



Genetic diversity assessment of the Mexican Simmental population through pedigree analysis

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ABSTRACT - The purpose of this study was to examine the genetic variability of the Mexican Simmental. Inbreeding was calculated by year for animals born from 1985 to 2014. Proportion of ancestors known, average equivalent complete generations, generation interval, and effective size, as well as the effective numbers of founders, ancestors, and founder genomes were calculated for animals born in six periods (1985-1989, 1990-1994, 1995-1999, 2000-2004, 2005-2009, and 2010-2014). The year 1985 was selected as the initial year to form the subpopulations since the registration of the first Simmental cattle born in Mexico began in this year. Gene contributions of ancestors with the highest genetic influence were also calculated, using data of animals born in the latter period. Coefficients of inbreeding were low, ranging from 0.0068 to 0.0165. The average number of equivalent complete generations increased from 3.71, for the 1985-1989 subpopulation, to 5.83, for the 2010-2014 subpopulation. The population showed an effective population size of 186.6 animals in the last period. The numbers of founders, ancestors, and founder genomes increased from 1985 to 2004, but decreased from 2005 to 2014. The ratio of effective number of ancestors to effective number of founders and the ratio of effective number of founder genomes to effective number of ancestors were 0.31 and 0.66 and 0.27 and 0.63 for animals born in the 2005-2009 and 2010-2014 periods, respectively, revealing loss of diversity due to bottlenecks and genetic drift in the last decade. One ancestor explained 3.4% of the total genetic variability of the progeny born from 2010 to 2014, whereas the first fifteen ancestors explained 20% of such variability. The pedigree analysis showed Mexican Simmental cattle are not currently endangered.

Key Words: effective number of ancestors, effective population size, inbreeding, marginal genetic contribution, Mexican Simmental cattle

Introduction

It has been widely demonstrated that pedigree analysis is an effective tool to monitor changes of genetic diversity of multiple breeds of cattle. The amount of genetic variability has been successfully estimated worldwide for dairy breeds as Brown Swiss (Hagger, 2005), Holstein Friesian (Maltecca et al., 2002), and Jersey (Sørensen et al., 2005) and for beef breeds as Alentejana (Carolino and Gama, 2008), Angus (McParland et al., 2007), Avileña, Alistana, Sayaguesa, Negra Ibérica, Morucha, Asturiana de los Valles, Asturiana de la Montaña, Pirenaica (Gutiérrez et al., 2003), Japanese Black (Honda et al., 2004), Japanese Brown (Honda et al., 2006),

Limousin (Boichard et al., 1997), Nellore (Brito et al., 2013), and Red Angus (Márquez et al., 2010), applying the methods developed by James (1972), MacCluer et al. (1986), Lacy (1989), and Boichard et al. (1997). Up to now, however, it seems that there are no pedigree analysis available (research papers) based on probability of gene origin for Mexican dairy and beef cattle populations. Specifically, no genealogical data analysis of the Mexican Simmental cattle population has been carried out; therefore, estimates of effective population size and effective numbers of founders, ancestors, and founder genomes, for instance, are not currently available. Since beef cattle breeding plays an important role in Mexican agricultural economics and the Simmental breed has exhibited great adaptation to different Mexican environmental conditions, except to tropical (Rosales et al., 2004), a comprehensive characterization of the genetic variability of this breed is needed. Based on the above-mentioned facts, it was thought useful to study the genetic variability in the registered Mexican Simmental cattle population, based on both probability of identity-by-

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descent of genes and probability of gene-origin methods, and the interrelations among the effective numbers of founders, ancestors, and founder genomes for several time periods to determine possible causes of genetic diversity loss.

Material and Methods

Data were provided by the Mexican Simmental-Simbrah Breeders Association. These data consisted of individual, sire and dam identification number, date of birth, sex, and herd of origin. Records were checked to ensure that sires only appeared as sires, but not as dams; dams only appeared as dams, but not as sires; progeny only appeared as progeny, but not as sire and/or dam in the same record; no progeny was born before neither of their two parents; and there were no duplicate records. After data checking, the final dataset used in the present study contained 141,600 genealogical records of animals born between 1963 and 2014.

Genealogical records were subdivided into five-year periods to study the trend of the estimates of the genetic variability parameters over time periods. To form the subpopulations, 1985 was selected as the base year because the Mexican Simmental-Simbrah Breeders Association registered the first Simmental cattle born in Mexico in this year. The average inbreeding coefficient was calculated per year for animals born from 1985 to 2014. The proportion of ancestors known, average equivalent complete generations, effective population size, and effective numbers of founders, ancestors, founder genomes, and non-founders were calculated for animals born in six different periods: 1985-1989, 1990-1994, 1995-1999, 2000-2004, 2005-2009, and 2010-2014. These six groups of animals constituted the different subpopulations evaluated. Average equivalent complete generations were also calculated by year, from 1985 to 2014. Effective population sizes were estimated from individual increase in inbreeding (Gutiérrez et al., 2009). In addition, total, marginal, and cumulated gene contributions of the first 1000 ancestors with the greatest genetic influence and the generation interval for each of the four parent-offspring pathways were calculated using the sixth reference population (animals born between 2010 and 2014). The measures to assess genetic diversity based on genealogical records are not outlined here; a detailed

description may be found elsewhere (e.g., Boichard et al., 1997; Gutiérrez et al., 2003).

The average inbreeding coefficient and effective numbers of founders, non-founders, and founder genomes were calculated with the CFC computer program (Sargolzaei et al., 2006). The ENDOG computer package (Gutiérrez and Goyache, 2005) was used to calculate the proportion of ancestors known (MacCluer et al., 1983), average equivalent complete generations, average generation interval, effective population size, and effective number of ancestors. Total, marginal, and cumulated gene contributions were calculated using the PEDIG software (Boichard, 2002).

Results

The number of individuals in the reference populations varied from 10,941 (1985-1989) to 21,795 (2005-2009) (Table 1). The number of individuals with only one known parent was very low; therefore, the proportion of individuals with two known parents was 0.99 in all subpopulations. The pedigree size (reference population plus ancestors) varied from 32,357 animals, for the 1985-1989 subpopulation, to 54,276 animals, for the 2005-2009 subpopulation. The number of animals in the pedigree decreased from the 2005-2009 period to the 2010-2014 period because, when the database was analyzed, it did not contain all the calves that were registered in 2014.

Proportions of ancestors known by generation significantly increased over periods (years) for paternal and subsequent generations. The proportions of parents known were very high, with values oscillating from 0.996 to practically 1 (Table 2). The proportions of grandparents and great-grandparents known ranged from 0.862 to 0.957 and from 0.727 to 0.919, respectively. As expected, the proportions of ancestors known were considerably smaller in the last two generations, varying from 0.539 to 0.842, in the fourth generation, and from 0.342 to 0.711, in the fifth generation; these ranges, however, also indicated that the proportion of ancestors known in the last two generations has significantly improved across periods. The average equivalent complete generations increased from 3.71, for the 1985-1989 subpopulation, to 5.83, for the 2010-2014

Table 1 - Pedigree description for each reference population

	1985-1989	1990-1994	1995-1999	2000-2004	2005-2009	2010-2014
Number of individuals in the reference population	10,941	17,391	19,377	20,712	21,795	14,939
Number of individuals in the pedigree	32,357	45,472	51,661	53,394	54,276	45,638
Total number of founders	8,563	9,469	9,711	9,422	8,543	6,989
Number of individuals with two known parents	23,453	35,599	41,479	43,462	45,320	38,361
Number of individuals with one known parent	341	404	471	510	413	288

subpopulation, also indicating that the degree of pedigree completeness improved across periods.

Coefficients of inbreeding were below critical levels, ranging from 0.0068 (2014) to 0.0165 (1997) (Figure 1). Inbreeding coefficients showed a relative stability evolution across years. However, the evolution of the average equivalent complete generations indicates a steady increase across years, from nearly 3.4 generations, for animals born in 1985, to nearly 6.0 generations, for animals born in 2014.

In general, generation intervals increased across periods for the four parent-offspring pathways. However,

Table 2 - Proportions of ancestors known by generation and reference population and average equivalent complete generations by reference population (ECG)

Subpopulation	Generation					ECG
	1	2	3	4	5	
1985-1989	0.9958	0.8621	0.7268	0.5391	0.3415	3.71
1990-1994	0.9974	0.9077	0.7966	0.6492	0.4623	4.29
1995-1999	0.9965	0.9159	0.8242	0.7081	0.5471	4.68
2000-2004	0.9969	0.9133	0.8354	0.7254	0.5880	4.97
2005-2009	0.9994	0.9277	0.8791	0.7721	0.6364	5.35
2010-2014	0.9999	0.9570	0.9188	0.8415	0.7114	5.83

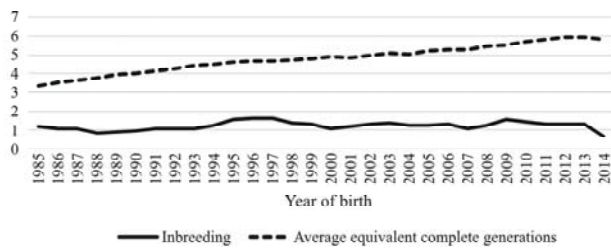


Figure 1 - Inbreeding (%) and average equivalent complete generations of the registered Mexican Simmental cattle population.

the two father-offspring generation intervals were greater than those two for the mother-offspring pathways (Table 3). In the last period, the average father-offspring generation interval was nearly two years longer than the average mother-offspring generation interval.

The population showed an increase in effective size since 1985 and until 2014 (Table 4). The effective numbers of founders, ancestors, and founder genomes increased from 1985 to 2004, but decreased from 2005 to 2014, indicating loss of genetic diversity in Mexican Simmental in the course of the last decade. Estimates for the last five-year period were 774, 209, and 131, respectively. The ratio between the effective number of ancestors (f_a) and the effective number of founders (f_c) indicated that the loss of genetic diversity was partially due to the presence of bottlenecks in the pedigree. The $f_a:f_c$ ratios were 0.38, 0.40, 0.39, 0.36, 0.31, and 0.27 for animals born in the 1985-1989, 1990-1994, 1995-1999, 2000-2004, 2005-2009, and 2010-2014 periods, respectively. On the other hand, the ratio between the effective number of founder genomes (N_g) and the effective number of founders is an indicator of the magnitude of genetic drift; smaller values indicate greater loss of genetic diversity. The $N_g:f_a$ ratios were 0.85, 0.80, 0.74, 0.69, 0.66, and 0.63 for progeny born in the 1985-1989, 1990-1994, 1995-1999, 2000-2004, 2005-2009, and 2010-2014 periods, respectively.

As expected, the majority (12) of the fifteen ancestors with the highest genetic contribution were males, whereas only three females made a significant genetic impact on the population (Table 5). The females ranked 7, 14, and 15. The genetic contribution of the most influential male ancestor was 3.4%, while that of the most influential female ancestor was 1.3% of the total genetic variability of the progeny born from 2010 to 2014. The first fifteen ancestors explained almost 20% of the total genetic variability.

Table 3 - Generation interval by parent-offspring pathway for the six reference populations

Pathway	1985-1989	1990-1994	1995-1999	2000-2004	2005-2009	2010-2014
Father-son	5.2±0.25	5.9±0.25	5.6±0.30	6.6±0.29	7.8±0.29	8.5±0.72
Father-daughter	6.2±0.19	5.9±0.19	5.9±0.23	6.3±0.19	6.6±0.19	6.3±0.45
Mother-son	4.2±0.12	4.4±0.14	4.5±0.16	4.9±0.17	6.1±0.19	5.9±0.44
Mother-daughter	4.3±0.12	4.6±0.12	5.2±0.14	5.7±0.11	5.9±0.12	5.4±0.29

Table 4 - Estimates of genetic variability for each reference population

	1985-1989	1990-1994	1995-1999	2000-2004	2005-2009	2010-2014
Effective population size	134.7±41	150.7±43	125.8±35	162.4±42	173.8±42	186.6±41
Effective number of founders	333.0	355.9	502.5	734.2	824.7	774.0
Effective number of ancestors	127.0	142.0	195.0	261.0	255.0	209.0
Effective number of founder genomes	107.8	113.0	145.0	179.3	167.9	131.3
Effective number of non-founders	159.4	165.7	203.7	237.2	210.8	158.2

Table 5 - The fifteen ancestors with the highest genetic contribution to the genome of the progeny born from 2010 to 2014

Ancestor	Sex	Birth year	Number of progeny	Genetic contribution (%)	
				Marginal	Cumulated
Great Guns Ferdinand 13Z	Male	1990	469	3.4	3.4
Balist	Male	1984	66	1.6	5.1
Bar 5 Western 856K	Male	2000	257	1.6	6.7
Signal	Male	1969	709	1.4	8.0
Siegfried	Male	1971	25	1.3	9.3
Bel CB Western 2nd	Male	1982	68	1.3	10.6
Lilli	Female	1982	13	1.3	11.9
Mr Miraflores 69A	Male	1991	183	1.2	13.2
BHR Doorn G629E	Male	1997	153	1.1	14.3
Mr Miraflores 50C	Male	1993	215	1.1	15.4
R&R Papillon 411W	Male	1987	128	1.0	16.5
Bar 5 Regency 864K	Male	2000	294	0.9	17.4
Balu 1383115	Male	1990	40	0.8	18.2
Miss Knight 155S	Female	1984	15	0.8	19.1
Toverberg Erika	Female	2006	9	0.8	19.9

Discussion

Proportions of ancestors known in the Mexican Simmental population are quite acceptable compared with those of other breeds. The proportions of ancestors known obtained by Carolino and Gama (2008) with the Alentejana breed for the first three generations for calves born in the period of 2000 to 2003 are similar to those of corresponding generations of the present study. Proportions of known ancestors for animals born between 1990 and 2001 reported by Cleveland et al. (2005) for parental and grandparental generations of US registered Hereford cattle are similar to corresponding proportions for the last population subset (2010-2014) of the current investigation. On the contrary, Gutiérrez et al. (2003) and Baro de la Fuente et al. (2007) reported much smaller proportions of parents, grandparents, and great-grandparents known for eight Spanish autochthonous breeds of beef cattle (Alistana, Sayaguesa, Avileña, Negra Ibérica, Morucha, Asturiana de los Valles, Asturiana de la Montaña, and Pirenaica).

Based on the average number of equivalent complete generations, the level of pedigree knowledge in the Mexican Simmental 2010-2014 subpopulation (5.83) is similar to those in the Bazadaise (5.8), Blonde d'Aquitaine (5.8), Flamande (5.8), and Parthenaise (6.2); smaller than those in the Aubrac (7.8), Charolais (7.9), Limousin (6.7), and Salers (8.0); and greater than those in the Ferrandaise (3.7), Gasconne (3.4), and Rouge des prés (4.8) cattle populations studied by Leroy et al. (2013). The average number of equivalent complete generations for the 2010-2014 subpopulation is also greater than those reported by Solkner et al. (1998), for Simmental (4.1); Baumung and Solkner (2002), for Tux-Zillertal (2.5); Pérez Torrecillas et al. (2002), for Chianina (2.88); Gutiérrez et al. (2003), for Asturiana de

los Valles (1.1); Bozzi et al. (2006), for Marchigiana (4.5); and Fernández et al. (2007), for Cachena (1.6).

Despite the observed increase in the average number of equivalent complete generations (Figure 1), inbreeding remained relatively stable across years (1985-2014). This phenomenon is not usual since inbreeding is supposed to increase with pedigree knowledge. However, this kind of result may happen when regular registration of animals with unknown ancestors is carried out, which is the case here, as even in the 2010-2014 period, 4.3% of grandparents and 8.1% of great-grandparents were unknown. These unknown ancestors were related to old and overseas AI sires with unknown genealogies at the moment of their registration in the Mexican Simmental-Simbrah Association. Boichard et al. (1997) observed that inbreeding is very sensitive to incomplete pedigrees, estimating that 10% incomplete data were enough to strongly underestimate inbreeding. Gutiérrez et al. (2003) stated that "an indepth analysis of the pedigree completeness level of breeds is important since all results in terms of inbreeding and relationship are dependent upon it".

Mean inbreeding coefficient of the 30 years (0.012) was smaller than those reported by other researchers for several breeds of beef cattle. Nomura et al. (2001), Cleveland et al. (2005), and Márquez et al. (2010) reported values of 0.05, 0.098, and almost 0.04 for American Hereford, Japanese Black, and American Red Angus, respectively. On the other hand, similar to the present mean estimate, a mean inbreeding coefficient of 0.01 was found in the American Limousin population (Gengler et al., 1998) and of around 0.02 in the Italian Chianina, Marchigiana, and Romagnola populations (Bozzi et al., 2006).

The discrepancy in generation intervals between the father-offspring and mother-offspring pathways found in

the present study may be attributed to the prolonged use of popular AI sires. In contrast, Gutiérrez et al. (2003) and Bozzi et al. (2006) reported that the father-offspring pathways showed shorter generation intervals than the mother-offspring pathways, attributing such difference to the early replacement of sires when artificial insemination is used. The consistent increment of the effective population size from 134.7 to 186.6 over the evaluated period (1985-2014) could be due to the artefact of increasing pedigree knowledge while inbreeding remained stable. The effective population size of the last period is nearly four times greater than the minimum size of about 50 animals per generation, recommended by FAO (1998), to maintain genetic variability for selection (Goddard and Smith, 1990) and conservation purposes (Meuwissen and Woolliams, 1994). The current effective population size for the 2010-2014 subpopulation (186.6) is smaller than the effective population sizes based on individual breeding rate for French Aubrac (291), Blonde d'Aquitaine (194), Charolais (646), Limousin (412), Parthenaise (263), and Rouge des prés (294), but greater than average equivalent sizes for French Bazadaise (104), Ferrandaise (58), Flamande (97), Gasconne (139), and Salers (136), reported by Leroy et al. (2013). However, some of these populations could probably have fewer registered cattle than the Mexican Simmental-Simbrah Breeders Association.

Estimates of effective numbers of founders, ancestors, and founder genomes could be also affected by loss of pedigree information, but to a smaller extent than inbreeding coefficients (Boichard et al., 1997). Current effective numbers of founders, ancestors, and founder genomes are greater than those reported for French Abondance, Limousin, and Normande (Boichard et al., 1997); Austrian Braunvieh, Grauvieh, Pinzgauer, and Simmental (Solkner et al., 1998); Swiss brown cattle (Hagger, 2005); Italian Chianina, Marchigiana, Maremmana, Mucca Pisana, and Romagnola (Pérez Torrecillas et al., 2002; Bozzi et al., 2006); and Irish Angus, Charolais, Hereford, Limousin, and Simmental (McParland et al., 2007).

In general, the marginal genetic contribution of the first fifteen ancestors was relatively uniform compared with the marginal genetic contribution observed in other beef cattle populations. For a Brazilian Nellore herd, Brito et al. (2013) found that 20.1% of the marginal genetic contribution was explained by only eight ancestors (half of the total ancestors of the present study), of which the most influential ancestor inherited 10.6% of the genes. Similarly, Solkner et al. (1998) reported that in the Austrian Braunvieh, Pinzgauer, and Grauvieh cattle populations, the most important ancestor contributed almost 10% of the genes to the

reference population, while in the Austrian Simmental cattle population, such contribution was 4.3%. In addition, these authors informed that the first ten ancestors explained 24, 32, 38, and 41% of the total genetic variability in each breed, respectively, suggesting that Mexican Simmental cattle are genetically more diverse than the breeds mentioned above.

Conclusions

The Mexican Simmental cattle population presents low levels of inbreeding, but has undergone some reduction in its genetic variability in the last ten years partly due to bottlenecks in the pedigree and partly due to random genetic drift. The scientific literature, however, suggests that the Mexican Simmental population is genetically more diverse than many other beef cattle populations, such as the Austrian Simmental population, since it has been reported that the amount of genetic variability in this latter cattle population was generated by only 94 non-related founders in 1995. Overall, the genetic status of the present evaluated population is not endangered, which could be partially due to the fact that expected progeny differences for growth traits (weaning and yearling weight, for example) are not extensively used for selection purposes, even though such BLUP estimates have been available for Mexican Simmental breeders since 2001.

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