ORIGINAL ARTICLE

Effect of the rob(1;29) translocation on the fertility of beef cattle reared under extensive conditions: A 30-year retrospective study

Jose Maria Jiménez[1] | Rosa Morales[2] | Antonio Molina[2] | Miguel Moreno-Millán[2] | Sebastián Demyda-Peyrás[3,4] 🔗

[1]CEAG Diputación de Cádiz, Jerez de la Frontera, España

[2]Departamento de Genética, Universidad de Córdoba, Córdoba, España

[3]Departamento de Producción Animal, Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, La Plata, Argentina

[4]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), La Plata, Argentina

Correspondence
Sebastián Demyda Peyrás, Departamento de Producción Animal, Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, Calle 60 y 118 S/N, La Plata, Buenos AIres, 1900, Argentina.
Email: sdemyda@fcv.unlp.edu.ar

Abstract

The Robertsonian translocation 1/29 (rob(1;29)) is the most worldwide widespread chromosomal abnormality in domestic animals. Previous studies have demonstrated its negative effect on fertility in dairy herds, but not in beef cattle extensively bred. In this study, we analysed the effect of rob(1;29) in a Retinta cattle breed data set gathered during the last 30 years. The data presented herein include rob(1;29) analysis of 11,505 cows from 251 herds, pedigree information of 24,790 animals and 67,457 calving records. Fertility was evaluated using estimated breeding values for the reproductive efficiency (Re), calculated as the percentage ratio between the number of calvings of an individual and the number expected in an optimal situation. Our results showed that cows carrying the heterozygote genotype showed a significant decrease in their Re (-5.10%, $p < .001$). No decrease was detected in free rob(1;29) animals and homozygous carriers. In addition, the incidence of rob(1;29) in the breed fertility was decreased to very low values after 30 years of avoiding selection of bulls' carrier as stallions. The effect of rob(1;29) on cattle fertility is only significant when the prevalence of carrier individuals is high. Selecting against the disease only by the paternal side reduced the incidence to negligible values.

KEYWORDS
age at first calving, beef cattle, calving interval, cytogenetic analysis, reproductive efficiency, Robertsonian translocation

1 | INTRODUCTION

The occurrence of a Robertsonian translocation rob(1;29) in cattle was first reported in 1964 in Sweden by Ingemar Gustavsson (Gustavsson, 1964). After this, it was rapidly detected in numerous breeds and countries, leading to the creation and development of several chromosomal screening programmes in farm animals, particularly in Europe (Ducos et al., 2008).

Although its origin has not been fully determined, the most accepted hypothesis is the occurrence of a centric fusion between BTA1 and BTA29 into a dicentric bi-armed chromosome, which occurred in a common ancestor even before the breeds were established in

cattle (Iannuzzi et al., 2009). This original occurrence was followed by a series of complex evolutive rearrangements, including the loss of small portions of DNA and the transposition and the inversion of a small pericentromeric region from *p* to *q* arms to the present form (Chaves et al., 2000; Escudeiro et al., 2021; De Lorenzi et al., 2012).

A major characteristic of this (Ellsworth et al., 1979; Miyake & Kaneda, 1987) translocation is the absence of morphological alterations in the phenotype of carriers, which cannot be distinguished from normal individuals without a specific analysis (Iannuzzi et al., 2021) (Gustavsson et al., 1976). However, a reduction in the fertility of rob(1;29) carriers has been documented in several breeds (Gustavsson, 1979; Lonergan et al., 1994; Schmutz et al., 1991). This effect is triggered by the formation of zygotes with trivalent meiotic configurations produced by unbalanced gametes, which become non-viable at the early stages of development. This original hypothesis was confirmed by in vitro studies in which the existence of abnormal meiotic segregation of gametes produced by rob(1;29) heterozygous bulls and cows was established (Bonnet-Garnier et al., 2006, 2008). However, in both cases, the percentage of unbalanced gametes observed was low, and therefore, the existence of other impairing mechanisms cannot be excluded.

Fertility traits are characterized by interactions between a large number of genes and environmental factors. Therefore, any successful attempt to evaluate its variation due to genetic causes is dependent on quantitative approaches, rather than comparing differences in phenotypes (such as non-return or pregnancy rates) or using binary models (Cammack et al., 2009; Gómez et al., 2020; Matos et al., 1997). Even so, the accuracy of these analyses relies on the existence of large and accurate data sets of reproductive data, which should be preferably collected from different herds and during a considerable number of seasons. To our knowledge, a quantitative approach aiming to determine the reproductive effects produced by the rob(1;29) translocation has not been done yet, even less in beef cattle reared in extensive conditions, in which the reproductive data set is more scarce.

Retinta is a Spanish autochthonous breed largely raised extensively on the south and southeast region of the Iberian Peninsula (Morales et al., 2020), in an environment characterized by pasturelands with scarce production and a dry and hot climate. This breed was selected for its adaptability to those conditions, as well as by longevity, during the last 50 years (Morales et al., 2017). However, it was 30 years ago (1991) when an official breeding programme was established, aiming to select long-lived and fertile cows highly adapted to the environment. Currently, many cows have more than 15 calvings, so we can determine that the selection in that sense has been successful. To achieve those goals, among other measures, it was decided since the beginning that only those bulls which were tested free of rob(1;29) can be used as breeders (Moreno-Millán, 2004). Since this bylaw remains until our days, we were able to collect a large and reliable data set of chromosomal analysis during the last three decades.

In this study, we aimed to determine the evolution of the rob(1;29) incidence in a population selected against carrier individuals and its effect on fertility at extensive field conditions. To this, we combined a genetic approach, including quantitative modelling of the genetic and environmental effects with the existence of a large chromosomal and reproductive data set gathered during the last 30 years.

2 | MATERIAL AND METHODS

2.1 | Animals

In this study, we analysed reproductive data, pedigree information and karyotypes from individuals belonging to the breeding programme of the Retinta breeders association (ANCRE). Reproductive data and pedigree information were gathered between 1970 and 2020 only by ANCRE technicians. Karyotypes were performed in the laboratory of animal applied cytogenetics of the University of Córdoba (Spain) from 1991 to 2020. All the samples were collected in compliance with the ethical guidelines from the ANCRE and the University of Córdoba.

2.2 | Karyotyping

Karyotypes of 5,721 animals from Retinta breed cattle (4,625 bulls and 1,096 cows) were determined on G-banded metaphases obtained from lymphocyte cultures according to our routine methodology (Rodero-Serrano et al., 2013). In addition, the rob(1;29) genotype was determined by an imputation process using AlphaPeel (Whalen et al., 2018). This imputation included all the pedigree data available in the breed database, comprising in total 258,961 animals, bobtaining results with an imputation probability greater than 95% for 137,025 animals (49,082 cows). After analysis, the individuals were assigned to one of the three categories: free (F) and heterozygous (He) or homozygous (Ho) carriers of the rob(1;29) translocation.

2.3 | Reproductive data

The raw data set included 49,082 cows from 505 herds. Initial filtering was performed to eliminate anomalous calving intervals and age at first calving (AFC) of the dam produced by the delivery of crossbreed calves (which are not registered in the ANCRE). After this, 11,505 cows with at least three calving records, obtained from 1,260 sires and 8,059 dams (3,194 included in the data vector), from 251 herds were retained, which produced 67,457 calving records (5.9 calvings per cow). In a final step, a robust extended pedigree of the cows (including 1,881 sires and 22,909 dams; maximum, complete and equivalent generations average equal to 8.94, 3.20 and 4.96, respectively) showing a moderate inbreeding value (5.82% in average, 4,601 outbred cows) and a low average relatedness (1.57%) were obtained analysing all the available pedigree information in the official breed database ($n = 24,790$ animals).

2.4 | Estimation of reproductive efficiency

The fertility of the individuals was assessed using the reproductive efficiency (Re) parameter (Ziadi et al., 2021), estimated as the deviation in percentage of the number of calvings that an animal has at each age, from the number of calvings that it could have had in optimal conditions. In the Retinta breed, the optimum age at first calving was considered 2 years and one year for the optimal calving interval, as in the majority beef cattle breed.

2.5 | Statistical model

The data were analysed using a univariate animal model, as follows:

$$y = + Xb + Z_1a + Z_2pe + Z_3hys + e,$$

where y is the vector of observed Re (RE at each age calving); 1 was the vector of ones μ the general mean; b is the vector of systematic fixed effects; a is the vector of cow additive genetic effects; pe is the vector of permanent environmental effects of the cow; hys is the vector of contemporary group effect of the herd combined with the year and season; e is the vector of residual effects; and X and Z_1, Z_2 and Z_3 are the correspondent incidence matrices. The values de a, pe, hys and e were assumed to follow a normal distribution with a ~ $N(0, \sigma_a^2 A)$, pe ~$N(0, \sigma_{PE}^2 I)$, hys ~$N(0, \sigma_{hys}^2 I)$ and e ~ $N(0, \sigma_e^2 I)$, being A the numerator relationship matrix.

The **b** vector included the age at first calving of the dam class (AFC; 3 classes: monthly intervals from ≥20 < 30; ≥30 < 36; and ≥36 < 42.5 months), a fixed effect of the cytogenetic genotype of the cows class (CG; 3 classes: *F* (Free, 2n= 60,XX); He (Heterozygous carriers, 59,XX rob(1;29)) and Ho (Homozygous carriers, 58,XX rob(1;29)), and two covariate effects (FC: inbreeding coefficient of the cow and CA : calving age of the cow).

The contemporary group effect of the herd combined with the year and season (hys) at mating (5,820 classes with restrictions set to a minimum of 5 records per group) was included as a random effect. Four seasons, December to March, April to June, July to August and September to November, were defined according to the weather characteristics of these regions.

Individual inbreeding values were estimated using ENDOG software (Gutierrez & Goyache, 2005). Variance components were estimated using a restricted maximum likelihood method implemented in AIREMLF90 software of the BLUPF90 software family (Misztal et al., 2002).

3 | RESULTS

3.1 | Detection of rob(1;29) genotype

The results revealed that 11,081 individuals were free of rob(1;29) translocation (2n = 60 XX, 96.31%), 412 were heterozygous carriers (2n = 59 XX, rob(1;29), 3.58%), and 12 were homozygous carriers (2n = 58 XX, rob(1;29),rob(1;29), 0.11%). These observations are not in equilibrium for H-W There was a clear negative trend in the incidence of He individuals in the whole population during the last 30 years, decreasing from 15.73% in 1992 to 1.06% in 2020. In the same period, the opposite (a slow but steady increase) was observed in the phenotypic values of Re (Figure 1).

In addition, the observed frequency of rob(1;29) carriers remains below the expected frequency during most of the years included in this analysis, according to H-W analysis (Figure 2), revealing the existence of selective breeding practices against the rob(1;29) carriers. However, it is necessary to take into account, at the beginning of the breeding programme, the existence of several herds with animals with a wide range of ages that were analysed in the same moment, as well as the continuous incorporation of new herds to the breeding programme (and the departure of others that have been purified for translocation), which suggests caution in the analysis of
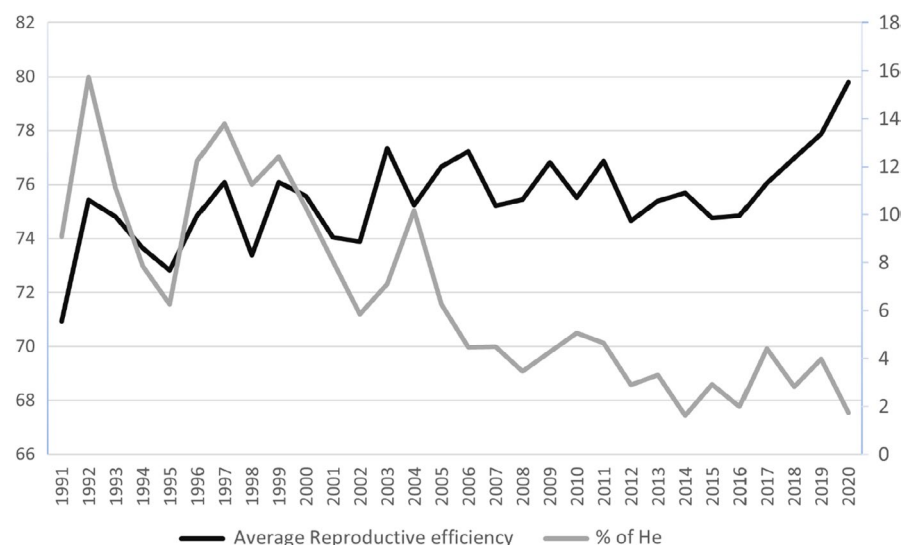

FIGURE 1 Evolution of percentage of heterozygotes (right *Y*-axes) and reproductive efficiency average (left *Y*-axes) in the last 30 years. Re is expressed in percentage. He: rob(1;29) heterozygous carriers
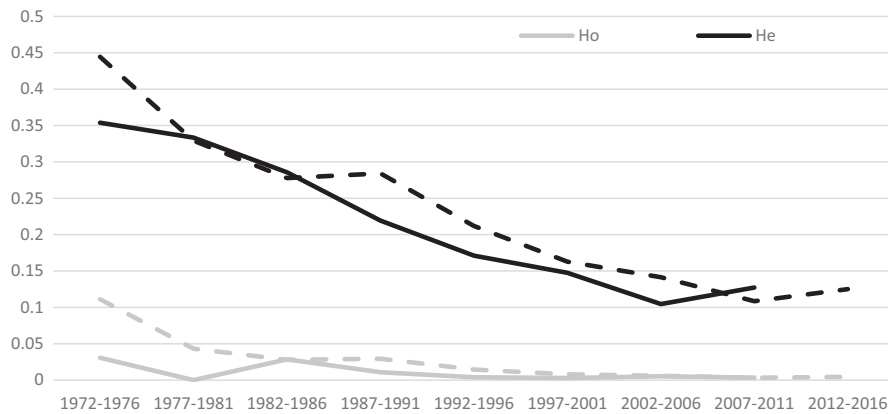
FIGURE 2 Evolution of the observed (full line) and expected (dashed line) frequencies of heterozygous (He) and homozygous (Ho) rob(1;29) carriers according to H-W. Data were analysed by generational intervals (5 years)

TABLE 1 Descriptive statistics for input data

Parameter		Mean	Minimum	Maximum	Coef. Var.
Reproductive efficiency (%)	F	76.77 ± 10.18	40	100	13.25
	He	73.46 ± 9.49	48	100	12.91
1st calving age (months)	F	34.01 ± 4.01	20	42	0.21
	He	34.71 ± 4.38	25	42	0.59
Cow inbreeding		0.06 ± 0.08	0	0.46	145.12
Calving age (months)		79.40 ± 39.41	20	285	49.62

Note: F: free rob(1;29), He: heterozygous carriers rob(1;29).

the H-W evolution over the time. Finally, although this increase of Re can be related to the decrease in the translocate rate, it may be also explained in part by to other effects improvements related to animal management and/or a better reproductive register and control. On the contrary, the decrease in rob(1;29) carriers was produced by the selection against translocated bulls (mandatory karyotype analysis is performed on every bull previous to its acceptance as active breeder) by the ANCRE breeding programme. However, it is worth mentioning the existence of Retinta herds outside the breeding programme in which its rob(1;29) incidence is still high (the highest rate detected was 19.23% in 2019; data not shown).

3.2 | Reproductive and genetic analysis

In general, the Re was high in Retinta cows, despite that AFC is delayed 8 months on average from the optimal value (2 years from the point of view of the maximum number of calving that can be obtained from a cow; Table 1). This latter result could be produced by the fact that some herds implemented a delay in the first mating to reduce the calving problems on heifers when they are used in crossbreeding. Interestingly, both parameters (Re and AFC) showed a reduced variation coefficient (C.V.) (Abanikannda & Olutogun, 2019; Bresolin et al., 2015; Mwatawala & Kifaro, 2009; Stefani et al., 2021), suggesting a high degree of homogeneity and reliability in Re and (indirectly) the existence of homogeneous reproductive management among Retinta farms as well as a high adaptation of the cows to the

environmental conditions where they are bred. On the contrary, inbreeding values showed a large variability among individuals (ranging from 0% to 46.5%); nevertheless in general, they were moderate to high, with an average near to 6%. The analysis of the variance components and heritability showed a large influence of the permanent environmental and HYS effects (37% and 16%, respectively, Table 2). However, the Re heritability remains moderate (0.17), which allows an effective selection for this trait in the Retinta breed.

Genetic analysis revealed a large effect of AFC on Re (Table 3), which is expected since a delay at the first calving (levels 2 and 3) is difficult to compensate, even in cows with high longevity. In addition, our results showed a negative effect in Re produced by heterozygous rob(1;29) carriers (−5.50, $p < .001$), which was absent in the two remaining levels (Ho and F). Finally, although both covariates analysed (CA and FC) were statistically significant, they have a minimal incidence in terms of Re.

4 | DISCUSSION

In this study, we aimed to determine the reproductive effect of the most widespread chromosomal abnormality in cattle, using a quantitative approach and a data set gathered over more than 30 years.

To this time, more than 50 Robertsonian translocations were reported in cattle (reviewed by Iannuzzi et al. (2021)); however, most of them were dicentric, thus disappearing after some generations due to the instability produced by two active centromeres. In contrast, a

TABLE 2 Variance components and parameter estimates for reproductive efficiency (Re)

Effect	Variance components	Parameter estimates
Additive genetic effect	20.91 ± 1.587	0.17 ± 0.012
Permanent environmental effect	37.0 ± 1.277	0.30 ± 0.003
Herd–year–season effect	15.88 ± 0.459	0.13 ± 0.001
Residual effect	51.19 ± 20.324	

TABLE 3 Solution for estimated effects of the model in reproductive efficiency (Re)

Effect	Level	Solution
AFC	1	0
	2	−13.90 ± 0.184***
	3	−21.62 ± 0.217***
rob(1;29)	F	0
	He	−5.48 ± 0.426***
	Ho	−0.38 ± 2.390^{ns}
		Regression coefficient
Calving age		−0.12 ± 0.001***
Cow inbreeding		−3.81 ± 1.261**

Note: AFC: 3 classes of monthly intervals 1 ≥ 20<30; 2 ≥ 30<36; 3 ≥ 36<42.5.

Abbreviation: Ns, non-significant.

*,**,*** significative at 0.05, 0.01, or 0.001 significance level.

complex series of chromosomal rearrangements producing a monocentric and stable configuration were responsible for the onset of rob(1;29) (Escudeiro et al., 2021). This stability across generations has allowed its spread worldwide (De Lorenzi et al., 2012), particularly in some small breeds of Europe, in which its prevalence is still high (Iannuzzi et al., 2008; Rodero-Serrano et al., 2013). Despite that, there is a consensus on the negative effect of this translocation on fertility in cattle; specific studies in extensive conditions are still missing.

To date, the largest study on the incidence of rob(1;29) on reproduction, health, morphology and productive traits was conducted by Gustavsson (1969) in SRB dairy cattle. After that, Kovacs (1994) and Gustavsson (1969) reported a negative effect of the rob(1;29) on fertility after the diagnosis as heterozygous carriers of two dairy bulls intensively used as breeders. After that, several additional efforts were made in European countries to characterize and control the rob(1;29) spread, by developing cytogenetic screening programmes including hundreds of individuals of beef and dairy breeds (Lonergan et al., 1994). However, despite the consensus generated regarding the reproductive effect of this trait, none of them have quantified to what extent fertility is affected by rob(1;29) in extensive breeding conditions. In contrast, this study, performed using a quantitative

approach in a large data set, allows us to demonstrate accurately that the effect produced by the rob(1;29) on fertility in beef cattle is limited, even more compared with those produced by additive and environmental effects.

The only known phenotypic change reported in rob(1;29) carriers is a reduction in fertility in individuals with a heterozygous genotype (Gustavsson, 1969). This phenotypic decrease was demonstrated analysing data from commercial herds (Kovacs, 1994) and I.A. (Gustavsson, 1969) and IVF programmes (Lonergan et al., 1994). Such reduction is caused by chromosomally unbalanced oocytes and spermatozoa (Bonnet-Garnier et al., 2006) produced during the meiotic segregation in heterozygous animals. During fertilization, such gametes will produce aneuploid zygotes which only develop until early stages of embryonic life. In practice, all the cows carrying aneuploid embryos will return to heat in the next cycle since all these events are produced before the uterine implantation. However, it is noteworthy that only heterozygous carriers are able to produce aneuploid gametes, and therefore, the reproductive effect should be absent in homozygous carriers of the rob(1;29). Our results fully agree with that hypothesis, since only rob(1;29) heterozygous carriers (He) were less fertile compared with homozygous or non-translocated animals, in which no reduction in fertility was appreciated. However, it is worth mentioning that the number of homozygous carriers analysed was low (compared with F and He groups), suggesting some caution by acknowledging the results obtained in that group.

Although that rob(1;29) genotype could be treated as a 'monogenic' effect affecting fertility, the whole trait reproductive phenotype is heavily influenced by environmental factors (Pryce et al., 2004; Short et al., 1990). This is particularly true in beef breeds raised under extensive grazing conditions, in which reproductive phenotypes are more difficult and expensive to determine (Naya et al., 2017). Even though we detect a large influence of the environmental factors on Re, the negative effect of rob(1;29) genotype was significant, showing a magnitude similar to calving age and cow inbreeding effects together. Despite the rob(1;29) translocation has a direct effect on reproductive outcome, our results demonstrate that the variations in the fertility among the individuals are triggered by multifactorial causes, including genetic and non-genetic effects. In addition, it demonstrates that the reduction in fertility caused by the rob(1;29) on populations with a moderate-to-low percentage of carriers is extremely low (less than 0.01% of the decrease in Retinta Cattle in 2020).

Our study also analysed cows with an inbreeding load that could be considered extremely high ($F > 20\%$), without showing a negative effect. However, those values were associated with reductions in fitness, adaptability and fertility in cattle (Carolino & Gama, 2008; Santana et al., 2010), including Retinta breed (Dorado et al., 2017). Three situations can explain the differences. First, the number of individuals with increased inbreeding was low (less than 9% of the total, data not shown) in comparison with the total number of cows analysed, thus diluting the phenotypic depression in the whole population. Second, some individuals are more 'resistant' to the harmful effects of inbreeding on the

phenotype (by harbouring a reduced depression load (Poyato-Bonilla et al., 2020)), and therefore, they could remain in some herds despite their inbreeding values if their fertility is not affected. Finally, our previous studies evaluating the effect of inbreeding on the fertility of Retinta animals suggested that such decrease is associated with negative changes in sperm quality in bulls rather than an effect caused by the fertility of the cow (Dorado et al., 2017; Teran et al., 2021).

Similarly, the regression coefficient for calving age was low (−0.123% of average reduction in Re per year), suggesting that the reproductive efficiency is barely affected by the age of the cow (at least to advanced cow ages). This result fits with the regularity observed in Retinta breed, in which cows are extremely longevous maintaining higher fertility rates even at very old ages (Morales et al., 2017). The medium-magnitude heritability obtained (0.17) presents a high level of significance due to its low estimation error; in addition, the methodology used (REML) ensures an estimation free of biases (e.g. assortative matings). Furthermore, this result together with the h^2 value estimated, 0.17, and the trait repeatability of 0.46 suggests that Re is an interesting trait to evaluate the fertility in large populations of cows reared under extensive conditions. The high trait repeatability allowed an evaluation of the animal fertility at relatively early ages, making it possible to take into account this parameter (Re) for the election of breeders' next generation.

Finally, our results showed that the prevalence of rob(1;29) could be controlled and reduced if this 'trait' is included as negative selection criteria within a breeding programme. This fact was proposed previously by Ducos et al. (2008), which gathered information on several breeds and countries across Europe 15 years ago. However, their reports were collected during a reduced period, and therefore, they were not able to conclude on long-time consequences of such breeding practices. Our analysis demonstrates that the exclusion of heterozygous and homozygous bulls for the rob(1;29) translocation (without culling any affected cow) was able to reduce, in a lapse of 30 years, the incidence of this genetic disease by more than 15-fold to the current values (close to 1%). At the same time, this practice was able, together with a better animal management of environmental factors, to increase the fertility of Retinta cows without any notorious reduction in the census and genetic variability of the breed.

5 | CONCLUSIONS

In this study, we were able to validate and quantify, using a large data set and a quantitative approach, the negative effect of the rob(1;29) translocation on the fertility of beef cattle reared in field conditions. Our results showed that the loss of reproductive efficiency in populations with a moderate–high prevalence of rob(1;29) (15% as the initial incidence in this breed 30 years ago) is noteworthy, but its effect may go unnoticed, without a specific analysis, masked by the environmental factors, particularly under extensive conditions. On the contrary, in populations with a very lower prevalence of rob(1;29) translocation such as the current Retinta breed, no significant effect on fertility can be seen, and economic losses could be negligible. For this reason, the use (and maintenance) of screening programmes for this genetic disease will allow minimizing their influence on the future fertility of the herds.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

AM, MMM and SDP contributed to conceptualization; RM, JMJ and MMM retrieved the data; RM and AM contributed to EVB´s estimation; JMJ, RM and SDP analysed the data; MMM and SDP contributed to karyotyping; SDP contributed to project management and overseeing; all the authors collaborated with writing and correcting the manuscript.

DATA AVAILABILITY

The data sets employed in this study are property of the Asociación Nacional de Criadores de Ganado Vacuno Selecto Español (ANCRE) and were provided for scientific purposes under a specific collaboration arrangement. The data set could be provided for scientific purposes to further authors under reasonable request in the ANCRE technical department (retinta@retinta.es).

ORCID

Sebastián Demyda-Peyrás https://orcid.org/0000-0003-3286-2441

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