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Genetic structure and inbreeding in Romney Marsh sheep in Brazil

Estrutura genética e consanguinidade de ovinos Romney Marsh no Brasil

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Highlights

Inbreeding coefficient explained with historical evidence.
The Romney Marsh breed has 82.55% of inbred animals in the 2018 records.
The Romney Marsh breed is long-lived and prolific.

Abstract

According to the last livestock census, Brazil has 17,976,367 head of sheep. Approximately 23.69% of this herd is located in the south region, where wool or wool and meat-producing breeds are predominately farmed. Inbreeding, or consanguinity, is defined as the mating of related individuals, which tends to occur when herds are small or originate from few parents. This study proposes to investigate the genetic structure and diversity of the Romney Marsh sheep herd in Brazil. The pedigree data used were obtained from the Brazilian Association of Sheep Breeders (ARCO), which keeps the sheep register database. For a more complete analysis, data from the Purebred Register Books were used. The population herein referred to as "total" comprised 22,833 individuals, whereas the population termed "reference" consisted of 17,053 records. Individual and average inbreeding coefficients, as well as overall frequencies, were calculated using SAS software. Demographic indicators were determined using ENDOG software. The average inbreeding coefficient found was 2.90% in the total population and 3.55% in the reference population. The minimum inbreeding value found in the studied population was 0.01% and the maximum was 43.47%. Inbred animals in the complete reference population were 10.31%. In 2018, inbred animals represented 82.55% of the registered population. The average generation interval was 4.0488 years. Due to the intensive use of few breeding lines and the high degree of genetic uniformity in the population, the Romney Marsh breed has

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narrow pedigree bottlenecks. The current population of the Romney Marsh breed has only two genetic origins, warranting the introduction of new genes to avoid genetic erosion and severe losses due to inbreeding.

Key words: Ancestors. Average relatedness. Founders. Inbreeding. Pedigree information.

Resumo

O último censo pecuário informa que o Brasil possui 17.976.367 cabeças de ovinos. Aproximadamente 23,69% desse efetivo está localizado na região sul do país, onde predomina a criação de raças produtoras de lã, ou lã e carne. Endogamia ou consanguinidade é definida como o acasalamento de indivíduos relacionados, e tende a ocorrer quando os rebanhos são pequenos ou provenientes de poucos genitores. Este estudo teve como objetivo estudar a estrutura e a diversidade genética do rebanho ovino da raça Romney Marsh no Brasil. Os dados de pedigree utilizados foram obtidos na Associação Brasileira de Criadores de Ovinos (ARCO), que é a mantenedora do banco de dados de registro de ovinos. Para uma análise mais completa foram utilizados dados dos Livros de Registro Puro de Origem (PO). A população referida como “total” foi composta por 22.833 indivíduos, e a população referida como “referência” composta por 17.053 registros. Os coeficientes de consanguinidade individual e médio, bem como as frequências gerais, foram calculados usando o software SAS. Os indicadores demográficos foram determinados a partir do software ENDOG. O coeficiente de consanguinidade médio encontrado na população total foi de 2,90%, e na população de referência foi de 3,55%. O valor mínimo de consanguinidade encontrado na população estudada foi de 0,01% e o máximo, foi de 43,47%. Animais consanguíneos na população de referência completa foi de 10,31%. Em 2018 os animais consanguíneos representavam 82,55% da população cadastrada. Intervalo médio de gerações 4,0488 anos. Devido ao uso intensivo de poucas linhas de reprodutores e ao alto grau de uniformidade genética da população, a raça Romney Marsh apresenta estreitos gargalos nos pedigrees. A população atual da raça Romney Marsh provém de apenas duas origens genéticas, sendo necessário introduzir genes novos para evitar a erosão genética e perdas por consanguinidade acentuada.

Palavras-chave: Ancestrais. Endogamia. Fundadores. Informações de Pedigree. Relacionamento médio.

Introduction

According to the last census, Brazil has 17,976,367 head of sheep. Approximately 62% of this herd is located in the northeast, while 23.69% is in the south region of the country (Instituto Brasileiro de Geografia e Estatística [IBGE], 2022), where wool or wool and meat-producing breeds predominate.

The Romney Marsh is a dual-purpose sheep breed with 60% aptitude for meat and 40% for coarse wool production. Thanks to its great hardiness, it properly withstands the conditions encountered in humid areas. As a prolific breed, twin births are frequent and triplet births are not uncommon. The Romney Marsh are thought to have been first introduced in Brazil around the 1910s, and the first animal born in the country was registered in 1926 a male owned by Dr. Serafim Prates Garcia in the municipality of Santana do Livramento, RS (Ferreira & Gonçalves, 2016; Machado, 2019; Osório et al., 2020).

Consanguinity, or inbreeding, is defined as the mating of individuals more closely related than the average of the breed. It leads to an increase in prepotency, resulting from greater homozygosity, and its consequence is less variability in the genetic makeup of the inbred individual, whose offspring will be more similar. Inbreeding was used to a greater or lesser extent in the early phases of establishment of virtually all breeds, mainly to facilitate the fixation of some simple genes associated with the definition of the breed standard (Gama, 2002). Crossbreeding usually began with the selection of individuals that best embodied the "ideal biotype"; then, these were mated with their progeny or with their parents to fix the desired qualities in the new breed.

Nonetheless, inbreeding can have deleterious effects on a herd. The traits most affected by inbreeding depression also happen to be those with higher heterosis values and tend to have a low heritability. These are mainly traits associated with reproduction and survival (Gama, 2002; Machado et al., 2020). Therefore, it is important to know the pedigrees of the animals to be used, particularly those that will leave a large number of progeny.

Inbreeding does not result in disaster when its use is concentrated in genetically superior individuals. When combined with selection, it may be of some zootechnical interest, especially as it facilitates the detection of carriers of recessive genes and contributes to a faster fixation of some genes (Machado et al., 2020).

There has been a considerable decline in the population of Romney Marsh sheep in Brazil in recent years, which may result in a dangerous narrowing of their gene pool. However, these observations are based on empirical data from breeders, so a scientifically based study is warranted to determine whether new lines will be needed in the short or medium term. Thus, the aim of the present study was to examine the genetic structure and diversity of the Romney Marsh sheep herd in Brazil.

Material and Methods

The pedigree data used in this study were obtained from the Brazilian Association of Sheep Breeders (ARCO), an entity assigned by the Ministry of Agriculture, Livestock, and Supply of Brazil for the collection, structuring, and maintenance of the database forming the National Zootechnical Archive. For a more in-depth analysis of inbreeding in the herds, we used data from the Purebred Register Book, which contains sufficient generations and ancestors to meet the need for knowing the pedigree of all animals in the population (Olori & Wickham, 2004).

Although over 38,069 animals are registered at present, the analyses are limited to the animals available in the digitalized system of ARCO. In this study, we used information of 22,833 animals registered in the Purebred Book. Information on father, mother, sex, and date of birth was collected from each animal. These data were used to calculate the consanguinity of the population. The other population parameters were calculated from a population herein defined as the "reference", which is made up of animals born from 1980 onwards. Thus, we analyzed the pedigree of 17,053 animals, from register no. FBB 19,685, added in 1980, to FBB 38,069.

The following demographic parameters were analyzed: Evolution of registers; Generation interval (L); Pedigree completeness level; Number of known generations (ni); Individual inbreeding (Fi); Degree of relatedness between individuals (aij); Increase in inbreeding per year (ΔF/year) and per generation (ΔF/generation); Effective population size (Ne); Average relatedness (AR); Genetic contribution of founders (qk) and ancestors (pk); Effective number of founders (fe); and Effective number of ancestors (fa).

Individual and mean inbreeding coefficients were calculated using the PROC INBRED procedure of the SAS software (Statistical Analysis System Institute [SAS Institute], 2009). The frequencies of sires and dams were obtained by PROC MEANS.

To calculate the demographic parameters, we also used computational applications developed by Carolino & Gama (2002), which include validations and filtering of the data to be submitted for analysis, to detect and eliminate possible errors.

Demographic indicators, namely, average relatedness (AR), were determined using ENDOG software, developed by Gutierrez and Goyache (2005).

Individual inbreeding (Fi) represents the probability that two alleles at the same locus are identical by descent (Wright, 1923), whereas the degree of relatedness (aij) between two individuals (i and j) represents twice the probability that, at a given locus, an allele drawn at random from individual i and an allele drawn at random from individual j are identical by descent. The general equation that allows the calculation of the inbreeding coefficient of an individual (Fi) from its pedigree is given as follows:

$$Fi = (1/2)\ n-1\ (1+Fc),$$

where n is the number of generations between the parents of i “through” the common ancestor, and Fc is the inbreeding coefficient of the common ancestor (Gama, 2002).

In case there is more than one common ancestor between the parents of i, Fi will be the result of the sum of the contributions of the several common ancestors (Ci):

$$Fi = \Sigma i[(1/2)\ n-1\ (1+Fc)].$$

The degree of relatedness between two individuals can, in very simple terms, be regarded as the proportion of genes they have in common, which is described by the function below:

$$aZY = 2\ \phi ZY \text{ and } RZY = aZY / \surd\ (1+FZ)(1+ FY).$$

By definition, the degree of relatedness between Z and Y is twice the probability that, at a given locus, an allele drawn at random from Z and an allele drawn at random from Y are identical by descent, i.e. copies of the same gene. This implies that, in the case of inbreeding, the degree of relatedness will be higher than the values mentioned above (Gama, 2002).

The annual increase in inbreeding (ΔF/year) was estimated by regression of the individual inbreeding coefficient (Fi) on the year of birth, using the following linear model:

$$Fij = b0 + b1yeari + eij,$$

where Fij: individual inbreeding of individual j born in year i; b0: intersection; b1: linear regression coefficient of individual inbreeding on the year of birth; and eij: error associated with observation ij. From ΔF/year, we were able to determine the increase in inbreeding per generation (ΔF/generation), calculated as follows:

$$(\Delta F/year)*L,$$

where L: average generation interval, corresponding to the average age of the parents at the time the offspring that will replace them are born.

The number of known generations (ni) was obtained individually for all animals in the database (n=22,833), by the following expression:

$$ni = \{(nf + 1)/2\} + \{(nm + 1)/2\},$$

where nf and nm: number of known generations of the father and mother, respectively. In case the father or mother of an individual is unknown, nf or nm assumes the value of -1.

According to Falconer and Mackay (1996), the effective size of a population (Ne) is defined as the number of individuals in a population with a non-ideal structure, which would originate a certain inbreeding rate if its structure were ideal (e.g. equal numbers of males and females, with no selection, random mating, etc.). In the demographic characterization, Ne was calculated by the expression shown next:

$$Ne = 1/2(\Delta F/generation),$$

where ΔF/generation: increase in inbreeding per generation.

The effective number of founders (fe) and ancestors (fa), as well as the genetic contributions of founders (qk) and ancestors (pk), were determined via computational applications developed by Carolino & Gama (2002).

The effective number of founders (fe) represents the number of founders (f) that would originate the genetic diversity observed in the population under study if all founders contributed equally. This variable was calculated as follows:

$$fe = 1/\Sigma^{f}_{k=1}\, q_k^{2},$$

where qk: proportional contribution of each founder k to the population under study (e.g. animals born in a certain period), considering founders as animals with unknown father and mother, or the unknown parent of an animal with only one known parent.

The effective number of ancestors (fa) is defined as the number of ancestors (founders or non-founders) explaining the complete genetic variability of the population under study if all ancestors contributed equally. It is determined by the following expression:

$$fa = 1/\Sigma^{f}_{k=1}\, p_k^{2},$$

where $p_k = q_k\ (1 - \Sigma^{n-1}_{i=1}\ a_{ij})$ and where pk: marginal contribution of an ancestor, that is, the contribution not yet explained by its already calculated ancestors; qk: proportion with which each ancestor k contributes to the population under study (from which the contribution of all its relatives whose contributions have already been determined is subtracted); and aij: relationship between k and each of its n-1 ancestors.

Results and Discussion

The number of animals in the total population reached 22,833 individuals (53% females and 47% males). Thus, despite some gaps found in the pedigrees, it was possible to analyze a large number of animals with consistent pedigree to obtain reliable information about the current situation of the breed. This number of animals in the total population is only lower than those described in the studies by Vostry et al. (2018), with the Romanov breed, and by Rodriguez-Ramillo et al. (2019), with French Lacaune. However, the reference population of the present study is the largest and has been registered the longest, compared with those analyzed in other studies (Vostry et al., 2018; McManus et al., 2019; Illa et al., 2019; Vatankhah et al., 2019; Mchugh et al., 2022).

The average inbreeding coefficient in the total population was 2.90%, with a coancestry coefficient of 0.82%, whereas in the reference population it was 3.55% with an average inbreeding coefficient among inbred animals of 10.31%. The male population had 3% inbreeding and 0.9% coancestry, and the female population 2.82 and 0.76%, respectively. These values are similar to those reported in studies that used breeds with ancient and complete pedigree records. Rochus and Johansson (2017) found an inbreeding coefficient of 1.8% in Gute sheep, whereas Prieur et al. (2017) observed 3% using molecular markers and 1.51% by pedigree analysis in New Zealander Romney Marsh. They are also similar to the results of Rodriguez-Ramillo et al. (2019) with the French breeds Basque Bearnese (2.96%), Manech Tête Noire (2.98%), Manech Tête Rousse (2.39%), Lacaune Confed (2.34%), and Lacaune Ovitest (3.11%). In contrast, the literature cites inbreeding values higher than those observed in this study with Brazilian Romney Marsh sheep, e.g. 5.5% in Romanov (Vostry et al., 2018), 4.54% in Iran Black (Rashidi et al., 2018), and 6.73% in Morada Nova (McManus et al., 2019). Nevertheless, some sheep breeds exist that, even in small populations, show inbreeding values lower than those described in the present study, such as those observed by Venkataramanan et al. (2013) in Nilagiri in southern India. According to the author, the population of the breed was approximately 8,000 animals in 1973, which declined to less than 1,000, yet with an average inbreeding of 2.17%.

By analyzing the evolution of the inbreeding coefficients in the reference population, grouped in time spaces, we observe an increase in average inbreeding in the registered population, which was 1.29% between 1980 and 1984 that grew to 9.60% after 34 years (2015-2018) (Figure 1).

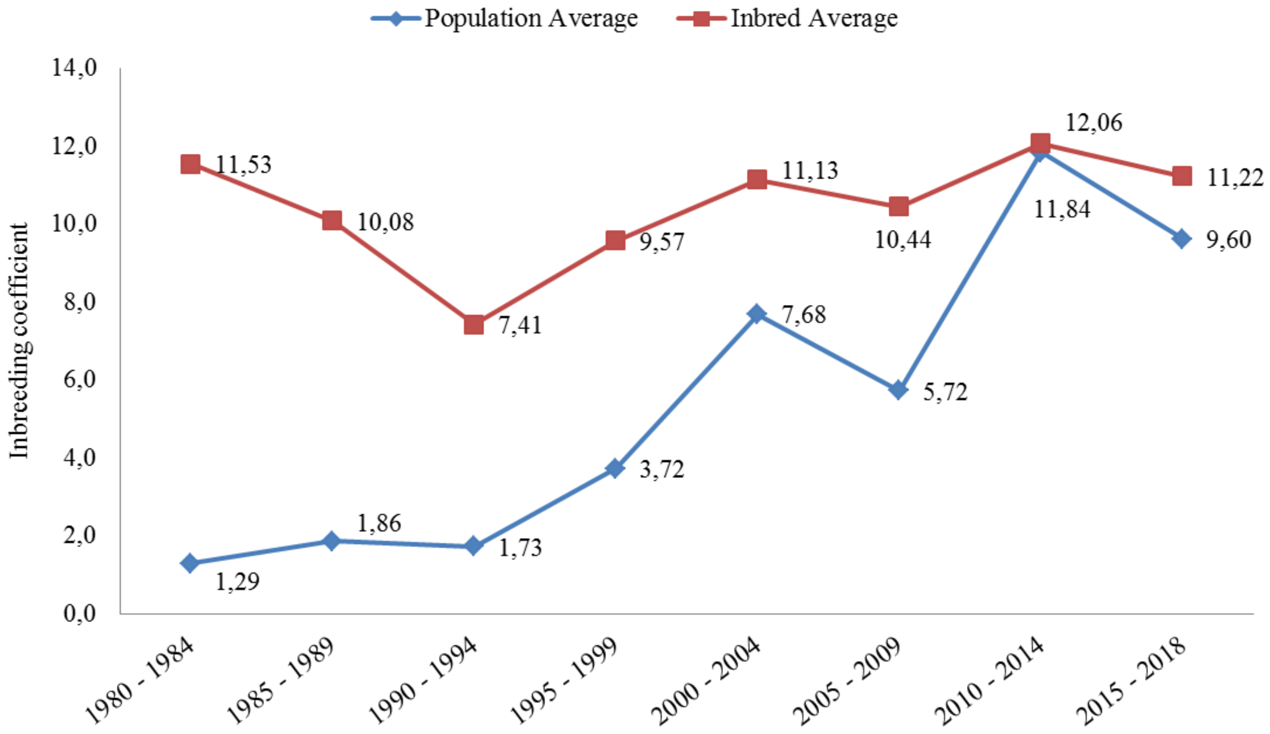

Figure 1. Inbreeding coefficient of the reference Romney Marsh population and among inbred animals, from 1980 to 2018.

The average inbreeding between animals with some degree of relatedness (Table 1) was 30% higher than that found in the Iran Black breed and more than 60% than those described in the Baluchi, Zandi (Rashidi et al., 2018), and Lori-Bakhtiari (Vatankhah et al., 2019) breeds.

Table 1
Demographic parameters obtained from the Romney Marsh population registered with ARCO and its ancestors

Parameter	Value
Number of animals in the total population	22,833
Number of animals in the reference population	17,053
Average inbreeding, total population	2.90%
Average inbreeding, reference population	3.55%
Average inbreeding among inbred animals, total population	0.82%
Coefficient of relatedness	2.04%
Inbred animals total population	34.48%
Inbred animals reference population	5,880
Average inbreeding among inbred animals, reference population	10.31%
Maximum inbreeding coefficient	43.47%
Increase in maximum inbreeding per generation	1.02%
Effective population size	48.99
Average of complete generations	1.50
Increase in inbreeding per complete generation	3.69%
Effective population size	13.57
Average of equivalent generations	2.23
Increase in inbreeding per equivalent generation	2.41%
Effective population size	20.77
Effective population obtained from regression on date of birth	2.34
Effective population obtained from log regression on date of birth	1.84
Base population with one or more unknown parents	1,444
Current base population with one unknown parent = half founder	1,369
Effective founder population size	55.26
Inbreeding expected from unbalanced founders' contribution	0.90%
Effective number of founders/ancestors for the reference population	47/47
Number of ancestors explaining 50% of the gene pool	16
Mating between full sibs	0.05%
Mating between half-sibs	6.71%
Mating between father or mother and offspring	2.91%
Generation interval: father - son	3.4472
Generation interval: father - daughter	3.4972
Generation interval: mother - son	4.6834
Generation interval: mother - daughter	4.4406
Generation interval: total	4.0488

The percentage of inbred animals (34.48%; Table 1) is similar to the 33.59% cited by Rashidi et al. (2018) in Zandi. Higher values were described by the same author in Iran Black (51.47%); by Vostry et al. (2018) in Romanov (93%); and by Vatankhah et al. (2019) in Lori-Bakhtiani (47.18%). It should be emphasized that the Romney Marsh registry studied here has had animals with higher inbreeding values in the last decades (Figure 1) and with a population that is being registered with an ever smaller herd (Figure 2).

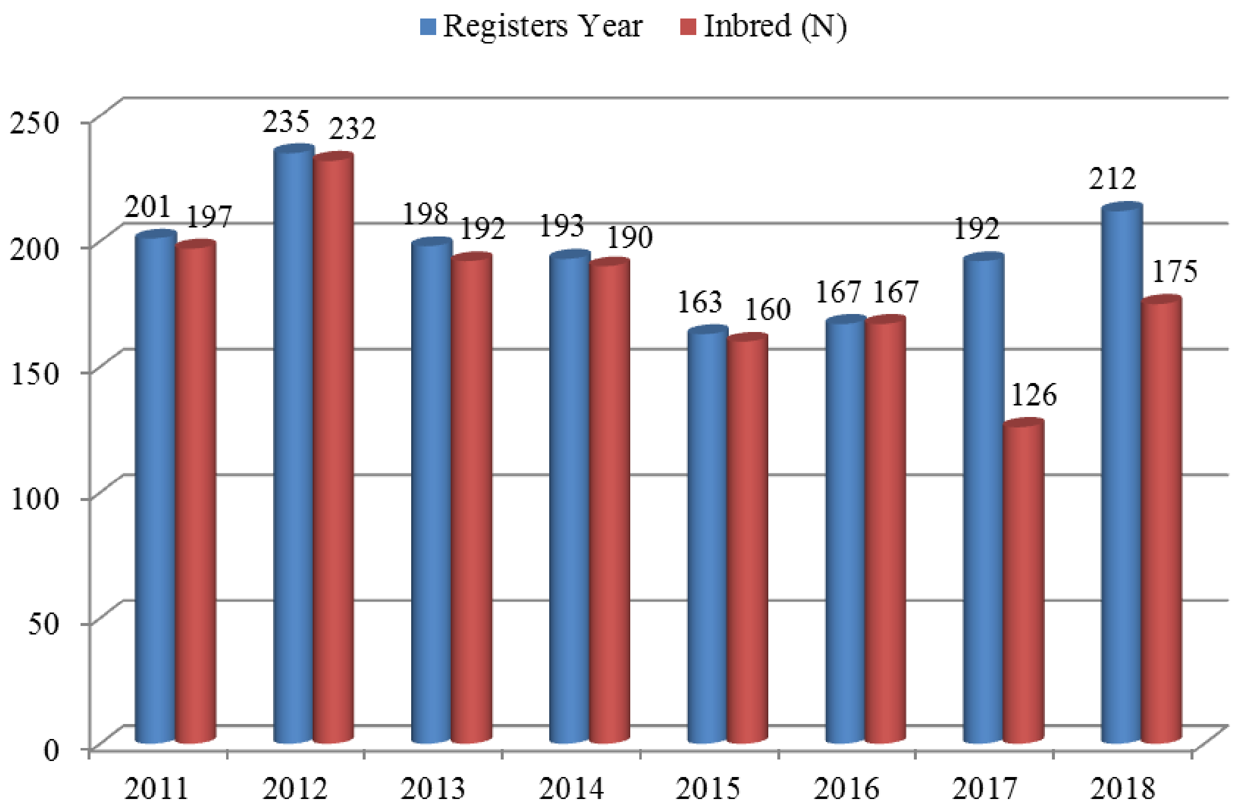

Figure 2. Number of annual records and inbred animals from 2011 to 2018.

In the present experiment, the lowest non-zero inbreeding coefficient found in the reference population was 0.01%, in 45 animals, whereas the highest coefficient (43.47%) was found in only two individuals. Inbreeding coefficients greater than 6.25% considered the maximum acceptable value by most researchers (Machado et al., 2020) corresponded to 22.15% of the registered herd. Vostry et al. (2018) found a similar value in the Romanov population (40.66%). In a study with Nilagiri, Venkataramanan et al. (2013) found a maximum coefficient of 33.59%. Prieur et al. (2017) described lower values in Romney Marsh (32.49%), Coopworth (26.20%), Perendale (14.45%), Texel (25%), and the RCP and RCPT compounds (15.44% and 12.70%), but this last population has unknown ancestors due to the nature of its formation, which involves several breeds.

The coefficient of relatedness observed in the Romney Marsh breed (Table 1) is within the parameters found in other studies, but higher than that obtained in the Brazilian Morada Nova breed (1.46%) by McManus et al. (2019). These authors evaluated a smaller population, yet with a higher inbreeding coefficient. Other studies show higher coefficients of inbreeding as well as relatedness, demonstrating greater genetic erosion.

The increase in maximum, complete, and equivalent inbreeding per generation (Table 1) denotes a tendency towards an increase to levels higher than those accepted by the FAO (Food and Agriculture Organization). The institution recommends a 1% increase in inbreeding per complete generation, in aiming to maintain the genetic variability of the population (Machado et al., 2020).

Effective size per complete generation was 20.77 (Table 1). An important aspect in pedigree analysis of a population is the study of the probability of gene loss between generations and the consequent decrease in genetic variability. Knowing the effective size of the population over time allows determining changes in genetic variability, as it is a reflection of the number and choice of breeding animals in previous generations. However, effective population size is a parameter extremely sensitive to the quality of the pedigree file data and makes more sense in long-term analyses (Machado et al., 2020).

Rego Neto et al. (2018) examined the effective size per complete generation in the Santa Inês breed and found oscillation due to variations in the inbreeding coefficient over generations. The effective size ranged from 283.5 to 5.3, with the minimum value obtained in the sixth generation. The explanation for the reduction in effective size and the increase in inbreeding coefficient was mainly related to the decrease in the number of animals for reproduction.

The number of founders in this study (47; Table 1) was similar to those found by McManus et al. (2019) and Illa et al. (2019) but lower than the 92.96 animals of the Romanov breed described by Vostry et al. (2018); the 47 animals by Illa et al. (2019); and the 109 Lori-Bakhtiari sheep by Vatankhah et al. (2019). In terms of effective ancestors (Table 1), our results were somewhat similar to those reported by Vostry et al. (2018) with Romanov (47.41) and McManus et al. (2019) with Morada Nova (42), but higher than the 37 found by Ill Illa et al. (2019). The number of effective ancestors is the minimum number of ancestors. This value complements the information provided by the effective number of founders that represent the losses of genetic variability generated by the unbalanced use of breeding animals that produce genetic bottlenecks in the population.

The number of ancestors that explain 50% of the genetic variability in the population was only 16 (Table 1), which reveals an unbalanced contribution of ancestors to the genetic diversity of the Romney Marsh breed in Brazil. Therefore, matings must be managed carefully to avoid inbreeding-related problems.

One of the reasons for the genetic erosion of a population is a decrease in its effective population, which has been occurring with the Romney Marsh breed in Brazil. Average inbreeding in the population during the 1980s was within an acceptable level, around 1.29%, even though the average inbreeding among inbred animals was high (11.53%; Figure 1). This is due to the dilution of homozygosity of inbred individuals in the calculation of the population average. In addition to the mathematical factor itself, this dilution also occurs due to the greater number of individuals within the breed, which allows for greater exchange of genes between herds.

The number of Romney Marsh animals registered has decreased in recent decades. As can be observed, the number of animals with some degree of genetic homozygosity tends to increase within the population as the registrations of individuals decrease. During the early 2010s, the number of inbred individuals and their average inbreeding was almost equal to the average inbreeding of animals registered in that quadrennium.

The Romney Marsh breed appears to be sensitive to the introduction of new genetic material. This clearly shows that outcrossing can have a decisive effect on the refreshment of a closed population. There was a decline in the number of inbred animals in the 2017 registrations (Figure 3). In the previous year, a ram from Uruguay with fully open pedigree was imported into the national herd, and there was a decrease in the registration of inbred animals in the following year. Despite the slight increase in average annual inbreeding, the average inbreeding of inbred individuals persisted with a slight decline.

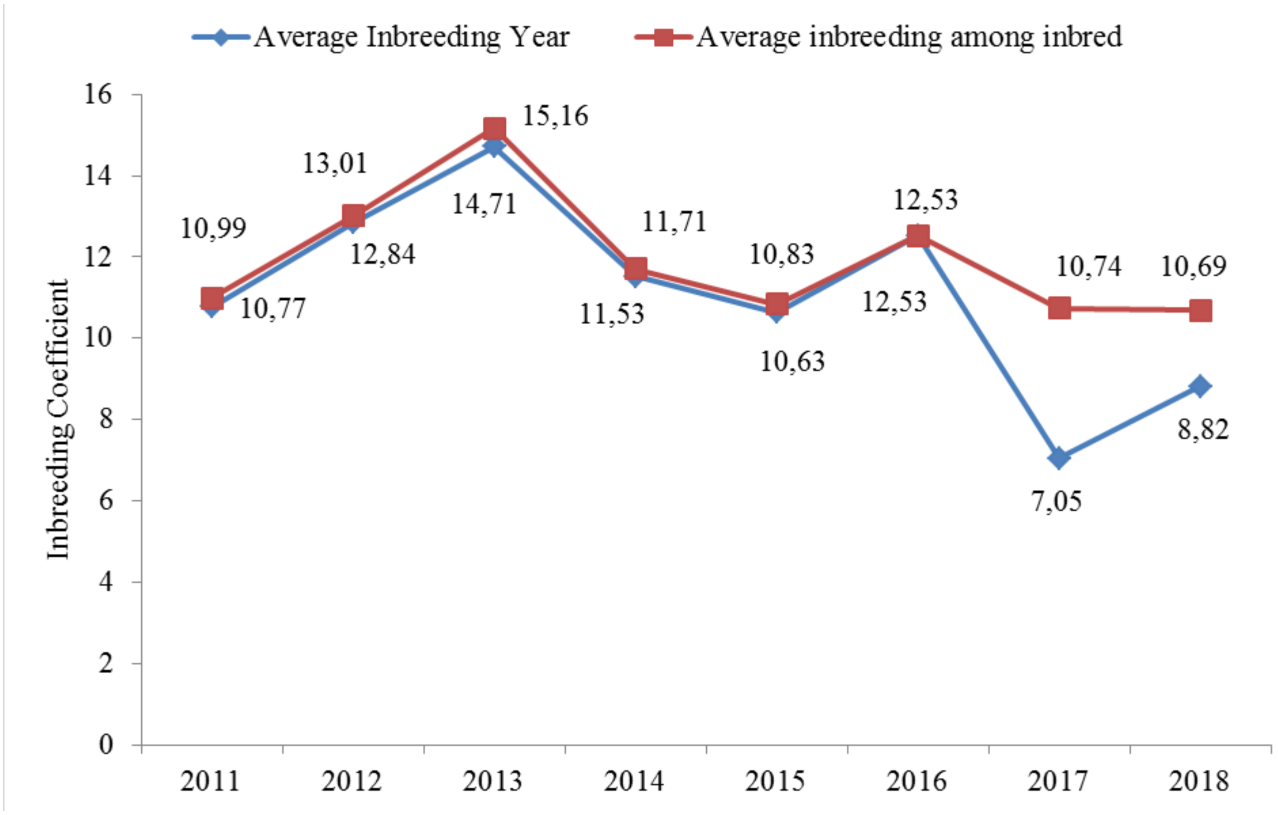

Figure 3. Average annual inbreeding in the reference population and inbred animals, from 2011 to 2018.

In this scenario, the key point is that there is a need for new blood to be introduced. Even if few, imported animals and animals deriving from outcrossing already show some relief from the pressure of inbreeding in the population. However, it is crucial that these imports of genetic material follow an organized scheme, where matings are consciously directed and that the chosen breeding stock have something new to add to the existing population.

As for prolificacy, we found that 85% of wombs bear, on average, up to five offspring throughout their reproductive life. Around 1% of the wombs have more than 10 offspring registered, with a maximum of 16 offspring for two wombs. The incidence of twin births was observed in 2,239 wombs. There were four wombs with six twins, six wombs with five twins, and 20 wombs with three twins. Triple births occur in the breed, but at low frequency.

The interval between generations was 4.0488 years (Table 1), a value close to those reported in other studies. In the population of the sheep conservation center in Sobral, state of Ceará, Brazil, the Santa Inês, Morada Nova, and Somalis Brasileiro breeds showed generation intervals of 3.54, 4.08, and 3.40 years, respectively (Tino et al., 2020). The average interval between generations in the Nilagiri breed was 3.36 years (Venkataramanan et al., 2013). Rochus and Johansson (2017) evaluated Gute sheep from Sweden and found a generation interval of 3.6 years.

Generation intervals are different for males and females. In general, males must be replaced earlier, and, therefore, generational intervals are shorter. Most young females are kept for replacement, which leads to low selection intensity in this sex, but also longer intervals between generations, since females are kept for a longer period of their reproductive life on the property. Still, if the peculiar longevity of the Romney Marsh breed makes the wombs remain longer in reproduction, especially those that give birth to twins, selection is performed for this trait.

Shorter generation intervals provide a higher annual rate of genetic gain for the selected traits. One of the probable explanations for the high average generation interval is the continuous use of certain breeding animals, without a rapid replacement with their descendants.

Conclusion

Due to the intensive use of few breeding lines and the high degree of genetic uniformity in the population, the Romney Marsh breed has narrow pedigree bottlenecks.

Despite the increase in the number of breeding animals, the current population of the Romney Marsh breed has only two genetic backgrounds. Thus, new genes must be introduced to refresh their lineages, avoiding genetic erosion and losses due to elevated inbreeding.

The increase in inbreeding per generation and the growing average inbreeding of the current population, equaling the values shown by inbred animals, makes the Romney Marsh a breed with strong genetic erosion in a short time frame.

Conflict of interest

The authors declare that there is no conflict of interest.

Declaration on animal rights

The present study has no implications to be appreciated by the Ethics Committee on Animal Experimentation of the institution (CEEA/ UFPel). This statement is underpinned by the use of information from an already consolidated database that holds zootechnical bookkeeping records of several livestock establishments.

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