

Genetic structure of the Montana Beef Composite, a program to increase beef production in tropical and subtropical environments

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Abstract. The aim of this paper is to describe in detail the development, over 30 years, of a large-size composite cattle population, destined for meat production in challenging environments in the tropical and sub-tropical regions of South America. Montana cattle were developed using crosses between *Bos taurus* and *Bos indicus* animals, and here we present details regarding the evolution of the breed, both numerically and in terms of the racial composition of the animals, and we assess the levels of heterosis and recombination and the genetic structure of the breed. Overall, given the continuous introduction of external germplasm, Montana

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Composite cattle have retained high levels of heterosis while maintaining inbreeding at very low levels.

INTRODUCTION

Livestock production in Brazil has changed considerably in recent years, when compared with the situation reported by Ferraz and Felício (2010) some years ago. According to ABIEC (2023), the cattle herd in Brazil is around 202 million heads, with a growth of 3.3% compared to 2022, while the area dedicated to pastures declined by 5.7% over the same period, to 154 million hectares, with a significant increase in productivity and a stocking capacity of 1.32 head/ha. According to this publication, the Brazilian herd currently has around 58 million beef cows and 15 million dairy or dual-purpose cows, for a total of approximately 73 million cows of reproductive age.

Furthermore, according to ABIEC (2023), the estimated number of cattle slaughtered is 42.31 million, corresponding to around 10.79 million tons of carcass equivalent, with an average carcass weight of 255.13 kg. According to this source, the beef industry accounts for around 41.6% of Brazil's agribusiness GDP. Updated information from CEPEA (2024) shows that beef production in Brazil reached a record of 8.9 million tons in 2023, 11.2% higher than in 2022. Of the total number of animals slaughtered, around 18.2% were finished in confinement. Therefore, 71.8% of Brazilian production is carried out in extensive systems, with animals produced on pasture (ABIEC, 2023).

According to Baruselli (2023), estimates of cattle semen sales in 2022 were around 25.6 million doses, of which around 97.7% were used in fixed-time artificial insemination procedures. Translated into pregnancy rates, this technique has an average efficiency of 50%, which means that less than 13 million calves born were sired by semen from bulls maintained in artificial insemination centers. This figure is confirmed by the ASBIA (2023), which reports that around 26% of Brazilian beef cows are inseminated. Within this context and considering the average efficiency rates of the artificial insemination process in the country, around 87% of calves born are the result of natural mating. Considering the sale of semen from European breeds and the number of calves born to bulls of these breeds, it can be estimated that around 12 to 15% of calves born in the country are considered to be *Bos taurus* x *Bos indicus* crosses, with a small percentage of purebred *Bos taurus* in Southern Brazil, the rest being of the *Bos indicus* subspecies.

There is no doubt that organized crossbreeding is a very attractive alternative for increasing beef cattle productivity (Dickerson, 1969, Dickerson, 1973), as it allows a reduction in age at slaughter, improves reproductive efficiency and, thus, contributes to the sustainability of this industry (Gama et al., 2022, Snelling et al., 2022). In tropical environments, crosses with *Bos indicus* are very common, especially due to their adaptability to climate-related factors (Ferraz and Felício, 2010). The development of composite populations is one of the possible alternatives of adopting crossbreeding, because they can be managed as in purebred production systems, while at the same time exploiting the combination of additive effects of the breeds involved, and maintaining some of the benefits of heterosis (Koch et al., 1985). However, the effects of the gene combinations obtained when using crossbred breeding stock tend to be broken down in the formation of gametes, in what has been called *recombination loss* (Dickerson, 1969, Kinghorn, 1980),

and this can, to some extent, compromise the gains obtained by heterosis (Brotherstone and Hill, 1994).

Organized crossbreeding programs have not been very successful in Brazil, due to various reasons, including: i) the choice of genetic material that is unsuitable for the different production systems; ii) the technical difficulties of using artificial insemination, such as adequate facilities and human resources; iii) the lack of suitable production systems, especially the availability and quality of food and the greater needs of crossbred animals; iv) the lack of adaptability of bulls to tropical and sub-tropical environments.

Considering these limitations, and the numerous experiments conducted in the development of the *USDA Germplasm Project MARC types*, at the USDAMARC - Clay Center, USA (Gregory et al., 1985, Gregory and Cundiff, 1999), a group of beef cattle breeders decided to establish a program to form a population of composite cattle aimed at producing quality beef, without losing the adaptability of the animals (especially the bulls), with the ability to overcome the challenging climates of Brazil's largest beef producing regions, including the Southeast, Midwest and North of the country. Thus, the Montana Composite program was started in 1994, initially based on herds made up of crossbred cows, with a known and highly variable breed composition, as well as a large population of Nelore cows. The focus of the program was to increase the productivity of the animals, both in terms of reproductive efficiency, rapid growth and meat quality, based on the exploitation of the complementarity between breeds and retained heterosis, while maintaining the adaptability of the animals, through the balanced contribution of zebu and taurine breeds adapted over time to tropical conditions, allowing the use of composite bulls in natural matings in those regions, with better fertility and longevity than *Bos taurus* bulls.

There are several studies in the literature on the Montana Composite (Ferraz et al., 1999a,b; Mourão et al., 2007, 2008; Marson et al., 2008; Dias et al., 2011; Bueno et al., 2012; Petrini et al., 2012, 2015; Santana Jr et al., 2012, 2013, 2014; Bocchi et al., 2016; Peripolli et al., 2020; Grigoletto et al., 2019, 2020, Kluska, 2021). Preliminary studies on this population were presented at the 12th World Congress on Genetics Applied to Livestock Production, on reproductive traits (Gama et al., 2022) and growth (Ferraz et al., 2023), both addressing issues related to heterosis, recombination and the effects of biological types.

OBJECTIVE

This paper aims to describe the experience, started in 1994, of developing the Montana composite beef cattle population, to be raised in tropical and subtropical regions of South America. Based on accumulated information, we provide baseline information on the breed characteristics and describe the details of its formation, analyzing in detail its evolution in terms of census, racial composition and breed structure.

MATERIAL AND METHODS

The Montana Composite program was started with strict data control, specific norms regarding breed composition of animals and a genetic evaluation program, such that it was the first program in Brazil where it is mandatory for all animals to be genetically evaluated. From then on, only the top animals (maximum 30% of the crop) can be sold as breeding stock, in a program certified by the Ministry of Agriculture, Livestock and Supply,

called Special Certificate of Identification and Production (Certificado Especial de Identificação e Produção – CEIP).

In the framework of this program, data are collected regarding:

Productive traits

Identification of the animal, sire and dam
Birth weight, with corresponding date and management group
Weaning weight, with corresponding date and management group
Yearly weight, with corresponding date and management group
Scrotal circumference, with corresponding date and management group
Visual scores for conformation, precocity of finishing, muscularity, preputial sheath
Carcass assessment measurements at around 16 months, with ultrasound (ribeye area, backfat, rumpfat, marbling)

Reproductive traits

Age at first calving Calving interval Date of calving Cow annual productivity (kg calves/year) Longevity (Stayability)

In addition, genomic information has been collected in animals born over the last 13 years, and currently includes genotype information on nearly 4000 animals.

For this preliminary study, we obtained pedigree and phenotype information from the breed database and exported the files to carry-out the corresponding analyses. The information available in the database was used to display the geographical distribution of Montana cattle in Brazil.

Each animal in the program had its racial composition computed by breed (to 4 decimal places), considering the genetic background of the parents. Due to the wide diversity of the cows that started the program, and in order to facilitate the interpretation of results, in our analyses the founder breeds were grouped into four biological types: **N** (animals of *Bos indicus* origin, including the Brahman, Gir, Guzerath, Nelore, Sindi, Tabapuã and Tuli breeds), **A** (*Bos taurus* animals adapted to the tropical environment, where the main breeds were Bonsmara, Caracu, Romosinuano and Senepol), **B** (*Bos taurus* of British origin, such as Aberdeen Angus, Devon, Hereford, Red Angus) and **C** (*Bos taurus* of continental origin, such as Charolais, Gelbvieh, Limousin, Marchigiana, Simenthal), as described in Ferraz et al. (1999a, 1999b), and Ferraz et al. (2023).

For an animal to be considered Montana Composite, its biological type composition must be in the ranges defined in Table 1 (adapted from Sumário de Touros Montana, 2023); otherwise the animal is not registered as Montana.

The expected breed composition of all animals in the data set, computed from pedigree information, was used to evaluate how it has changed over time. These expectations were also used to compute the expected heterosis and recombination rate of every individual, following the procedures outlined by Dickerson (1969) and Van Raden

(2003). The expected heterosis and recombination rate in an individual, resulting from the heterozygous combination of breeds i and j, was computed as follows:

$$Het_{ij} = 1 - \sum_{i=1}^{n} (\alpha_i^s \times \alpha_i^d)$$
 (Eq. 1)

$$Rec_{ij} = 1 - \sum_{i=1}^{n} \frac{(\alpha_i^s)^2 + (\alpha_i^d)^2}{2}$$
 (Eq. 2)

where i and j represent two breed sources, while α^s and α^d represent the corresponding breed fraction in the sire and the dam, respectively.

Table 1. Required breed composition for an animal to be certified as Montana Composite.

Biological type	Minimum	Maximum
Number of breeds	3	No limit
Group N	0	6/16
Group A	2/16	14/16
Groups $N + A$	4/16	16/16
Group B	0	12/16
Group C	0	12/16
Groups B + C	0	12/16

Phenotypic data collected over time were validated and analyzed with the GLM procedure of SAS, to obtain baseline information on production traits collected in Montana commercial farms.

Population structure analyses were carried out using Endog 4.8 (Gutierrez and Goyache, 2005) and CFC (Sargolzaei et al, 2006). The degree of pedigree completeness was assessed by calculating an equivalent number of complete generations known per animal, as in Picolli et al. (2014). The mean additive genetic relationship between pairs of animals and the individual coefficient of inbreeding (F_i) were obtained from the numerator relationship matrix (Van Vleck, 1993). An inbreeding level of zero was assigned to individuals with one or both parents unknown.

The rate of inbreeding per generation was obtained from the individual rate of inbreeding (δF_i), which was computed as in Gutiérrez et al. (2009):

$$\delta F_i = 1 - \sqrt[n_i - 1]{1 - F_i}$$
 (Eq. 3)

where F_i is the coefficient of inbreeding of an individual and n_i is its equivalent number of complete generations known. The δF_i for animals in the population were averaged, in order to obtain a mean rate of inbreeding per generation (ΔF_i). The estimated rate of inbreeding per generation was used to estimate the effective population size (N_e), which was computed as in Falconer and Mackay (1996):

$$N_e = \frac{1}{2 \Delta F_i}$$
 (Eq. 4)

For the calculation of genetic contributions from founders and ancestors, a reference population intended to represent the current gene pool of the breed was assumed (Boichard, 1997). In our analyses, the reference population corresponded to the group of calves born between the years 2019 and 2022, and the genetic contributions of founders and ancestors were computed, as described by James (1972) and Boichard et al. (1997), and the effective number of founders (f_e) and ancestors (f_a) was calculated. For the purpose of these calculations, founders were considered both the individuals in the pedigree with no parents known, and the unknown parent of an animal with only one parent known.

All demographic and statistical analyses were carried out within-breed, using the ENDOG V.4.8 software (Gutiérrez and Goyache, 2005). This software computes individual inbreeding coefficients based on the algorithm proposed by Meuwissen and Luo (1992), assigning a null coefficient of inbreeding to animals that do not have both parents known.

RESULTS AND DISCUSSION

Breed census

The evolution of the population size of the Montana composite is shown in Figure 1. With the first animals registered in 1995, the breed showed a steep increase in number of registrations until 2001, when almost 40000 animals were registered. Afterwards, a decline in registrations was observed. Many reasons are responsible for that, such as the redirection of the use of land in several farms, from cattle to agricultural production, mainly to soybeans and corn, changes in administration and or ownership of the farms, changes in the market of bulls and prices and profitability of the beef industry.

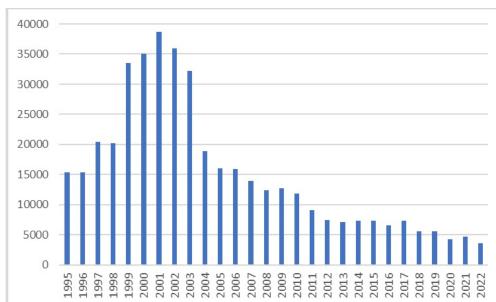


Figure 1. Number of animals born per year in the Montana Composite Population

Geographical distribution

The location of the farms where the animals that made up the Montana Composite program were raised over time is shown in Figure 2a for the early stages of the program, and Figure 2b for the herds currently enrolled. In both cases, it is clear that Montana herds are located mostly in southern and central-western Brazil, supporting the suitability of their fitness to challenging conditions, in view of the need to develop animals adapted to produce in tropical and subtropical environments.

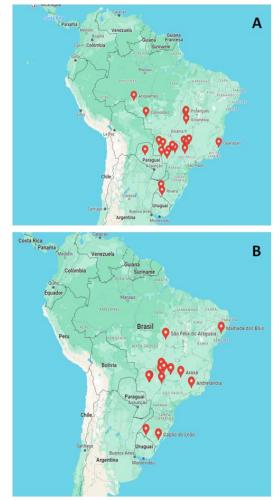


Figure 2. Distribution of Montana herds in Brazil. a) in 1995; b) presently.

Phenotypic information

Descriptive statistics for production traits recorded for the whole Montana population are shown in Table 2. The large number of records for the main traits, together with the very variable breed composition and environments where animals were raised was very important to create a suitable data bank to study many effects in this composite

population, which motivated our group to start such studies in 2021, mainly to consider the introduction of the effect of recombination in the genetic analyses.

Table 2. Descriptive statistics for phenotypic records in the Montana Composite population.

Trait	N	Mean	Standard deviation
Birth weight, kg	387,986	33.40	5.01
Weaning weight, kg	405,624	195.23	39.41
Weaning age, days	405,624	213.15	28.73
Weight gain, from weaning to yearling, kg	403,440	189.90	47.92
Yearling weight, kg	161,609	274.54	60.34
Yearling age, days	161,609	411.77	37.13
Scrotum perimeter, cm	59,270	28.50	4.30
Muscle score (1-5)	143,057	4.30	1.32

Contribution of different biological groups

As outlined in Table 1, there are specific limits for the breed composition allowed in Montana cattle, and the breeding system is established having in mind the goal of maintaining breed composition within those limits. Over the years, the contribution of the four biological types contributing to Montana genetic composition has changed, as shown in Figure 3. In the initial years, the *indicus* group (N) had a contribution of over 50% to the Montana gene pool, which then declined to about 20% nowadays, similar to the contribution of the British group (B). The group of continental breeds (C) has shown a very stable contribution below 10% throughout the years. On the other hand, the contribution of the group of adapted breeds (A) increased rapidly to about 40% in 2004, then remained stable, and showed a further increase to nearly 50% in recent years.

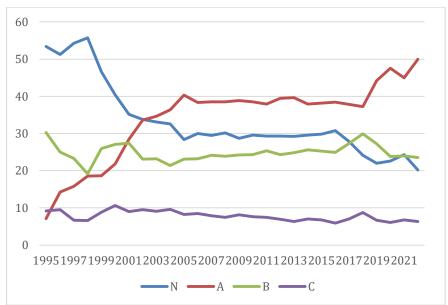


Figure 3. Evolution of the genetic contribution of different biological types to the genetic pool of Montana Composite cattle, by year of birth.

These changes probably reflect the tendency of producers to reduce the genetic supply originating from the N biological type, while increasing the proportion of genes originating from the A group. This could, to some extent, reflect changes in breeding objectives over the years, or be a consequence of changes in geographical dispersion in recent years, where the zebu influence could possibly be less desirable. It is, nevertheless, interesting to notice that the major genetic contribution currently results from the group of "adapted" breeds (A), which has gained some preponderance recently. Additionally, the contribution of the breeds of biological type A contributed to change de size and weight of animals, without loss of adaptability, resulting in animals with intermediate frame and good carcass composition, adequate to the needs of the Brazilian beef industry. As Brazil is the leader country in the market share of international meat market, the needs of the industry have strongly changed in recent years, mainly because the international market requires meat from animals slaughtered with a maximum age of 30 months.

Breeding and genetic diversity indicators

There were 635,963 animal records in the data set analyzed, including 4013 sires and 282993 dams (Table 3), and there were 265816 calves registered as Montana Composite.

Table 3. Indicators of genetic diversity and erosion in Montana cattle.

Indicator	Estimate	
Total number of animals	635963	
Number of sires	4013	
Number of dams	282993	
Number of registered Montana calves	265816	
Average number of offspring per bull	73.3 ± 330.6	
Average number of offspring per dam	1.92 ± 1.93	
Mean equivalent number of complete generations	1.59 ± 1.24	
Parent-offspring and matings between sibs (%)	0.17	
Average inbreeding coefficient (%)	0.09 ± 0.92	
Inbred animals (%)	3.14	
Average inbreeding coefficient for inbred animals (%)	2.88 ± 4.39	
Maximum inbreeding coefficient (%)	37.50	
Average relatedness (%)	0.13 ± 0.18	
Rate of inbreeding/generation (%)	0.16	
Effective population size	311.43	
Number of founders	217382	
Number of ancestors	95318	
Effective number of founders(f _e)	459	
Effective number of ancestors (f_a)	260	
Number of founders explaining 50% of the gene pool ^a	471	
Number of ancestors explaining 50% of the gene pool ^a	206	
Mean heterosis (%)	81.12 ± 16.76	
Mean recombination rate (%)	61.98 ± 7.83	

^a Contribution to the current population (calves born between 2019 and 2022).

Reproductive rates

A total of 4013 bulls produced 294062 registered Montana calves with known sire (Table 4), with a mean number of 73.3 ± 330.6 calves per sire. The distribution of number of offspring per sire (Table 3) indicates that nearly 48% of the bulls produced about 1% of the

calves, while 1.3% of the bulls produced 41% of the calves, such that the bull with the largest number of recorded offspring sired 9375 calves.

The 543100 registered calves with dam known were produced by 282993 cows (Table 4), with a mean of 1.92 ± 1.93 calves per dam. The distribution of number of offspring per dam (Table 5) indicates that nearly 49% of the calves were produced by cows having only 1 or 2 calves, and about 24% of the calves were offspring of cows producing more than 5 calves. Nearly 0.3% of the total calves registered resulted from 30 cows with more than 20 offspring, reflecting the limited use of embryo transfer in this population, which has, however, become more common in recent years.

Table 4. Distribution of bulls and calves by classes of number of offspring per sire.

No. offspring/sire	Bulls		Calves	
	No.	%	No.	%
<5	1913	47.67	3056	1.04
05/10	414	10.32	3271	1.11
10/50	955	23.80	23633	8.04
50-100	275	6.85	19676	6.69
100-200	170	4.24	24522	8.34
200-500	162	4.04	48429	16.47
500-1000	73	1.82	50891	17.31
>1000	51	1.27	120584	41.01
Total	4013	-	294062	-

Table 5. Distribution of cows and calves by classes of number of offspring per dam.

	Cows		Calves	
No. offspring/dam	No.	%	No.	%
1	187204	66.15	187204	34.47
2	39637	14.01	79274	14.60
3	20587	7.27	61761	11.37
4	12267	4.33	49068	9.03
5	7231	2.56	36155	6.66
06/10	14007	4.95	103287	19.02
11/20	2030	0.72	24886	4.58
>20	30	0.01	1465	0.27
Total	282993	-	543100	-

Population structure

The proportion of ancestors known for animals born in the current population is shown in Figure 4. As expected, the fact that Montana has an open herdbook, which allows the registration of animals resulting from the use of sires or dams of the "allowed breeds", even though they are not registered themselves, results in some gaps in pedigree recording. Figure 4 shows the proportion of ancestors known for animals in the current population, and it is clear that pedigree knowledge is less consistent on the sire side, but there are, nevertheless, nearly 50% of current animals which have great-grandparents known.

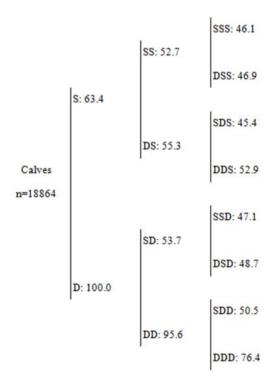


Figure 4. Average percentage of sires (S), dams (D), paternal and maternal grandparents (SS, DS, SD, and DD), and great-grandparents (SSS, DSS, SDS, DDS, SSD, DSD, SDD, and DDD) known for calves in the current population (calves born between 2019 and 2022).

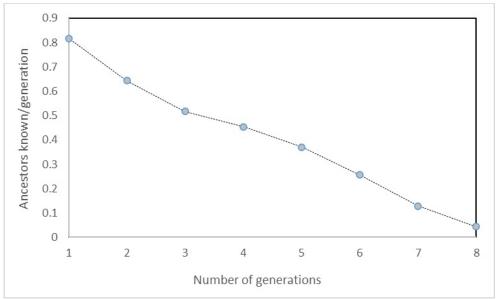


Figure 5. Proportion of known ancestors by generation, for animals in the current population (calves born between 2019 and 2022).

Genetic erosion

Since the beginning of its development, the Montana cattle population has remained open to the use of outside animals in breeding, as long as they belong to the established breed groups, and the resulting offspring had breed proportions in the range defined in Table 1. Therefore, it is expected that the evolution of inbreeding should not be as much of a concern as it is in closed populations. As a matter of fact, the overall mean inbreeding coefficient is only 0.09%, and the mean relationship is 0.13% (Table 3).

Inbred animals represent only 3.14% of the population, with a mean level of inbreeding of 2.88%. Still, a few animals have high levels of inbreeding (with a maximum of 37.5%), and 0.17% of the matings are considered highly inbred.

The modest rate of inbreeding of 0.16%/generation resulted in an estimate of N_e =311.43 for effective population size (Table 3), which is much higher than the minimum of N_e =50 recommended by the FAO for maintaining appropriate levels of genetic diversity for the future.

Genetic contributions of founders and ancestors

The results of the retrospective evaluation of cumulative genetic contributions of founders and ancestors to the reference population (animals born between 2019 and 2022) are summarized in Table 3 and represented in Figure 6. Overall, there were 217,382 founders and 95,318 ancestors in the database. The cumulative genetic contributions of the most important founders and ancestors (Figure 6) show a steady increase in the early stages of the curves, particularly for ancestors, indicating that a limited number of animals have a stronger influence on the breed. Overall, 50% of the genetic pool is accounted for by the contributions of 471 founders and 206 ancestors (Table 3), with the most influential ancestor contributing 4.6% of the genetic pool while the top 5 ancestors contributed 13.0%. The effective number of ancestors and founders (260 and 459, respectively) indicates that the Montana population maintains a wide diversity of genetic contributions, as would be expected from its open genetic management.

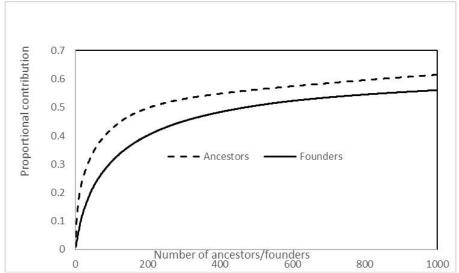


Figure 6. Cumulative genetic contribution to the current population (Montana calves born between 2019 and 2022) of the 1000 most influential founders and ancestors.

Heterosis and recombination

The evolution of heterosis and recombination over the years (Figure 7), indicates that an important reduction in heterosis has occurred over time. This Figure, analyzed together with Figure 3, indicates that, from the standpoint of heterosis, there is a higher than desirable predominance of the A biological group, which has resulted in a decline in heterosis. On the other hand, recombination rate has remained quite stable over the years. These results may serve as a basis to support the need to infuse new sources of genetic diversity into the herd, possibly considering a higher percentage of C-type cattle, to recover some of the heterosis that has been lost.

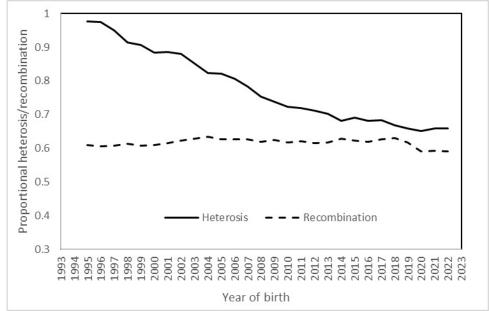


Figure 7. Evolution of mean heterosis and recombination rate by year of birth for registered Montana cattle.

CONCLUSIONS

Overall, our results indicate that the Montana composite breed has gone through changes in its census and geographic distribution, reflecting market and production trends, but remains a viable alternative for beef production in the tropics.

The main reasons for developing a population of composite cattle are to exploit heterosis and breed complementarity, in this case favoring adaptability to tropical and subtropical climates and their challenges. The increased predominance over the years of the A biological type of cattle has resulted in some reduction of heterosis, suggesting that the breeding strategy in Montana cattle may need to be revised. In this case, an introgression of biological type C genes, from cattle of Continental origin, may be advisable, in order to recover the desired levels of heterosis, increase carcass size and weight, but with special attention to meat quality, especially fat cover and marbling, which are often problematic characteristics in these breeds.

As for other cattle breeds, the use of artificial insemination may have caused genetic bottlenecks in Montana, and the resulting inbreeding could compromise the benefits of heterosis and possibly reduce genetic diversity, which would hamper further genetic progress. Our results indicate that, so far, inbreeding is under control, even though the intensive use of a few ancestors may have detrimental consequences in the long run, and should be appropriately addressed.

The *specificities* of composite cattle populations place important challenges to genetic improvement programs, as the roles of heterosis and recombination should be taken into account when estimating breeding values. Furthermore, the proposal of alternative ways of expressing the genetic value of animals (Arnold et al., 1992), including the effects of both biological types and the additive genetic effects of the animals (which are commonly predicted in genetic evaluations), should be investigated and possibly adopted in the Montana Composite breeding program.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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