Genetic variability in Colombian Creole cattle populations estimated by pedigree information[1]

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ABSTRACT: The genetic structure of 4 Colombian Creole cattle breeds, namely, Costeño con Cuernos, Blanco Orejinegro (BON), Romosinuano (ROMO), and Sanmartinero (SM), was studied with an analysis of the available pedigree data. The comparison between the effective number of founders (f_e) and the effective number of ancestors (f_a) revealed a decrease in the genetic variation that was rather important for the ROMO and San Martinero breeds, which had the lowest f_a/f_e ratios (0.34 and 0.53, respectively). All breeds showed similar values for the number of equivalent generations traced, ranging from 3.1 in BON to 4.8 in ROMO. These 2 populations also had the lowest and the highest population sizes, respectively. The lowest average inbreeding coefficient considering the whole pedigree was obtained by BON (0.18%), whereas the highest was attained by ROMO (1.22%). Finally, the percentage of individuals with an inbreeding level greater than 6.25% in the reference population was high, indicating that the existing conservation management strategies could be improved to successfully maintain the genetic variability of these populations.

Key words: Creole cattle, inbreeding, pedigree analysis

INTRODUCTION

Cattle herds in Colombia were initially composed of crossbred animals brought by the Spanish in the 16th century (Jordan, 1993). However, during the first decades of the past century, these Creole breeds were indiscriminately crossbred with imported taurine breeds from temperate countries and also with zebuine breeds, which contributed to the genetic erosion of these important tropical cattle genetic resources (Hall and Ruane, 1993). Today, Creole cattle account for only 0.01% of the national bovine population, and this proportion experienced a 23% decrease from 1989 to 1999. The last population census available, which was carried out in 1999 by the Ministry of Agriculture together with the Breeders Federation (FEDEGAN), reported 3,173 animals in 13 herds for Romosinuano (**ROMO**), 1,522 animals in 3 herds for Costeño con Cuernos (**CCC**), 3,968 animals in 27 herds for Blanco Orejinegro (**BON**), and 765 animals in 5 herds for Sanmartinero (**SM**; Asocriollo, 2003).

These breeds, of *Bos taurus* origin, have essential genetic properties for survival and reproduction in the tropics, so their preservation for future use is important (Syrstad and Ruane, 1998). For example, a higher level of resistance to brucellosis was found in the BON breed with an in vitro assay of macrophage infection, and a level of heat tolerance similar to that of *Bos indicus* breeds was described in the Romosinuano breed (Hammond et al., 1996; Hernández-Cerón et al., 2004). Chase et al. (1997) found important adaptive traits related to puberty, growth, heat tolerance, and reproductive efficiency in subtropical ecosystems of the United States segregating at high levels in some of these populations.

The aim of this paper is to provide results of population genetic variability parameters in 4 Colombian Creole cattle breeds maintained as genetic conservation pools. In addition, we discuss the possible influence the genetic strategies used in the management of these breeds have had.
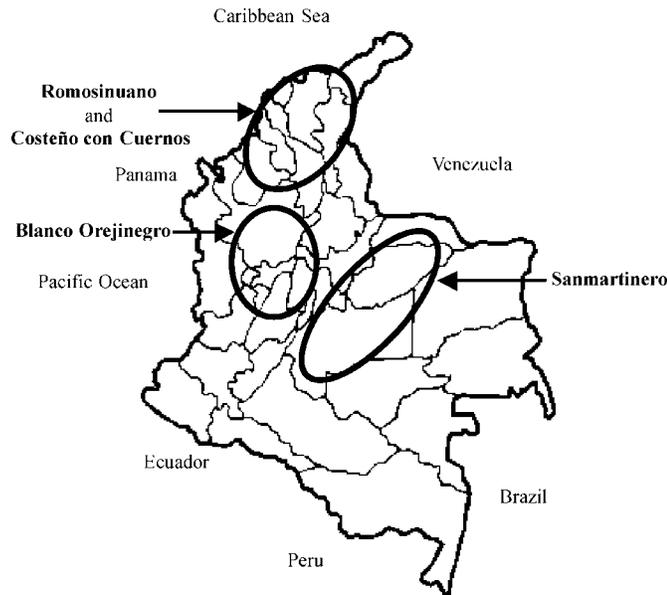
Figure 1. Approximate geographical distribution of the 4 Creole cattle breeds in Colombia.

MATERIALS AND METHODS

Breed Management and Available Data

The breeds considered in this study were located in the North coast (ROMO and CCC), in the mountains of the central region (BON), and in the East savannas region (SM; Figure 1). Animal Care and Use Committee approval was not obtained for this study because the data (genealogical information) were obtained from existing herd books. Mating strategies to control the rate of inbreeding, as described by Nomura and Yonezawa (1994) and implemented in several conservation programs of rare livestock breeds (Alderson, 1990), are being applied to these closed populations. Populations are subdivided into a number of family groups, and the mating males are transferred to neighboring groups in a circular pattern. The mating system in each breed differs depending on the number of family groups (SM, n = 10; ROMO, n = 8; CCC, n = 8; and BON, n = 8), the rate of female replacement, which is a function of the number of steers born each year, and other random factors such as the proportion of individuals with unknown sires, which is usually greater in CCC, ROMO, and SM because of management of the sires on the farms.

Although the conservation program began in 1994 with animals born from 1980 onward, both parents of each animal entering the program had to be known. The pedigree information analyzed included the parents of those animals and totaled to 2,339, 3,610, 1,625, and 4,844 animals registered for CCC, SM, BON, and ROMO, respectively. Animals born from 2000 to 2004, with at least the sire known, were used as the current populations to perform the analysis of the genetic variability parameters of interest.

Characterization of the Pedigree Information

Three parameters were used to characterize the pedigree completeness level of the reference populations: 1) the percentage of known ancestors per generation, 2) the number of equivalent complete generations, and 3) the maximum number of generations traced. For each of the 4 reference populations, the percentage of known ancestors was computed by counting the number of equivalent complete generations, calculated as the sum over all known ancestors of the terms $(1/2^t)$, where t is the ancestor's generation number (1 for the parents, 2 for the grandparents, etc.; Maignel et al., 1996), and the maximum number of generations traced was obtained as the number of generations between an individual and its earliest ancestor. These parameters were calculated by using the PEDIG software (Boichard, 2002; http://www-sgqa.jouy.inra.fr/sgqa/article.php3?id_article=110 Accessed Jan. 25, 2008).

Demographic Parameters

Generation lengths were computed for the 4 possible genetic pathways (sire-son, sire-daughter, dam-son, and dam-daughter) as the average age of parents at the birth of their offspring that become breeding animals.

Genetic Variability Measurements

The individual inbreeding coefficients were computed for all animals in the pedigree file as the probability of an individual having 2 alleles identical by descent, using the Meuwissen and Luo (1992) algorithm implemented in the PEDIG software (see above).

The rate of inbreeding in the last generation (ΔF) was estimated as in Gutiérrez et al. (2003) by using the following expression:

$$\Delta F = \frac{F_t - F_{t-1}}{1 - F_{t-1}}.$$

To calculate ΔF, the increase in inbreeding between 2 generations ($F_t - F_{t-1}$) was obtained by combining the annual rate, the regression coefficient (b) of the average inbreeding on the year of birth, and the average generation length (l) as follows: $F_t - F_{t-1} = lb$, and F_{t-1} is computed as $F_t - lb$, with F_t the mean inbreeding in the last year. The effective size of each breed was then computed as $\frac{1}{2\Delta F}$. To classify the endangerment of the breeds, we used the maximum values of inbreeding after 50 yr of conservation (Simon, 1999), computed as $F_t = 1 - (1 - \Delta F)^t$ (Falconer and Mackay, 1996).

The average relatedness of each individual is defined as the probability that an allele randomly chosen from the whole population in the pedigree would be identical to any of those carried by the individual. It

Table 1. Pedigree completeness level for the reference populations (animals born from 2000 to 2004) in the 4 Colombian Creole cattle breeds[1]

Item	CCC	SM	BON	ROMO
Maximum no. of generations traced	5.2	6.1	4.2	6.9
No. of complete equivalent generations traced	3.7	3.8	3.1	4.8
Percentage of known ancestors from the:				
First generation (parents)	100.0	97.5	100.0	99.9
Third generation	88.0	72.1	79.6	91.7
Fifth generation	20.4	41.0	3.6	66.9
Seventh generation	<1.0	2.8	<1.0	5.2

[1]CCC = Costeño con Cuernos; SM = Sanmartinero; BON = Blanco Orejinegro; ROMO = Romosinuano.

was calculated as the average of the coefficients in the row corresponding to the individual in the numerator relationship matrix (Dunner et al., 1998), and its computation was formalized by Gutiérrez and Cañón (1997).

The effective number of founders (f_e; Lacy, 1989), defined as the number of equally contributing founders that would be expected to produce the same genetic diversity as that observed in the population under study, was computed as the reciprocal of the probability that 2 alleles drawn at random came from the same founder. However, Boichard et al. (1997) showed that f_e overestimates the effective number of founders if the population has suffered an important bottleneck, and they proposed as an alternative the effective number of ancestors (f_a). This was defined as the minimum number of ancestors, founders or not, accounting for the complete genetic diversity of a population, and it was calculated as the reciprocal of the probability that 2 alleles drawn at random came from the same ancestor. In other words, the f_e and f_a were calculated as the reciprocal of the square average relationship coefficients across founders and across ancestors, respectively.

RESULTS

Pedigree Completeness Level

Values for the maximum number of generations and of equivalent generations traced, and the percentage of known ancestors for the first, third, fifth, and seventh generations are given in Table 1 for the reference popu-

lations of each breed. Breeds with lower population sizes showed the lowest pedigree depth. In particular, the lowest pedigree depth was observed in BON, which showed the lowest percentage of known ancestors for the fifth and seventh generations (3.6 and 0.0, respectively). In addition, SM and ROMO showed the greatest proportion of known ancestors in the fifth generation (41.0 and 66.9, respectively) and seventh generation (2.8 and 5.2, respectively), possibly as a consequence of using some relatively old parents when the conservation program started. For instance, 33 dams and 12 sires in the SM breed, and 86 dams and 11 sires in the ROMO breed were born in the 1960s.

Demographic Parameters

The average generation lengths between parents of the whole population are displayed in Table 2. The greatest generation length was for SM (6.8) and the lowest values were for CCC and BON, which performed similarly (5.38 and 4.66, respectively). Generation lengths were shorter for the sire-offspring pathways than for the dam-offspring pathways except in SM, in which they were similar. In BON, ROMO, and CCC, the generation length was almost twice as great for the dam-son or dam-daughter pathway as for the sire-son or sire-daughter pathway. Within sire, generation length was longer for daughters than for sons, with the exception of SM. The use of the circular mating system is a possible cause of these patterns, because the selection of replacement females took place after that of the males, which resulted in longer generation lengths for the females than for the males.

Table 2. Generation intervals (years) estimated from the parents of the calf crop in the 4 Colombian Creole cattle breeds

Breed[1]	Sire-son		Sire-daughter		Dam-son		Dam-daughter		Average	
	n	Years	n	Years	n	Years	n	Years	n	Years
CCC	75	3.8	470	4.3	76	6.8	488	6.5	1,109	5.4
SM	153	7.3	559	6.4	158	7.2	624	6.9	1,494	6.8
BON	98	3.7	319	3.9	100	5.4	341	5.5	858	4.7
ROMO	131	4.9	789	5.4	133	5.9	827	6.2	1,880	5.7

[1]CCC = Costeño con Cuernos; SM = Sanmartinero; BON = Blanco Orejinegro; ROMO = Romosinuano.

Table 3. Parameters of gene origin for the reference populations (animals born from 2000 to 2004) in the 4 Colombian Creole cattle breeds[1]

Item	CCC	SM	BON	ROMO
Total no. of founders				
Both parents unknown (f)	220	435	180	583
At least 1 parent unknown	441	1143	277	968
Effective no. of founders (f_e)	50	91.9	89.4	67.1
Effective no. of ancestors (f_a)	33	49	58	23
No. of most contributing ancestors to a 50% cumulative				
expected contribution of the genes	12	22	22	8
f_e/f ratio	0.23	0.21	0.50	0.12
f_a/f_e ratio	0.66	0.53	0.65	0.34

[1]CCC = Costeño con Cuernos; SM = Sanmartinero; BON = Blanco Orejinegro; ROMO = Romosinuano.

Probabilities of Gene Origin

Table 3 shows the results of the analysis of probabilities of gene origin. The greatest total number of founders was found in ROMO, but the largest f_e, which depended on both the total number of founders and the imbalance between their expected contributions to the gene pool, was found in the SM and BON. A substantial imbalance between the number of founders and the number of ancestors was found in all the breeds, but it was especially significant for the largest breed, ROMO. It had the largest f value (583) and the lowest f_e/f (0.12) and f_a/f_e (0.34) ratios. The CCC and BON breeds showed similar values for the latter (0.66 and 0.65, respectively).

Inbreeding and Relatedness

The results for inbreeding and average relatedness in the whole pedigree and in the reference populations are given in Table 4. The ROMO breed showed the greatest proportion of inbred animals and the BON breed the smallest, probably because the pedigrees in this breed were known to a substantially lower extent than in others. This would also explain why the BON breed showed the lowest average inbreeding coefficient, both for the whole pedigree and for the animals in the reference population. The values of inbreeding and average relatedness in inbred animals were similar for all the breeds and were more than 3 times greater than those found for the whole pedigree. These values were also very similar for males and females (data not shown). The proportion of coefficients greater than 6.25%—the result of mating 2 animals sharing 2 grandparents—was substantial. The greatest proportion was found in ROMO, probably because of the high number of complete equivalent generations known. The average coefficient of inbreeding was substantially lower than the average relatedness for all breeds. It is well known that, assuming random mating in a population, the inbreeding rate in each generation is approximately half the average relatedness in the previous one, but the values here were even below that.

The rate of inbreeding for the last generation, and the realized effective population size for the 4 breeds, can be seen in Table 5. The smallest value of inbreeding by equivalent generations was found for BON, with CCC and SM scoring similarly greater figures. When generation intervals were considered, relative values of these parameters in the 4 breeds changed, and then the greatest rate of inbreeding in the last generation was that of SM. Consequently, this breed showed the lowest effective population size. Further inbreeding results are given in Table 4. The BON breed showed the lowest average inbreeding coefficient in the whole pedigree (0.18%), whereas ROMO scored the highest (1.25%).

DISCUSSION

Of the 8 Creole cattle breeds officially described in Colombia, only the 4 included in this study (CCC, SM, BON, and ROMO) have been managed under conservation programs across the entire country and have been maintained for 20 yr under the same genetic management strategies, with a constant breed population size, a circular mating system, and low rates of inbreeding. The other 4 Creole breeds (Casanare, Chino Santandereano, Hartón del Valle, and Caqueteño) can also be considered endangered breeds based on their reduced population sizes, and local governments are now undertaking strategies for their conservation. The picture of the different breeds is quite different depending on the parameter taken into consideration, and it is not possible to find common patterns throughout the different criteria.

The generation length estimates in the Colombian Creole breeds were similar to those reported by Cañón et al. (1994) and Gutiérrez et al. (2003) in several Spanish local beef breeds, in which the generation intervals for the sire-offspring pathway were always lower than those of the other gene transmission pathways. In our Creole populations, the use of a circular mating system led to sires being replaced earlier than dams. Longer generation intervals in the female pathways have also been reported previously for other beef breeds, for example, in Australian Shorthorns (Herron

Table 4. Average values of inbreeding and relatedness in the whole pedigree, the reference populations (animals born from 2000 to 2004), and the inbred animals in the 4 Colombian Creole cattle breeds

Breed[1]	Percentage of inbred animals	Mean of coefficients of inbreeding percentage in:			Percentage[2] of coefficients greater than 6.25%		Average relatedness percentage in:		
		Whole pedigree	Reference population	Inbred animals	Whole pedigree	Reference population	Whole pedigree	Reference population	Inbred animals
CCC	24.6	0.79	1.3	3.2	17.0	4.7	2.9	3.8	4.2
SM	29.2	0.87	1.4	3.0	12.8	2.5	2.0	2.5	3.4
BON	5.8	0.18	0.5	3.0	13.7	10.1	1.5	2.0	2.1
ROMO	30.8	1.22	3.1	4.0	20.1	9.9	2.2	3.9	4.1

[1]CCC = Costeño con Cuernos; SM = Sanmartinero; BON = Blanco Orejinegro; ROMO = Romosinuano.
[2]Percentage relative to the inbred individuals.

and Pattie, 1977), British Herefords (Özkütük and Boichard, 1977), and Avileña-Negra Ibérica (Vassallo et al., 1986). Generation intervals in the ROMO and SM could be biased upward because of the age of some of the parents of animals included in the conservation program. An increased generation interval may be desirable to reduce the loss of genetic variation per unit of time.

Disequilibrium between expected contributions of the founders was greater in the ROMO breed, which also had the largest population size. Although the 4 breeds have been managed in a similar way, a lower number of ancestors were used in the ROMO breed at the beginning of the conservation program. This indicates an excessive use of some animals as parents, which is also reflected by the low number of ancestors explaining 50% of the genetic variability of this breed (8).

Overall, the comparison between the f_e and f_a revealed a decrease in genetic variation in the populations passing through a bottleneck (Boichard et al., 1997). This decrease was more important in the SM and ROMO breeds, for which the lowest values of the f_a/f_e ratio (0.21 and 0.12, respectively) were observed. This large difference between f_a and f_e can be partially explained by the relatively high level of pedigree completeness of these 2 breeds.

The f_e has been used to measure the overall founder representation in a managed population, accounting for the loss of genetic variability from unequal founder contributions (Lacy, 1989; Rochambeau et al., 1989).

In our results, SM and BON showed the greatest f_e and f_a, although BON had the lowest population size and also low pedigree completeness (3.6% of known ancestors in the fifth generation and only 3.1 complete equivalent generations in the reference population). This parameter is directly related to genetic diversity and showed a similar pattern when using molecular information. Using microsatellite information, Barrera et al. (2006) reported a greater genetic diversity in BON compared with SM, CCC, and ROMO, and the greatest loss of genetic diversity occurred in ROMO.

The estimated f_a for the reference populations of the 4 Colombian Creole cattle breeds were within the range (23 to 58) of published estimates for several European beef cattle breeds (Boichard et al., 1997; Solkner et al., 1998; Gutiérrez et al., 2003), even though they had low population sizes, and of those reported by Sorensen et al. (2005) for selected dairy populations of Holstein, Jersey, and Red Danish (20.6, 23.8, and 34.6, respectively).

Population parameters as the f_e (Lacy, 1989), the f_a (Boichard et al., 1997), or the founder genome equivalents (Lacy, 1995) are also directly related to genetic diversity and have been used in the management of small populations. They provide complementary information to the traditional estimates of the effective population size and the evolution of inbreeding levels. The founder genome equivalent is related to the coancestry, the probability that 2 alleles in 1 locus from 2 individuals drawn at random from the population are identical by descent. Mating animals in such a way

Table 5. Rate of inbreeding for the last generation, realized effective population size in the last generation, and inbreeding rate after 50 yr of conservation in the 4 Colombian Creole cattle breeds

Breed[1]	Rate of inbreeding for the last generation, %	Effective population size	Inbreeding rate, % over 50 yr of conservation
CCC	0.35	143	3.2
SM	1.85	27.1	12.8
BON	0.20	260.0	2.0
ROMO	0.76	66.1	6.4

[1]CCC = Costeño con Cuernos; SM = Sanmartinero; BON = Blanco Orejinegro; ROMO = Romosinuano.

that the next generation has the lowest average coancestry has been pointed out to maximize genetic diversity (Lacy, 1995). Moreover, minimization of the average coancestry has been theoretically proven to be an efficient method of preserving genetic diversity (Caballero and Toro, 2000, 2002).

Average coefficients of inbreeding in the BON breed have been the lowest, as happened as well with the pedigree completeness level. The inbreeding coefficients were probably underestimated, as was the number of founders and ancestors. The percentage of inbred animals was very similar in all breeds (26 to 31%), except in BON (6%) because of its low pedigree depth.

Inbreeding has an adverse effect on all performance traits of several species, as shown in beef and dairy cattle (Croquet et al., 2006) and sheep (Ercanbrack and Knight, 1991). However, inbreeding depression effects are more severe in populations developed under rapid inbreeding systems, particularly in animals with inbreeding coefficients greater than 20% (Burrow, 1993). In general, the average coefficient of inbreeding was low; only the ROMO showed an inbreeding value greater than 1%, and only 8% of the individuals had a coefficient greater than 5%. In the other breeds, less than 5% of the individuals exceeded this 5% inbreeding level. These results were lower than those reported by Gutiérrez et al. (2003) for Spanish local beef cattle breeds, with values ranging from 1 to 3% and similar pedigree completeness levels. Therefore, the values found here can be considered far from high risk.

The minimization of genetic variation loss, which is related to the rate of inbreeding per unit of time, is an important aspect to consider from a conservation perspective. However, the rate of inbreeding obtained by regressing inbreeding coefficients on time cannot be considered a good criterion because of its strong dependence on the pedigree completeness level. In such situations, the use of average relatedness offers a good complement to predict future inbreeding. Theory shows that, under random mating, the average inbreeding coefficient in a generation equals half the average relatedness of the previous one. Average relatedness can then be used to balance the genetic contribution at different levels, lines, or families of founders or ancestors.

Even though prioritizing breeds for conservation at any level depends on several criteria, the inbreeding rate or the resulting effective population size are frequently used as the most important risk factors for rating breeds and forming classes of endangerment (Food and Agriculture Organization of the United Nations, 1998; Bennewitz et al., 2007). A desired effective population size of approximately 50 animals per generation (Food and Agriculture Organization of the United Nations, 1998; Scherf, 2000) leads to a 1% rate of inbreeding per generation, which is considered acceptable for conservation purposes by the European Association of Animal Production, which recommends the use of the maximum value of inbreeding after 50

yr of conservation (Bennewitz et al., 2007). According to these criteria, only the SM breed would be considered as potentially endangered (Simon, 1999). However, additional variables such as the number of breeding females and males, trends in population size, percentage of pure breeding, and number of herds provide a general perception of endangerment for all the breeds. Unfortunately, this perception cannot be accurately assessed, because there is no easy way to model these parameters into an objective risk index. Some attempts have been made to build an extinction probability based on these kinds of parameters (Reist-Marti et al., 2003), but there is a strong component of arbitrariness to the definition. Regardless of these difficulties, these additional variables should be taken into account when scarce pedigree information affects the reliability of average inbreeding estimates.

Further studies should include the use of molecular markers to complement weak pedigree information. Within- and between-breed diversity, as well as conservation priorities, the uniqueness level of the populations, or the relationship between inbreeding or fitness and within-breed diversity can be assessed with molecular tools.

Several authors (Caballero and Toro, 2000; Eding and Meuwissen, 2001) have proposed the use of molecular information to estimate the pairwise kinship between animals, but high sampling variance is a well-known problem for this methodology. The use of molecular information to estimate the between-population kinship has shown an acceptable efficiency in terms of low prediction error (Eding and Meuwissen, 2001); on the other hand, individual inbreeding measured by using molecular information and its true value are poorly associated unless a high number of markers are used (Balloux et al., 2004). Therefore, when the interest is focused on the analysis of isolated populations with abundant and accurate genealogical information, the cost of performing the molecular analyses to estimate population parameters is difficult to justify, because estimation using the available genealogies will be more accurate than those based on molecular information. The case of Colombian Creole breeds, for which there is limited genealogical information, up to the point of having annual inclusion of animals with an unknown sire, is open for the application of these methodologies so that the results presented here can be extended and complemented.

Recent studies have applied phylogenetic methods based on genetic distances to set priorities for the conservation of domestic animal breeds (Weitzman, 1993). Although these methods may be appropriate for between-species conservation, some authors argue that they are clearly inappropriate for within-species breed conservation, because they ignore within-breed variation (Caballero and Toro, 2002), whereas others have extended them to incorporate this variation (García et al., 2005; Ollivier and Foulley, 2005). It would also be interesting to apply these methods to establish a

prioritization scheme for the conservation of genetic diversity in the Colombian Creole breeds.

CONCLUSIONS

Although all the breeds had small effective sizes and a limited number of commercial populations, only the SM breed could be considered as endangered, according to the criteria established by the Food and Agriculture Organization of the United Nations and the European Association of Animal Production. At present, only the CCC and SM breeds have reported fewer than 5 herds and 1,500 animals (Asocriollo, 2003). The ROMO breed has the greatest population size but also a low f_a and f_e/f ratio. Thus, a decrease in its genetic variation can be expected. The mating system devised to minimize the rate of inbreeding needs urgent revision in this breed, and inclusion of the most convenient breeding practices to maintain genetic diversity must be addressed. Nevertheless, considering all the results, monitoring of the inbreeding index, the use of the largest possible number of sires, and circular mating have proven to be useful for the maintenance of genetic variability, in spite of low population sizes. In general, the conservation program for Colombian Creole cattle has had relative success in maintaining a constant population size and population variability, but it is imperative to find mechanisms to increase the effective population indicators before any genetic breeding program can be implemented.

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