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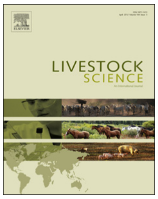

Assessment of pedigree information in the Quarter Horse: Population, breeding and genetic diversity

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ABSTRACT

This study aimed to evaluate population parameters and to describe the genetic diversity of Quarter Horse breed (QH) in Brazil, reported for the first time in the literature. The pedigree data comprised 131,716 animals representing the total population (TP), with records of animals born between 1747 and 2008. The reference population (RP) representing the last generation was applied in this study considering 47,861 animals born between 2000 and 2008. The average generation interval was 9.6 and 10.8 years in TP and RP, respectively. The average equivalent complete generations (EG) were 5.09 (TP) and 6.24 (RP). The inbreeding coefficient (F), average relatedness (AR) and the increase in inbreeding by generation (ΔF) was 1.07%, 0.95% and 0.24%, respectively, for TP. The effective population size (N_e) based on ΔF was 195 and 164 for TP and RP, respectively. The effective number of founders (f_e) was 1045 and 811 for TP and RP, respectively, that of ancestors (f_a) was 156 and 113, and that of founder genomes (f_g) was 105 and 66. The f_e/f_a and f_e/f_g ratios in TP were 6.70 and 9.95, respectively, and an increase was observed in RP, indicated a strong bottleneck effect. The total genetic diversity of the QH breed was explained by 4780 ancestors, with 50% of diversity being explained by only 121 and 72 ancestors in TP and RP, respectively. The thoroughbred stallion Three Bars is the most influential ancestor with the largest marginal genetic contribution for TP (5.73) and RP (5.94%). The results demonstrate a large number of founders and ancestors, but a small ancestor group was responsible for the continuity of the QH breed in Brazil. These finding highlight the importance of monitoring genetic diversity, including follow-up by breeding programs, to permit control of the next generations.

1. Introduction

The Quarter Horse (QH) breed originated in the United States in the 17th century from the crossing of stallions from Arabia and Turkey, characterized by resistance and elegance, with fast and muscular English Thoroughbred dams, resulting in a compact and muscular horse that is agile when used as a working horse and fast in short-distance races (ABQM, 2017). The versatility of the QH breed was investigated recently in the genomic study of Petersen et al. (2014), who described six groups (halter, western pleasure, reining, working cow, cutting, and racing short distances) within the breed. In Brazil, the first animals were imported from the state of Texas (USA) in 1955 and the Brazilian Association of Quarter Horse Breeders (ABQM) was founded in 1969. The Association registers the births of the animals and considers them to be of pure origin when their parents are registered in their Studbook or by the American Quarter Horse Association (AQHA). The Brazilian Studbook contains no information about the performance group of the animals, such as those cited by Petersen et al. (2014). Between 2012 and 2016, the ABQM recorded financial transactions in auctions throughout Brazil of about USD 302 million, with the sale of approximately 27,000 animals. About 310,000 professionals directly work on horse farms distributed over an area of approximately 1 million hectares, with an estimated value of more than USD 6 billion (ABQM, 2017).

Studies addressing important topics for the development and design of genetic breeding programs are necessary to guide technicians and breeders in the continuous improvement of the QH population. Parameters such as pedigree completeness (MacCluer et al., 1983), generation interval (GI), inbreeding coefficient (Wright, 1931) and the probability of gene origin (Boichard et al., 1997) are important to

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design an animal breeding program. The data obtained permit to verify the genetic diversity and changes over time (Maignel et al., 1996). The objective of the study was to evaluate population parameters and to estimate the genetic diversity of QH in Brazil based on pedigree records.

2. Material and methods

2.1. Data and statistical analysis

The pedigree data, including records of the animal, sire, dam, sex and date of birth, were provided by ABQM. Ancestors of sires not present in the file that are necessary to increase the quality of the pedigree were added. The data of these ancestors were obtained from the internet: Pedigree Online's All Breed Pedigree Database (www.allbreedpedigree.com). The total population (TP) consisted of 131,716 animals born between 1747 and 2008, with records of 60,933 males and 70,783 females born to 11,838 stallions and 34,028 mares. The reference population (RP) representing the last generation was applied in this study considering 47,861 animals born between 2000 and 2008, with records of 23,041 males and 24,820 females (36% of TP), born to 4503 stallions and 17,763 mares.

Preparation of the data and statistical analysis were performed using the MEAN and FREQ procedures of the SAS software (SAS, 2011). The population and reproductive parameters, probability of gene origin and genetic diversity were obtained with the ENDOG V4.8 program (Gutiérrez and Goyache, 2005).

2.2. Reproductive parameters and generation interval

The reproductive parameters including the mean, median, minimum, mode and maximum number of offspring, number of sires and mare-stallion ratio were calculated only for TP. The GI was obtained in both populations based on the average age of the parents at the birth of offspring that reproduced (James, 1972) and was calculated for the four different path of selection: sire-son, sire-daughter, dam-son, dam-daughter, and all parent-offspring.

2.3. Quality of pedigree data

Pedigree completeness was calculated as the proportion of ancestors known in each ascending generation (MacCluer et al., 1983) and ancestors with no known parent were considered founders as described by Gutiérrez and Goyache (2005). Providing equal information about the quality of pedigree data, the number of generations was computed in three different ways: (1) number of full generations traced (FG), which corresponds to the number of generations with both parents known; (2) number of equivalent complete generations (EG), which is calculated as the sum over all known ancestors based on $(1/2)^n$, where n is the number of generations between the animal and each known ancestor, and best represents the pedigree information (Maignel et al., 1996); (3) maximum number of generations traced (MG), which provides the number of generations that separate the individual from its furthest ancestor, regardless of whether or not the parents are known.

2.4. Inbreeding parameters

The individual inbreeding coefficient (F) is defined as the probability that an individual has two identical alleles by descent (Wright, 1931) and was calculated using the algorithm proposed by Meuwissen and Luo (1992). The average relatedness coefficient (AR) of each animal was described by Goyache et al. (2003) and Gutiérrez et al. (2003) as the representation of a given animal in the pedigree and was defined as the probability that an allele randomly chosen from the population belongs to a given animal. The increase in inbreeding by generation (ΔF) was calculated with the classical formula

$$\Delta F = (F_t - F_{t-1})/(1 - F_{t-1}) \tag{1}$$

where F_t and $F_{t\text{-}1}$ is the average inbreeding in the ith generation.

To calculate the effective population size (N_e), defined by Gutiérrez and Goyache (2005) as the number of breeding animals that would lead to the actual increase in inbreeding if they contributed equally to the next generation, was considered:

$$N_e = 1/2\Delta F \tag{2}$$

where ΔF indicates the average inbreeding increase per generation.

In addition, N_e was calculated based on the individual increase in inbreeding as suggested by Gutiérrez et al. (2009) and was used for the calculation of genetic drift.

2.5. Probability of gene origin and genetic drift

The effective number of founders (f_e) is given by the measurement of the contributions of the most influential founders. Lacy (1989) defines f_e as the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population studied. This parameter was calculated using the formula

$$f_e = 1/\sum_{k=1}^{f} q_k^2 \tag{3}$$

where q_k is the probability of gene origin of ancestor k and f is the real number of founders. The effective number of ancestors (f_a) is the minimum number of ancestors (founders or not) necessary to explain the genetic diversity of a population (Boichard et al., 1997). This parameter was calculated using the expression

$$f_a = 1/\sum_{j=1}^{f} p_j^2 \tag{4}$$

where p_j is the marginal contribution of ancestor j. The marginal contribution is the additional genetic contribution made by an ancestor that is not explained by another previously chosen ancestor (Boichard et al., 1997). The effective number of founder genomes (f_g) is defined as the number of founders that would be expected to produce the same genetic diversity as in the population under study if the founders were equally represented and no loss of alleles occurred (Lacy, 1989). This parameter was estimated as proposed by Caballero and Toro (2000) using the formula

$$f_g = 1/2C \tag{5}$$

where C is the average coancestry between individuals of the population.

Genetic drift is the random change in allele frequencies in a population, which occurs at a higher intensity when the population undergoes a drastic reduction in its effective size (Falconer and Mackay, 1996). The ratio between f_e/f_a permits to identify whether the use of breeding animals causes a genetic bottleneck in the population (Boichard et al., 1997). A ratio equal to or close to 1 indicates the absence of this effect. The ratio of f_e/f_g determines the effect of genetic drift in the population studied (Lacy, 1989). According to Sorensen et al. (1995), an f_e/N_e ratio > 0.5 in a population indicates the occurrence of changes in genetic drift. Stabilization of genetic drift in a population can be observed when f_e is close to $N_e/2$, suggesting a greater representation of founders (Caballero and Toro, 2000).

2.6. Genetic conservation index

The genetic conservation index (GCI) was proposed by Alderson (1992) and estimates the average effective number of founders in the pedigree of a given animal. Higher values indicate animals with a greater balance of genes transmitted by founders, i.e., greater genetic conservation of the breed. In addition, this index provides reliable

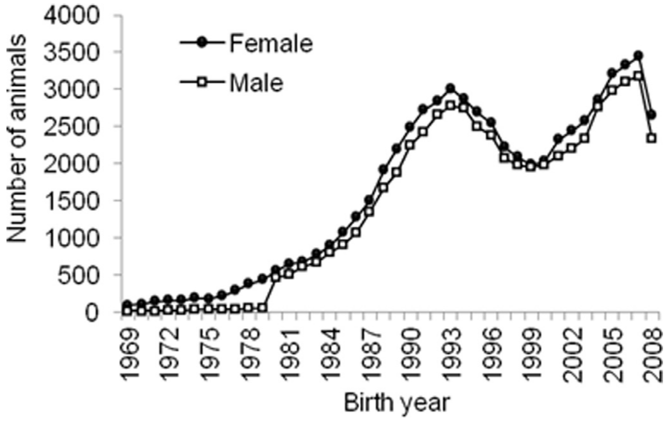

Fig. 1. Number of animals born (males, female) and registered in the Brazilian Quarter Horse Studbook by year of birth.

predictions of homozygosity in subsequent generations. The GCI was calculated from the genetic contributions of all founders identified for each animal using the formula

$$\text{GCI} = 1/\sum p_i^2 \tag{6}$$

where p_i^2 is the proportion of genes of founder i in the pedigree of an animal (Gutiérrez and Goyache, 2005).

3. Results

3.1. Number of births over time

The distribution of the official birth records (Fig. 1) includes only animals born after the opening (1969) of the Brazilian Studbook until 2008. In the first year, 104 births were recorded (18 males and 86 females), with the number of animals increasing gradually thereafter. However, a smaller number of males than females were registered until 1980 (Fig. 1). After this year, the number of animals of both sexes increased constantly until 1993. The average annual growth rate was 19.7%, reaching 5785 records in 1993, followed by a decline between 1994 and 1999, and again increasing from 2000 to 2007 (5.2% per year). A marked decrease in the number of registered animals was observed in the last year studied (2008).

3.2. Reproductive parameters and generation interval

Stallions and mares accounted for 19.4% and 48.1% of all animals, respectively. The average number of offspring per stallion and per mare in TP was 10.7 ± 29.9 and 3.7 ± 3.6, respectively (Table 1). Stallion Signed to fly and mare Princesa had the largest number of offspring (1006 and 186, respectively). The measures of central tendency (mode and median) of the number of offspring per breeding animal were the same and the ratio of the number of dams per sire in TP was 2.9.

Table 1
Summary descriptive statistics of reproductive parameters of Quarter Horse stallions and mares in Brazil.

Item	Total population	
	Stallion	Mare
Total animals (n)	60,933	70,783
Total breeding (n)	11,838	34,028
Total offspring (n)	126,311	126,083
Average ± SD (n)	10.7 ± 29.9	3.7 ± 3.6
Median (n)	2	2
Minimum and mode (n)	1	1
Maximum (n)	1006[a]	186[b]
Mare/stallion ratio	2.9	

n, number of the respective observations. SD, standard deviation

[a] Signed to Fly.

[b] Princesa.

Table 2
Summary statistics of the generation interval (years) between parents and sons/daughters that reproduced, and number of mean generations of the Quarter Horse breed in Brazil.

Item	Total population		Reference population	
	n	Mean ± SD	n	Mean ± SD
Generation interval				
Sire-son	10,090	10.0 ± 5.9	1384	11.5 ± 5.7
Sire-daughter	30,384	9.8 ± 5.5	3986	11.0 ± 4.9
Dam-son	10,055	9.3 ± 4.9	1384	10.5 ± 4.9
Dam-daughter	30,159	9.3 ± 4.8	3986	10.3 ± 4.6
Parents-offspring	80,688	9.6 ± 5.3	10,740	10.8 ± 5.0
Number of mean generation				
Equivalent complete (EG)	–	5.09 ± 1.76	–	6.24 ± 0.88
Full (FG)	–	3.99 ± 1.00	–	4.34 ± 0.63
Maximum (MG)	–	26.76 ± 8.59	–	31.42 ± 4.63

n, number of observations. SD, standard deviation.

The average GI was 9.6 ± 5.3 and 10.8 ± 5.0 years for TP and RP, respectively (Table 2). The GI was greater for the sire-son than for the sire-daughter pathway and shorter for the dam-progeny than for the sire-progeny pathway. On average, mares reproduce at a younger age than stallions, indicating a greater contribution of females to the decrease in this parameter.

3.3. Quality of pedigree data

Pedigree completeness (Fig. 2) in the three most recent generations (1st, 2nd and 3rd), was 96.2%, 92.0% and 83.6% in TP and 100.0%, 100.0% and 98.5% in RP, respectively. The combined average of the five most recent generations was 77.9% and 91.0% for TP and RP, respectively.

The results derived from the number of generations (Table 2) were 5.09 ± 1.76, 3.99 ± 1.0 and 26.76 ± 8.59 for EG, FG and MG, respectively, in TP. In the same order, these values were 6.24 ± 0.88, 4.34 ± 0.63 and 31.42 ± 4.63 in RP. In TP, the maximum number of FG and MG was 6 and 44 generations, respectively.

3.4. Inbreeding parameters

The F was 1.07% and 1.56% in TP and RP, respectively, although 70.89% (TP) and 92.88% (RP) of the animals had an F different from zero (Table 3). The ΔF was also low (0.24%), with a small increase of

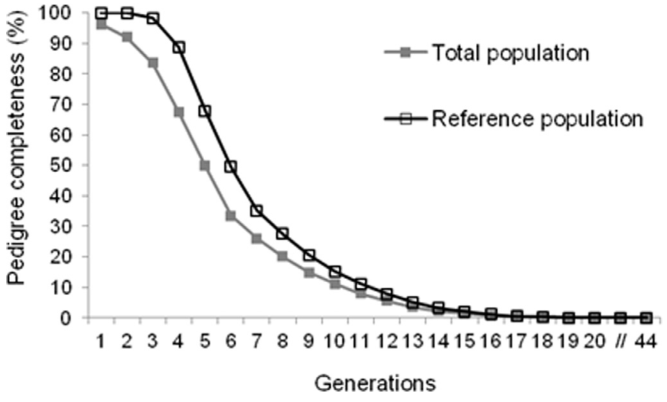

Fig. 2. Completeness of pedigree information for both populations per generation in Quarter Horses in Brazil.

Table 3

Summary statistics of parameters related to inbreeding, probability of gene origin, genetic drift and genetic contributions of founders and ancestors of the Quarter Horse breed in Brazil.

Item	Total population	Reference population
Total number of animals in the study	131,716	47,861
Parameters related to inbreeding		
Average inbreeding coefficient[a], F (%)	1.07 ± 2.72	1.56 ± 3.08
Average related coefficient[a], AR (%)	0.96 ± 0.54	1.16 ± 0.41
Increase in inbreeding[a], ΔF (%)	0.24 ± 0.82	0.30 ± 0.65
Animals with F different from zero (n)	93,359	44,456
Average inbreeding coefficient[b], F (%)	1.51 ± 3.12	1.68 ± 3.16
Average related coefficient[b], AR (%)	1.16 ± 0.44	1.20 ± 0.39
Increase in inbreeding[b], ΔF (%)	0.33 ± 0.96	0.32 ± 0.67
Effective population size[c], N_e (n)	195	164
Effective population size[d], N_e (n)	199	167
Probability of gene origin and genetic drift		
Effective number of founders, f_e (n)	1045	811
Effective number of ancestors, f_a (n)	156	113
Effective number of founder genomes, f_g (n)	105	66
f_e/f_a	6.70	7.18
f_e/f_g	9.95	12.29
$f_e/N_e > 0.5$	5.25	4.86
$f_e \sim (N_e/2)$	1045 ~ 100	811 ~ 84
Contributions of founders and ancestors		
Total number of animals with both parents known	125,913	47,861
Genetic conservation index (GCI)	14.83 ± 8.89	21.83 ± 8.11
Number of founders	5427	4815
Number of ancestors (100% of genetic diversity)	4821	2993
Number of ancestors (50% of genetic diversity)	121	72
Genetic contributions of the (%)		
10 most influential founders	3.10	4.02
100 most influential founders	20.07	25.09
500 most influential founders	53.65	62.92
10 most influential ancestors[e]	17.45	22.48
100 most influential ancestors[e]	46.92	55.63
500 most influential ancestors[e]	74.86	82.48

[a] All animals in the population studied.

[b] Only animals with an inbreeding coefficient ≠ from zero.

[c] Gutiérrez and Goyache (2005).

[d] Gutiérrez et al. (2009).

[e] Marginal genetic contributions.

0.06% in RP. The N_e obtained based on ΔF (most common parameter in the literature) was 197 (TP) and 164 (RP). Using individual increase in inbreeding, the N_e was 199 and 167 for TP and RP, respectively (Table 3).

3.5. Probability of gene origin and genetic drift

The three parameters of the probability of gene origin describe the genetic diversity of the populations (Table 3). The value of f_e represents 19.3% and 16.8% of founders in TP and RP, respectively. Parameter f_a had 889 ancestors less than f_e in TP. The value of f_g indicated that only 1.9% (TP) and 1.4% (RP) of the founder genomes are still represented in each population. Based on the total number of animals evaluated and when compared between each other, the parameters of the probability of gene origin, f_e, f_a and f_g (Table 3), are considered low and indicate how many of the founders (1045) remain in the herd as ancestors (156) and founder genomes (105). The ratios of f_e/f_a and f_e/f_g were 6.70 and 9.95 (TP), and 7.18 and 12.29 (RP), respectively (Table 3). The f_e/N_e ratio was 5.36 (TP) and 4.95 (RP), and the fe ~ (Ne/2) value was 1045 ~ 98 (TP) and 811 ~ 82 (RP).

3.6. Genetic conservation index

The mean GCI was 14.83 ± 8.89 and 21.55 ± 8.11 in TP and RP, respectively (Table 3). The indices lower than 2.0 and higher than 31.19 corresponded to the 5th and 95th percentiles, respectively (TP). There were 8023 animals with GCI values higher than 30.

3.7. Genetic contributions

The total number of founders and ancestors of the QH breed in Brazil represent 4.1% and 3.7% (TP) and 10.1% and 6.3% (RP) of the animals, respectively, in each population (Table 3). The number of animals that explain 50% of the genetic diversity of the breed was small and represents only 2.5% and 2.4% of all ancestors in TP and RP, respectively. The cumulative genetic contribution of the 10, 100 and 500 most influential animals was increased in RP by 0.9%, 5.0% and 9.3% (founders) and by 5.3%, 8.7% and 7.6% (ancestors), respectively, compared to TP (Table 3).

The marginal genetic contribution of the 15 most influential ancestors of the QH breed was 21.52% and 27.34% in TP and RP, respectively (Table 4). The two most representative ancestors (Table 4) are Three Bars (Thoroughbred) and Doc Bar (Quarter Horse), together accounting for 7.78% (TP) and 9.36% (RP). These animals were born in the United States, had sired 51 offspring each, and breeding time for 22 and 16 years, respectively. The marginal genetic contribution of the most influential mare, Poco Lena, was 0.81% and 1.52% in TP and RP, respectively. The number of ancestors with a contribution greater than 1.0% was 8 and 13 animals in TP and RP, respectively.

As also shown in Table 4, the mean breeding time was 14.1 ± 6.1 years in both populations, the mean number of offspring was 125 ± 129 and 170 ± 262 in TP and RP, respectively, and the mean EG was 5.65 ± 0.69 and 5.40 ± 0.73 in TP and RP, respectively.

4. Discussion

4.1. Number of births over time

The decline in the number of births observed in the 1990s (Fig. 1) resembles that observed for autochthonous horse breeds in Brazil, including the Campolina (Procópio et al., 2003), Mangalarga Marchador (Costa et al., 2005), and Mangalarga breeds (Mota et al., 2006). This period coincided with the implementation of the Brazilian government's economic plan (currency change), suggesting a cause-effect relationship as reported by Mota et al. (2006). The decrease observed in 2008 (Fig. 1) coincided with the period of the financial crisis in Europe and in the United States that led to a deacceleration in horse breeding in different parts of the world. A similar trend has been reported in studies on Lusitanos (Vicente et al., 2012) and Pantaneiros (McManus et al., 2013). Oscillations in the number of birth registrations observed in the 20th and 21st centuries are common in different continents and are influenced by economic-financial and social changes such as war.

4.2. Reproductive indices and generation interval

The difference between stallion and mare in terms of the number of offspring was significant. Especially in the average and standard deviation number of offspring per stallion (Table 1), indicates the concentration of progeny in a reduced number of breeding animals, a finding suggesting the use of reproductive technologies. Differences in the mean number of offspring have been reported in the literature. Mota et al. (2006) reported a mean number of 23.8 per stallion and of 4.4 per dam for Mangalarga horses, Vicente et al. (2012) of 13.1 per stallion and of 4.1 per dam for Lusitano horses, and McManus et al. (2013) of 12.8 per stallion and of 2.6 per dam for the Pantaneiro breed.

Table 4

Summary statistics of the marginal genetic contribution (in %) of the 15 most influential ancestors in the total and reference population of the Quarter horse breed in Brazil, and year of birth, sex, breed, birth of first and last progeny, breeding time, total number of progeny and equivalent generations.

Order	Name	Marginal contribution (%)	Birth year	Progeny			Breeding time (years)	EG (*n*)
				Birth of first	Birth of last	Total number		
Total population								
1	**Three Bars**[a]	5.73	1940	1946	1968	51	22	5.75
2	**Doc Bar**	1.95	1956	1961	1977	51	16	5.09
3	Leo	1.76	1940	1946	1966	28	20	5.81
4	Top Deck[a]	1.45	1945	1950	1966	21	16	4.60
5	**El Zorrero**	1.31	1969	1975	1993	382	18	5.48
6	**Dash for Cash**	1.11	1973	1979	1993	60	14	6.57
7	Mr San Peppy	1.10	1968	1974	1993	37	19	6.13
8	Sanjay[c]	1.05	1980	1982	1994	291	12	6.52
9	**Shady Apolo Bars**	0.99	1970	1973	1980	75	7	6.14
10	**Dan's Boy Skippy**	0.99	1969	1983	1993	311	10	6.02
11	Caracolito	0.91	1957	1961	1975	47	14	4.84
12	Catchme Ifyoucan[a]	0.84	1975	1977	1997	306	20	5.66
13	**Poco Lena**[b]	0.81	1949	1967	1968	3	1	4.23
14	The Aquarian	0.75	1972	1977	1982	107	5	5.96
15	**Easy Jet**	0.74	1967	1970	1988	99	18	5.91
Reference population								
1	**Three Bars**[a]	5.94	1940	1946	1968	51	22	5.75
2	**Doc Bar**	3.42	1956	1961	1977	51	16	5.09
3	Peppy San Badger	2.36	1974	1980	1993	94	13	5.29
4	Freckles Playboy	1.95	1973	1979	2000	55	21	5.43
5	**El Zorrero**	1.65	1969	1975	1993	382	18	5.48
6	**Dash for Cash**	1.60	1973	1979	1993	60	14	6.57
7	**Poco Lena**[b]	1.52	1949	1967	1968	3	1	4.23
8	**Shady Apolo Bars**	1.49	1970	1973	1980	75	7	6.14
9	**Dan's Boy Skippy**	1.45	1969	1983	1993	311	10	6.02
10	Leo San	1.10	1949	1956	1970	11	14	6.33
11	**Easy Jet**	1.07	1967	1970	1988	99	18	5.91
12	Peppy Belle[b]	1.06	1955	1961	1968	4	7	4.12
13	Trouble Two Times	1.04	1975	1978	2002	329	24	4.89
14	Beduino[a]	0.88	1968	1976	1987	25	11	4.74
15	Signed to Fly	0.81	1988	1993	2008	1006	15	5.02

[a] Throughbred.

[b] Female.

[c] Born in Brazil. EG, equivalent generation.

The number of offspring per dam was low and varied little among the breeds studied, but contrasted with the mean number of offspring per stallion (Table 1). Reproductive differences between sexes are observed in all horse breeds, indicating a greater participation of dams in maintaining the genetic diversity of each breed. The largest number of offspring (Tables 1 and 4) was observed for stallion Signed to Fly and mare Princesa. The large number of offspring can be explained by the sportive results of breeding animals in terms of conformation traits, western modalities and/or speed racing.

The GI was greater in RP (Table 2), reducing genetic gain probably because of the use of artificial insemination and/or embryo transfer, techniques that permit the reproductive use of deceased or older animals. The high standard deviations indicate differences in the GI within the population. Long GI as obtained in the present study have been reported in the literature for different horse breeds. Petersen et al. (2014) found a similar mean GI (9.5 years) for QH in the United States. Vicente et al. (2012) reported a longer GI (10.5 years) for Lusitano horses. The GI is a parameter that is monitored in breeding programs because its reduction promotes an increase in genetic gain. However, the QH of most Brazilian breeders have long GI, reducing the rate of genetic improvements in their populations.

4.3. Quality of pedigree data

Knowledge of the ancestors in the pedigree is necessary for characterizing the genetic diversity of breeds. According to (Cervantes et al., 2009), sets of incomplete data reduce the accuracy of the results. In the present study, in addition to the database of ABQM, the ancestors of Brazilian QH animals registered until the mid-18th century were used, permitting to evaluate the present genetic diversity of the QH breed in Brazil.

Cervantes et al. (2008), Medeiros et al. (2014) and Duru (2017) reported pedigree completeness in the first, second and third generations of 92.0%, 86.6% and 80.8% (Spanish Arab Horse in total population), 99.99%, 98.0% and 69.9% (Brazilian Sport Horse in reference population) and 98.2%, 96.6% and 95.0% (Turkish Arab Horse in reference population), respectively. Bartolomé et al. (2011), Roos et al. (2015) and Bhatnagar et al. (2011) described combined average pedigree completeness of the five most recent generations of 71.2% (Spanish Sport Horse in total population), 88.0% (Holstein in reference population) and approximately 70.0% (Norwegian Fjord Horse in North America), respectively. Similar to the literature, the increase in pedigree completeness in RP suggests improvement in the quality of the pedigree information of the ABQM registry (Fig. 2).

The mean number of EG obtained (Table 2) permitted to evaluate the changes in genetic diversity that occurred in the last generation (RP). The values reported in the literature of 0.7 in Pantaneiro (McManus et al., 2013), of 5.7 in the Spanish Arab Horse (Cervantes et al., 2008) and of 9.9 in Lusitano horses (Vicente et al., 2012) indicate the difference in knowledge of pedigree information for each breed. The evolution of EG shows improvement in the pedigree information of each animal. However, in the presence of a breed founded in the 17th century, suggesting that the Brazilian Studbook of the QH breed should be expanded to include all ancestors from the United States, United Kingdom and other origins.

4.4. Inbreeding parameters

Values of F (Table 3) have been reported in the literature, Bartolomé et al. (2011) and Hamann and Distl (2008) for the Spanish Sport Horse (0.66%) and Hanoverian horse (1.33%), respectively. High F values are observed mainly in the case of closed studbooks, for example Thoroughbred (Cunningham et al., 2001), Lipizzaner (Zechner et al., 2002) and Lusitano (Vicente et al., 2012), contrary to the file used in this study. The low F observed in the two populations evaluated suggests that breeders control inbreeding in QH, but should be considered by breeders given the growing trend in the number of related animals. The low AR (Table 3) was similar to that described in the literature for other breeds (Bartolomé et al., 2011; Vicente et al., 2012; McManus et al., 2013), indicating reduced representation of each individual in the whole breed, regardless of pedigree completeness.

N_e (ΔF) values of 372, 150, 226 and 55 have been reported for the Hanoverian (Hamann and Distl, 2008), Trakehner (Teegen et al., 2009), Spanish Sport Horse (Bartolomé et al., 2011) and Holstein (Roos et al., 2015) breeds, respectively. Studies describing high values of N_e suggest, by definition, reduced inbreeding because of the direct relationship between N_e and the inbreeding rate (Falconer and Mackay, 1996). However, the differences observed between the population studied and the literature are related to the number of animals in each breed and the probabilities of gene origin that maintain a close relationship with N_e. The FAO (1988) recommends a minimum N_e of 50. The value obtained in this study is not a matter of concern for the maintenance of genetic diversity, but the decrease in N_e observed in RP suggests the possible loss of genetic diversity.

4.5. Probability of gene origin and genetic drift

The results of probability of gene origin reported in the literature are heterogeneous. Roos et al. (2015), Delgado et al. (2014) and Vicente et al. (2012) found lower values for Holstein horse (f_e, 50; f_a, 29 and f_g, 17), purebred Arabian (f_e, 30; f_a, 13 and f_g, 6), and Lusitano (f_e, 28; f_a, 12 and f_g, 6), respectively. The higher values of the parameters obtained by Bartolomé et al. (2011) for the Spanish Sport Horse (f_e, 963; f_a, 407 and f_g, 254) and by Siderits et al. (2013) for the German Paint Horse (f_e, 963; f_a, 186 and f_g, 118) suggest the use of a larger number of animals for formation of the breeds. The diversity of the breeds observed in the literature, as well as of the probabilities of gene origin, suggests concern in the breeding of horses. However, the variation in the three parameters of the probability of gene origin obtained in this study (Table 4) was higher than that described in the literature. Care should be taken when comparing the data with the literature because each population has its own characteristics. Comparison should be made within each breed and considering the three parameters of each population. The lower values of f_e, f_a and f_g were found in RP compared to TP (Table 3), suggesting concentration of the population in a reduced number of breeding animals and loss of genetic diversity. The f_e in both populations, comparing the number of founders, indicates the preferential use of certain lineages of founders.

Parameter f_a complements the information provided by f_e, indicating losses of genetic diversity produced by the unequal use of breeding animals, with the observation of high bottlenecks in both populations (Table 3). The results contrast with those obtained for the Holstein (1.72), purebred Arabian (2.31), Lusitano (2.33) and Spanish Sport Horse (2.37) breeds studied by Roos et al. (2015), Delgado et al. (2014), Vicente et al. (2012) and Bartolomé et al. (2011), respectively, who observed lower bottlenecks in the formation of the populations when compared to the present study. The smaller the difference between f_e and f_a, the greater the number of founder animals in the population across generations, permitting the maintenance of the genetic base of the breed and of a large number of founders over time and consequently reducing the loss of genetic diversity, in contrast to what is observed in the QH breed. Values suggesting loss due to genetic drift have been reported for Hanoverians (Hamann and Distl, 2008) and the German Paint Horse (Siderits et al., 2013), but with smaller differences than those found in the present study (Table 3), indicating greater loss due to genetic drift in the QH breed in Brazil.

4.6. Genetic conservation index

In the literature, mean GCI of 1.3 and 9.5 and maximum indices of 7.2 and 19.2 have been reported for Pantaneiro (McManus et al., 2013) and Lusitano horses (Vicente et al., 2012), respectively. The differences compared to the present study can be explained not only by the better conservation of the QH breed, but also by differences in the quality of the pedigree information. Animals with high values (GCI) exhibit greater genetic conservation, i.e., a greater balance in the number of founders, and should be used in genetic selection programs designed to maintain the genes transmitted by founders (Alderson, 1992). However, does not take into account pedigree bottlenecks, which may have occurred through non-founder individuals. These animals should be preferred as breeding animals to ensure continuity of the genetic diversity of founders in the QH breed.

4.7. Genetic contributions

Genetic contributions have been described by Hamann and Distl (2008), with a marginal contribution of the 15 top ancestors of up to 35% in the Hanoverian breed. Roos et al. (2015) found that 15 ancestors (stallions) account for 50.0% of the total contribution, with a value of 11.6% for the most influential animals. Vicente et al. (2012) reported a marginal contribution of the main ancestor of 25% in the Lusitano breed. The differences found in the literature indicate that the QH exhibits greater genetic diversity in the 15 most influential ancestors. However, the increase in genetic contributions observed in RP (Tables 3 and 4) caused the loss of genetic diversity due to the preferential use of lineages of certain ancestors (founders or not).

The long breeding time and large number of offspring of the main ancestors (Table 4) increase the concentration of genetic contributions in a small number of ancestors of the QH breed, indicating the loss of alleles in the last generation studied. The lower genetic contribution of females, indicating a greater genetic distribution compared to males, which therefore contribute to the maintenance of genetic diversity in QH.

The values obtained do not compromise the evolution of the QH breed in Brazil. The breed continues to exhibit genetic diversity and a large number of ancestors in the formation of its population compared to the other breeds. However, a loss of genetic diversity could be observed (Tables 3 and 4) and may increase in future generations because of the lack of monitoring of the QH breed. Thus, the increase in genetic contributions must be monitored by ABQM and breeders to guide matings in order to obtain more balanced values and genetic diversity of the QH breed in Brazil.

5. Conclusion

The results highlight the importance of monitoring the population structure in breeding programs, as well as of guided matings using ancestors of different lineages, in order to increase the genetic diversity of the QH breed in Brazil. The expectation of annual genetic gain in the population was reduced because of the long GI. Selection of a larger number of young sires with a shorter breeding time will permit to increase genetic gain, to reducing bottleneck effects and minimizing the loss of genetic diversity.

Conflict of interest statement

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

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