0.20
Cerón-Muñoz 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 Orejinegro	AFC	1256	1256	0.15
		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.

Carcass quality and reproduction traits

Carcass quality traits face a similar scenario. The Brahman breed, which has the highest presence as a purebred for meat production in Colombia, was the first to undergo genetic estimates for carcass quality in 2010, based on approximately one thousand phenotypic records (Jiménez et al., 2010). The genetic evaluation conducted by Asocebú in 2022 included 10,332 records for loin eye area and back fat thickness. However, the accuracy for most selection candidates remained below 0.5. This underscores the urgent need for continuous efforts in updating information systems. The development of emerging technologies such as sensors, cameras, and microphones could partially address these obstacles, accelerating data collection and strengthening genetic evaluations for these traits.

Reproductive traits have been less explored, with research mainly focusing on calving interval and age at first calving (Rocha et al., 2012; Vergara et al., 2016; Amaya et al., 2020a;

Ramírez et al., 2021). While these two traits are directly linked to reproductive performance, management practices in Colombian production systems may deviate slightly from that focus. Age at first calving could serve as an indirect indicator of puberty age or the rate at which a female reaches sexual maturity. However, in Colombian cattle farming, this trait depends more on growth rate, as farmers prioritize weight over age when deciding the first service.

On the other hand, recording calving interval presents two major challenges; firstly, a preferential treatment for certain females may confound the genetic effect with environmental advantages, even when farm and year effects are accounted for in the model. Secondly, 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,

reconsidering the reproductive component in Colombian cattle by focusing on traits that are less affected by management practices or production conditions could be beneficial.

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 the restricted maximum likelihood methodology. Although there are other methodologies, such as Bayesian inference for variance component estimation, its application in Colombia is scarce, and as far as our search indicates, 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 focused on Holstein, Simmental, and Jersey dairy cattle breeds. The reported heritabilities for these traits range from 0.01 for somatic cell count to 0.46 for fat and protein production. Average heritabilities (0.2-0.4) are 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) range from 0.09 to 0.38 (Ossa et al., 2021a; Martínez et al., 2018), with lower heritability values 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 from 0.29 to 0.37; however, the reported errors for these estimations were higher (Jiménez et al., 2010) due to the 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 range between 0.0 and 0.15 (Rocha et al., 2012; Caivio-Nasner et al., 2021a). The lack of these estimations in Colombia could be due to the information systems implemented on farms, where farmers show greater interest in variables directly associated with the final product (meat and milk). Although most variables associated with reproduction are easily measurable and highly economically important (Amaya et al., 2020a; 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 varies from 620 to 25,608 cows (Cerón-Muñoz et al., 2001; Amaya et al., 2019). Regarding the number of animals included in the relationship matrix, populations range from 801 to 27,986 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 may 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 for the estimation of variance components and the genetic merit of animals.

The reports of genetic correlations are more diverse. For example, one correlation of interest is between age at first calving and calving interval. In the Simmental breed, this correlation was positive (0.25; Amaya et al., 2020a), which is favorable 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 issue could be addressed through the identification of animals whose breeding values are favorable for both traits, genetic progress would be slow, and the change in correlation could take place but only in the long term, hindering genetic gains and balanced selection. For this reason, the 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 and Zambrano (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 is proportionally associated with lower total solids content in milk. No reports of positive correlations between milk quantity and quality 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 are 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 to measure these traits should be increased by farmers and associations.

Regarding repeatabilities, the number of reports is lower than that found for heritabilities. The variables analyzed include birth and weaning weights of female offspring, calving interval, milk production, and services per conception (Montes et al., 2009; Rocha et al., 2012; Solarte and Zambrano, 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 and Zambrano, 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 and Zambrano, 2012), while birth and weaning weights of offspring had higher values of 0.11 and 0.19, respectively (Montes et al., 2009). These reports suggest a limitation in selecting young animals based on 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

indicates that genomic information did not produce significant changes in the estimation of heritability, at least for traits associated with beef production such as weight at different ages, milk production, age at first calving, and calving interval (Amaya et al., 2019; Amaya et al., 2020a; Ramírez et al., 2020).

In those evaluations, the number of genotyped animals ranged from 718 to 1,224, with genotyping densities of 30,106 to 50,932 molecular markers, respectively. One possible explanation is that most genotyped animals lacked enough offspring with phenotypic records, limiting the benefit of using genomic information for genetic estimates. Additionally, genotyped animals in Colombia are predominantly females with few progenies with phenotypes, further restricting the depth of pedigrees and the extent 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 genetic variance but also the empirical best linear unbiased predictor, which is a quantity associated with the breeding values of each parent. The breeding value of a parent can be defined as the ability of genetic factors to modify an overall mean within a specific population, meaning its assessment varies over time and space.

Genetic evaluations can be classified as single-breed if the target population belongs to a single genetic group, and multi-breed if the population belongs to various genetic groups or crossbred animals (Elzo, 2007). Regardless of whether the evaluation is single-breed or multi-breed, 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 across multiple traits simultaneously

within a population.

In Colombia, most genetic evaluations have been developed using single-breed methodology. However, more than 90% of the cattle destined for meat and milk production in the country have a multi-breed 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 multi-breed evaluations have been scarce and isolated in the country. The conclusion of all the consulted studies was the same: multi-breed evaluations are a more objective method of selection in 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 single-breed populations than among those who use crossbred animals. This condition further limits the implementation of multi-breed evaluations in the medium and long term.

Regarding single-breed genetic evaluations, the breeds with the largest participation in Colombian livestock are foreign, primarily Brahman, Holstein, Jersey, Normande, 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 for research, conservation, and dissemination of 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 have been more reports, evaluating variables such as milk yield, fat and protein production, linear classification, and somatic cell count (Cerón-Muñoz et al., 2001; Echeverri et al., 2014; Múnera et al., 2014; Amaya et al., 2019; Rincón et al., 2015; Solarte and Zambrano, 2012). The most explored reproductive traits include age at first calving, calving interval, and services per conception (Amaya et al., 2020a; Caivio-Nasner et al., 2021a; 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, precision is 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 production 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 for the animal (i.e., complete information per animal), the non-genetic effects considered in the models (quantification of the system and environmental variables), and the genetic correlations with other traits included in the evaluation.

Regarding the number of available records, according to the literature review, this could be the factor that contributes the most to low precision. Only two studies included 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, and 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. Another aspect, of equal importance, is the genetic connectivity required for genetic evaluations, which is usually low in Colombian herds and is also not evaluated a priori before the development of genetic evaluations, further limiting estimations and corrections for non-genetic effects (Kennedy and 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 so far 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 1,700 animals, and in the other breeds, it was fewer than 1,000 animals. Even reports on the Holstein breed had fewer than 150 animals. Although the accuracies of the breeding values for animals with genomic information may improve, the change is minimal or absent in 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 into 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 phenotypic data in a genomic program. Considering traits with medium heritability (0.3), we would need at least 4,500 animals in the reference population for the precision of the estimation of genetic values in animals without phenotypes to be approximately 0.5. In this context, and given the

theoretical requirements of genomic selection, the benefits in Colombian populations could occur, but only 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, their use must be analyzed in detail and with caution, given that genomic estimates, like quantitative estimates, depend on the genetic structure of each population and the environmental conditions in which animals are raised.

Environmental effects also require attention within genetic evaluations, especially when the response of a genotype varies according to the environment. Studies in Colombia that evaluated this effect are scarce (Cerón-Muñoz et al., 2004; Arboleda Zapata et al., 2010; Toro-Ospina et al., 2023). Cerón-Muñoz 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 regarding 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 also in zootechnical management. We found only one report evaluating the interaction of genotypes and environments within the country, conducted by Arboleda Zapata et al. (2010); however, its use for decision-making at a national scale is very limited because 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 single-trait or multi-trait, but the most recommended methodology is a multi-trait evaluation. One of the main advantages of this approach is an increased accuracy of breeding values, which is particularly beneficial for traits with low heritability (Mrode, 2014). However, genetic evaluations published in Colombia tend to be single-trait, 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 a Selection Index, which is, theoretically, the most efficient method (Hazel and Lush, 1942). The application of this methodology requires meeting two assumptions: estimating breeding values using multi-trait models and estimating economic values. However, most published genetic evaluations come from single-trait models, and more concerningly, they do not include economic analyses of the traits or their 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). The methodologies used to estimate the weights have been primarily regressions, principal component analysis, and relative importance based on the phenotypic variance of the traits. Economic approaches have also been applied, but to date, there are only two articles of this type (Amaya et al., 2020b; Amaya et al., 2022).

The use of these indexes is limited because they do not consider all the traits that farmers aim to improve. The indexes include between three and eight productive traits (Agudelo-Gómez et al., 2016; Amaya et al., 2022), but they are often highly focused on a specific group of variables. For example, for populations whose zootechnical objective is meat production, it was identified that weight at different ages accounted for 71-75% of the construction of the indexes (Ramírez et al., 2021; Agudelo-Gómez et al., 2016). For populations with a milk production objective, milk volume and quality 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 may 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 system.

In Colombia, some breeders' associations have incorporated indexes into the catalogs 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 to estimate 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 ultimate 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 economically evaluated, considering that the ultimate interest of farmers is increasing profitability, not just changing phenotypic traits.

According to our review, just a few scientific papers include economic aspects in 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 precision of estimated breeding values and absence of 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 urgently needed 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 average economic 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 production 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 is the estimation of the 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 below 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 cattle (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 the 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, and commercial farmers). As expected, the effective population size for animals categorized as part of the commercial farmers group 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, which involve 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 extensive and indiscriminate use of a small group of sires in artificial insemination programs, leading to a loss of genetic variability in the population.

In the Colombian Zebu 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 analyzing a pedigree of 77,311 animals, the estimated effective population size ranged between approximately 118 and 139 animals (Rodríguez et al., 2017). Although this same scenario has not been evidenced in scientific publications, it could be occurring in other foreign breeds in the country, such as Holstein, Jersey, and Ayrshire, where the extensive use of a small number of sires increases the 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 genetic structure and diversity parameters. While cattle breeders' associations require the genealogy of each animal for registration, most breeders are not affiliated with these associations, increasing the complexity of collecting information to evaluate genetic variability and progress.

Crossbreeding

Although crossbreeding systems are not within the structure of a genetic improvement program for a pure population, their use in animal breeding allows for greater profit given the effect of heterosis. Technically, crosses 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 that were methodologically designed to evaluate non-additive genetic effects in crossbreeding schemes have only been conducted by Elzo et al. (2001) and Martínez et al. (2012). In the first study, an incomplete diallel scheme was designed that considered the Zebu 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 differ significantly from the management practices of commercial farmers. In this same study, the authors recommended expanding these analyses in commercial herds, but to date, no studies have been found on a national or commercial scale.

In the second study, Martínez et al. (2012) used 37 bulls from nine breeds (Braunvieh, Limousin, Normando, Simmental, BON, Romosinuano, Gray Brahman, Red Brahman, and Guzerat) with 352 Brahman cows. This study was carried out in the Cesar region during 2008 and 2009. The traits evaluated were weight measurements, loin eye area, and backfat 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, and the authors recommended an estimation based on larger populations for more efficient decision-making. However, as in 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 based on 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 and Montoya, 2000). The number of animals in these studies varied between 10 (milk production per lactation) and 15,256 (birth weight). However, the databases came from one or a maximum of four farms, limiting the ability to infer the genetic parameters of crossbred animals and their benefits in commercial-scale crossbreeding schemes. Furthermore, the evaluations have been more focused on production comparisons than on the estimation of non-additive genetic effects.

Elzo (2006) describes that the multibreed databases available in countries that conduct productive monitoring are characterized by: 1) having an extremely unbalanced structure, 2) including a large number of parental breeds -many of them with very little information-, and 3) having a large percentage of production and pedigree records with incomplete information. The collection of this information has resulted from the collaborative work between associations of purebred cattle breeders and associations of commercial cattle producers. Although Colombia has associations of purebred cattle breeders, there is no official association for commercial breeders that monitors the productivity of crossbred animals.

Currently, purebred cattle associations lead programs related to genealogical registration and, to a lesser extent, the productive control of animals. However, logistics still depend largely on the willingness of affiliated farmers to report data, and these farmers are a minority compared to 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 coordination between government entities, livestock breeders' associations, and commercial farmers. Meanwhile, the isolated efforts of farmers, researchers, and private and public entities are unlikely to optimize cattle production

systems using 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 appear to 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 for implementing and directing genetic improvement programs becomes a challenge; one that 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, as this factor must be incorporated into the genetic selection procedures of Colombian cattle. In other regions such as Europe or North America, this issue either does not exist or does not significantly affect the outcome of genetic evaluations.

Declarations

Acknowledgments

Funding

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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