Ciência Rural, Santa Maria, v.53:4, e20210827, 2023

http://doi.org/10.1590/0103-8478cr20210827

ISSNe 1678-4596
BIOLOGY

Genetic diversity of Shepherd dog using pedigree analysis

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ABSTRACT: *The German Shepherd dog breed is the most popular breed globally and in Brazil. The study of the population structure through pedigree information is an essential tool to understand the history of the Brazilian German Shepherd dog breed. This study evaluated the status of genetic diversity and population structure of the Brazilian German Shepherd dog breed. The pedigree included a total of 77,938 animals born between 1970 and 2014. The average generation interval in this population was 3.91 years. Considering the reference population, 2,183 founders were identified. Approximately 3% of the genetic diversity of the current population (2010-2014) was lost, most of which was due to genetic drift. The effective population size was relatively small, and the pedigree showed bottlenecks indicating a loss of genetic diversity in this breed. These results indicated the need to adopt measures against the excessive increase in inbreeding and monitor effective population size to minimize genetic diversity loss.*

Key words: *conservation, inbreeding, pedigree analysis, population structure.*

Diversidade genética em cães da raça Pastor Alemão utilizando análise de pedigree

RESUMO: *A raça Pastor Alemão é uma das raças mais populares no mundo e no Brasil. O estudo da estrutura populacional por meio de informações de pedigree é uma ferramenta essencial para o entendimento da história dessa raça no Brasil. Objetivou-se com o estudo avaliar o status da diversidade genética e da estrutura populacional de cães da raça Pastor Alemão. O pedigree incluiu um total de 77.938 animais nascidos entre 1970 e 2014. O intervalo médio de geração nesta população foi de 3,91 anos. Considerando a população de referência, foram identificados 2.183 fundadores. Cerca de 3% da diversidade genética da população atual (2010-2014) foi perdida, a maior parte devido à deriva genética. O tamanho efetivo da população foi relativamente pequeno e o pedigree apresentou gargalos indicando uma perda de diversidade genética nesta raça. Esses resultados indicam a necessidade de adoção de medidas contra o aumento excessivo da endogamia e do monitoramento do tamanho efetivo da população para minimizar a perda de diversidade genética.*

Palavras-chave: *análise de pedigree, conservação, endogamia, estrutura da população.*

INTRODUCTION

The German Shepherd dog breed is the most popular breed globally and in Brazil. This breed is widely used in the police work, military working, border guard working, shepherding animals, agility, personal and residential guard, due to its intelligence, faithful, alertness, and learning ability (KANIA-GIERDZIEWICZ et al., 2013). The German Shepherd is widely used in police and military service in Brazil. Despite the numerous international studies on the pedigree analysis of dog breeds, including German Shepherd (KASARDA et al. 2007; KALINOWSKA et al. 2010; KANIA-GIERDZIEWICZ et al. 2011; MELLANBY et al., 2013), unfortunately, until today, nothing is known about the population structure and genetic diversity of Brazilian dog populations.

Pedigrees are a valuable data source for monitoring the genetic diversity and the structure of a given population of dogs (LEROY et al., 2006; LEROY, 2011). This genetic information is particularly useful in dogs, as repeated matings and numerous matings between close relatives also negatively influence genetic variability (GŁAŻEWSKA, 2008). Consequently, there are severe losses of genetic diversity and an increased incidence of inherited diseases (LEROY, 2011). According to JANUTTA et al. (2008), increased inbreeding coefficients were associated with a higher genetic disposition for hip dysplasia in German Shepherd dogs. Furthermore, pedigree information would enable different kennel clubs to manage the rate of inbreeding and maintain the genetic diversity of highly specialized dog breeds.

Received 11.22.21 Approved 04.14.22 Returned by the author 06.11.22
CR-2021-0827.R1
Editors: Rudi Weiblen Silvia Llambi

The study of population structure through pedigree information is an essential tool for understanding the history of Brazilian German Shepherd dogs. It can provide useful information for breed selection, conservation, and expansion programs. Thus, the objectives of the present study were to evaluate the status of genetic diversity and population structure of the German Shepherd dogs using pedigree analysis.

MATERIALS AND METHODS

Data

The pedigree of Brazilian German Shepherd dogs used in this study was obtained from the "Sociedade Brasileira de Cães Pastores Alemães" (SBCPA). The pedigree includes 77,938 animals born between 1970 and 2014. All population parameters were computed using pedigree analysis, with the entire and reference population defined as animals born between 2010 and 2014 (n = 11,299). This definition is equivalent to that of animals born in the last generation interval.

Analysis of pedigree

Pedigree analyses were performed using the PEDIG (BOICHARD, 2002), and CFC (SARGOLZAEI et al., 2006) software. The generation interval was defined as the average age of parents at the birth of their progeny, which was subsequently maintained for reproduction. Pedigree completeness was assessed by the number of equivalent complete generations (ECG) traced, computed as the sum of all known ancestors of the terms ($1/2^d$), where d is the ancestor's generation number, which is equal to one for the parents, two for the grandparents, etc. (MAIGNEL et al., 1996). F-statistics (WRIGHT, 1969) were computed to characterize the genetic structure of the population of Brazilian German Shepherd dogs. The average inbreeding coefficient of dogs was denoted F_{IT}, and the average inbreeding coefficient under random mating was denoted F_{ST}. F_{ST} was computed from a hypothetical population produced by randomly matching males and females. The F_{IS} statistic was calculated as follows:

$$F_{IS} = \frac{F_{IT} - F_{ST}}{1 - F_{ST}}$$

.

Effective population sizes were estimated based on the individual rates of inbreeding ΔF_i (GONZÁLEZ-RECIO et al., 2007, GUTIERREZ et al., 2009) and coancestry ΔC_{ij} (CERVANTES et al., 2011), considering: $\Delta F_i = 1 - \sqrt[t_i - 1]{(1 - F_i)}$ and $\Delta C_{ij} = 1 - \sqrt[(t_i + t_j)/2]{(1 - C_{ij})}$, where F_i is the inbreeding coefficient of the individual i, C_{ij} is the coancestry coefficient between individuals i and j, and t_i and t_j are their respective ECG. The following formulas were used: $NeF_i = 1/(2\overline{\Delta F})$ and $NeC_i = 1/(2\overline{\Delta C})$. The number of equivalent subpopulations was computed as suggested by Cervantes et al. (2008, 2011): $S = NeC_i/NeF_i$.

The principal ancestors (founders or not) of the reference population were identified as described by BOICHARD et al. (1997). The marginal contribution of each main ancestor was computed as the expected genetic contribution independent of the contributions of the other ancestors. The genetic contribution of a founder was calculated as the probability of selecting a gene randomly within the reference population that came from the founder (JAMES, 1972). The number of founders (f_e) and ancestors (f_a) was obtained to evaluate the concentration of the origin of both animals and genes. The parameter f_e is defined as the number of equally contributing founders that would be expected to produce the same genetic diversity as observed in the population under study (Lacy, 1989). This parameter was calculated as $f_e = 1/\left(\sum_{k=1}^{f} q_k^2\right)$, where q_k is the probability of gene origin of founder k. Parameter f_a is the minimum number of ancestors, not necessarily founders, explaining the complete genetic diversity of a population. This parameter was calculated as $f_a = 1/\left(\sum_{j=1}^{a} q_j^2\right)$, where q_j is the marginal contribution of ancestor j, which is the genetic contribution made by an ancestor that was not previously explained by other ancestors chosen before. The founder genome equivalent (f_g) can be defined as the number of founders that would be expected to produce the same genetic diversity as observed in the population under study if the founders were equally represented and no loss of alleles occurred (BALLOU & LACY, 1995). Following CABALLERO & TORO (2000), the parameter f_g was obtained by the inverse of twice the average coancestry of the individuals included in a pre-defined reference population.

Genetic diversity (GD) in the reference population was computed as: $GD = 1 - \frac{1}{2f_g}$ (LACY, 1989 and 1995). In domestic populations, bottlenecks and genetic drift frequently occurred, leading to a loss of genetic diversity. The genetic diversity lost in the population since the generation of the founder can be estimated by 1 - GD. The loss of genetic diversity due to unequal contributions of founders was estimated by 1 – GD^*, where

$GD^{*} = 1 - \frac{1}{2f_e}$ (CABALLERO & TORO, 2000). The difference between GD and GD^{*} indicates the loss of genetic diversity due to genetic drift that has accumulated since the founding of the population (LACY, 1995). Thus, this difference can be expressed as: $GD - GD^{*} = \frac{1}{2f_n}$, where f_n is the effective number of non-founders. This parameter was computed using the following expression proposed by CABALLERO & TORO (2000): $\frac{1}{fg} = \frac{1}{fe} + \frac{1}{fn}$.

RESULTS AND DISCUSSION

The pedigree included 77,938 animals that were born between 1970 and 2014 (Figure 1). There were 53.8% females and 46.1% males. During 1970–1985, only 862 dogs were registered. Starting from 1995, the lowest value was recorded in 2008, with 1,243 dogs, and the highest in 2002, with 4,001 dogs.

The percentage of the animals used for breeding was lower in males than in females (Figure 2). On the average, 19% of the males born in the 2000s were used for breeding; the proportion was 9% in females. Since 1995, the percentages of both males and females used for breeding have decreased. The average ratio of males to breeding females in the reference population was approximately 1:2.3. In contrast, this ratio was 1:2.43 between 1994 and 2009. This number reflects breeders' adoption of the reproduction system via polygamy.

Popular sires (defined as >100 recorded offspring) and popular dams (> 40 offspring) were identified. Popular sires were 102 (1.83% of the sires), while popular dams were 39 (0.30% of the dams). The most popular sires and dams in this study were Willy von der Ehrenfeste (556 progeny records) and Cheer Aus Agrigento (55 progeny records). CALBOLI et al. (2008) performed a study on German Shepherd dogs from the United Kingdom and reported 4% popular sires and 1% popular dams. The popular sire effect is one of the most significant contributors to the reduction in genetic diversity, inbreeding depression, inbreeding purging, and inherited disorders (WELLMANN & PFEIFFER, 2009; LEROY & BAUMUNG, 2011). Welfare concerns and effective population size should limit the use of popular sires. As a result, many more dogs are given the opportunity to breed, increasing the number of breeding dogs. Thus, more balanced use of breeding animals can be guaranteed.

The average generation interval for this population was 3.91 years. LEROY et al. (2009), MÄKI et al. (2010), and SHARIFLOU et al. (2011) reported an average generation interval similar in the German Shepherd. The generation intervals for the four different gametic pathways were similar and close to four years (Table 1). The long generational intervals could be attributed to the low replacement rate of breeders, as the most popular males and females have continued to contribute to their offspring for generations today (NAVAS et al., 2020). On average,

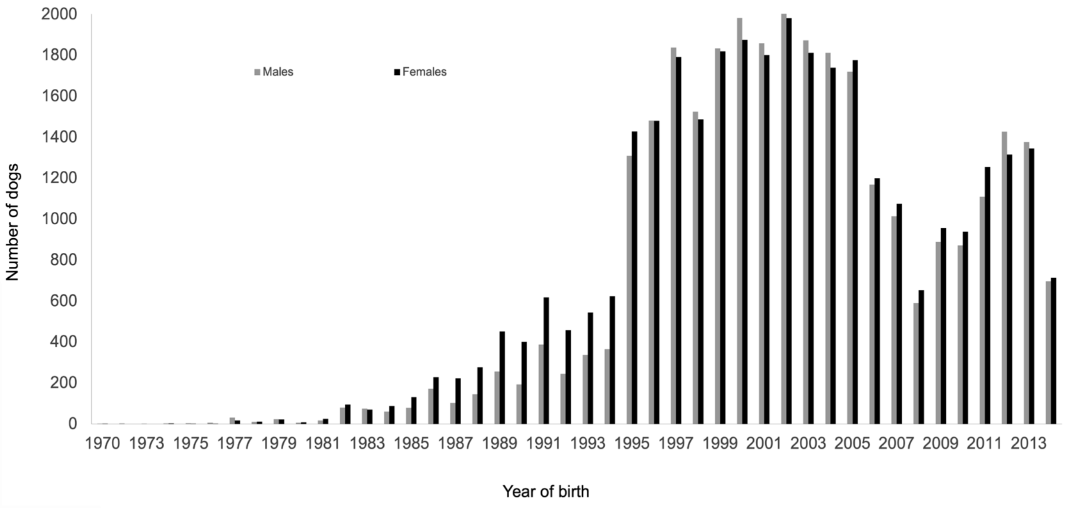

Figure 1 - German Shepherd number according to the year of birth and sex of the dogs.

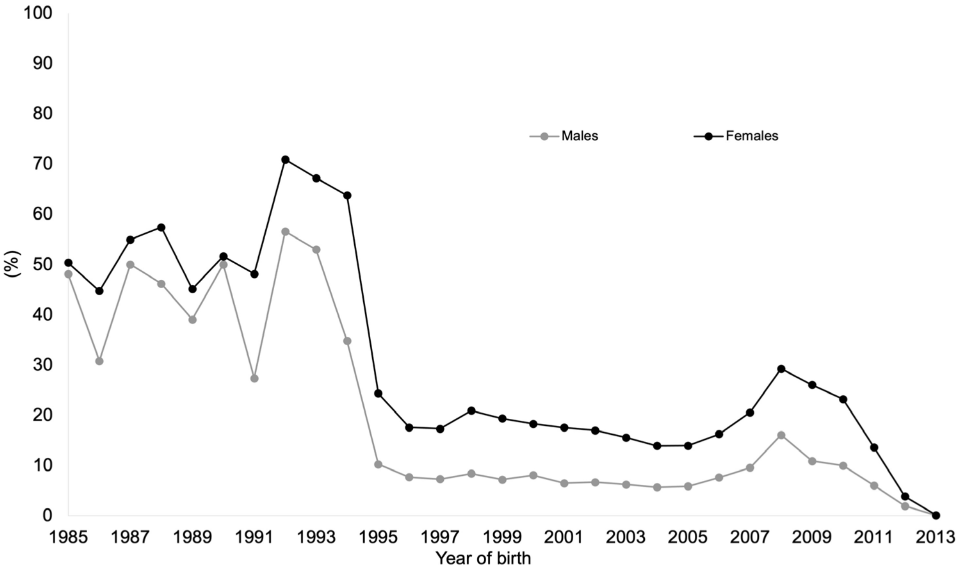

Figure 2 - Percentage of German Shepherd dogs used for breeding by year of birth.

breeding males were older than breeding females. This difference may be due to improved reproductive management. The intensive use of young females explains their shorter generation intervals as dams.

Until the 1990s, the average inbreeding coefficient (F_{IT}) was below 2%, probably towing to pedigree information changes (Figure 3). *F* reached its maximum value of 4% in 2006 and remained constant until 2014 (3.8%). This increase was mainly due to the increasing amount of pedigree information. COLE et al. (2004) reported that the populations of German Shepherd dogs exhibited an average inbreeding level of 26.2%. LEROY et al. (2009) studied French German Shepherd dogs and reported a value of 1.8%. According to BOICHARD et al. (1997), incomplete pedigree information can underestimate inbreeding levels. The ECG in this study was higher than the ones reported in other data sets of German Shepherd dogs (MÄKI et al., 2001; COLE et al., 2004; LEROY et al., 2009). Almost all the animals in the reference population were inbred (Table 2). As dog mating between close relatives is a practice, dogs with high inbreeding are, in general, the products of full-sibs or parent-offspring mating.

As a result of the regular recording of genealogical information, animals in the reference population had nine mean equivalent generations (Table 2). This result indicated that the pedigree is deep enough to provide a comprehensive picture of the evolution of genetic diversity in the Brazilian German Shepherd dog breed. LEROY et al. (2009) studied 61 dog breeds and reported mean equivalent generations of 9.1 and 9.2 for breeds such as Beauceron and Epagneul Breton, respectively.

Table 1 - Generation interval (in years) of Brazilian German Shepherd dogs.

Path	N	Average	Minimum	Maximum
Sire to sires	2082	3.92	0.74	10.81
Sire to dams	5247	3.96	0.56	11.00
Dam to sires	1884	3.74	1.15	10.01
Dam to dams	5079	3.81	0.67	11.33

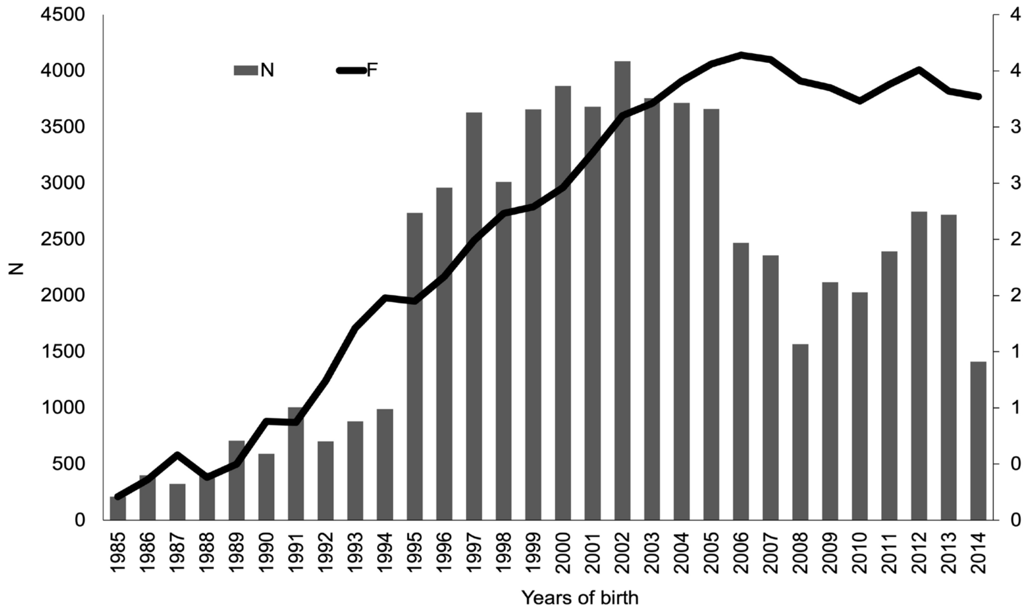

Figure 3 - Number of dogs registered (N, left axis) and average inbreeding coefficient (F, right axis) per year of birth.

Twenty-four breeds had a complete generation equivalent value higher than 6.

The high inbreeding values, connected to a lower inbreeding effective population size (Table 2), may increase the proportion of individuals affected by monogenic recessive genetic disorders concerning their allele frequency (LEROY & BAUMUNG 2011). SHARIFLOU et al. (2011) reported that the effective population size estimated from Australian German Shepherd dogs was more significant (250) than that in this study. According to LEROY et al. (2013), some measures should be recommended to limit close inbreeding practices, at least for breeds with effective inbreeding population sizes lower than 100, a very close scenario for the population of the Brazilian German Shepherd dog.

Based on the reference population, 2,183 founders were identified. These founders showed unbalanced genetic contributions because the effective number of founding dogs was only 103.70. The founder genome equivalents were 21.41 for the entire population and 17.13 for the reference population. According to NAVAS et al. (2020), a small number of founders leads to a decrease in genetic diversity. Only 20 ancestors explained more than 50% of the genetic contribution in the reference population, 92 contributed 75%, and 234 contributed 90% of the genetic contribution. It must be noted that these values indicated how much inbreeding is caused by the abusive use of specific studs.

The ten most influential ancestors of the Brazilian German Shepherd dog breed considering the reference population were Palme vom Wildsteiger Land (german female), Lasso di Val Sole (german male), Fedor von Arminius (german male), Irk von Arminius (german male), Wilma v.d. Kisselschlucht (german female), Zamb von der Wienerau (german male), Jeck vom Noricum (german male), Mischaland´s Chaplin (german male), Axel von der Lucio (german male), and Xinte v. d. Wienerau (german female) and the ancestors explained, 1.49%, 10.37%, 5.83%, 4.84%, 4.40%, 4.03%, 3.01%, 2.47%, 1.83% and 1.72% of the genetic pool, respectively. Four of these dogs were influential ancestors of the Polish-German Shepherd (KANIA-GIERDZIEWICZ et al., 2013), Jeck vom Noricum 6.98%, Fedor von Arminius 6.68%, Zamb von der Wienerau 3.98%, and Irk von Arminius 1.20%. The ten most influential ancestors were responsible for 40% of the gene pool in the reference population. Some ancestors have also contributed significantly to the inbreeding of the population over the last few

Table 2 - Summary of the parameters obtained from the pedigree analysis of Brazilian German Shepherd dogs.

	Entire population (1970-2014)	Reference population (2010-2014)
Number of animals	77,938	11,299
Average inbreeding, F_{IT} (%)	2.63	3.86
Maximum inbreeding coefficient (%)	44.40	33.49
Inbred animals (%)	74.69	96.34
Mean equivalent generations	6.34	9.05
Effective population size computed via individual inbreeding rate (NeF_i)	104.70	105.80
Effective population size computed via individual coancestry rate (NeC_i)	219.10	150.80
Number of equivalent subpopulations (S)	2.09	1.43
Number of ancestors explaining 50% of the gene pool	53	20
Total number of founders	3,535	2,183
Total number of ancestors	18,793	10,690
Effective number of founders (f_e)	113.70	103.70
Effective number of ancestors (f_a)	106.39	40.40
Founder genome equivalents (f_g)	21.41	17.13
f_a/f_e ratio	0.94	0.39
f_g/f_e ratio	0.19	0.17
1– GD (%)	2.34	2.92
1 – GD* (%)	0.44	0.48
GD* – GD (%)	1.90	2.44
F_{ST} (%)	1.84	2.91
F_{IS} (%)	0.81	0.98

1 – GD = genetic diversity lost in the population since the founder generation; 1 – GD* = loss of genetic diversity due to the unequal contributions of founders; GD* – GD = loss of diversity by genetic drift accumulated over non founder generations.

years. Palme vom Wildsteiger Land (11.14%) and Lasso di Val Sole (3.31%) alone contributed 14.45%, and the top 10 contributed 27.25%, demonstrating their relevant influence on the present population.

According to BOICHARD et al. (1997), genetic diversity within populations after a small number of generations can be measured using parameters derived from gene origin probabilities. The estimated parameters derived from the probability of the gene origin are listed in table 2. The estimates of f_e,f_a, and f_g were relatively low. This was probably due to the intensive use of few dogs as breeding animals. The f_a parameter complements the effective amount of founder information by accounting for the genetic variability losses caused by the unbalanced use of reproductive individuals, which produces population bottlenecks. According to the definition of LACY (1989), considering the reference population, only 17 unrelated founders would be necessary to generate the genetic diversity for that period.

The lowest fa/fe ratio indicated bottlenecks in the pedigree of the German Shepherd dog in Brazil. CECCHI et al. (2009) observed a similar pattern in the fa/fe ratio of an Italian population of German Shepherd dogs. Bottlenecks in pedigrees are a common problem in domestic populations and contributed to a reduction in genetic diversity (HUBY et al., 2003). The fa/fe ratio was lower, reflecting a higher impact of random genetic drift on the loss of genetic diversity in the population. The small number of founder animals shows the need to control inbreeding levels, maintain desirable allele founders, search for control tools, and even introduce animals not directly related to the principal ancestors in the population. Approximately 3% of the genetic diversity of the current population (2010-2014) has been lost. SHARIFLOU et al. (2011) reported that 1% of the genetic diversity of Australian German Shepherds was lost. These results suggest that genetic drift is a common cause of genetic diversity loss in Shepherd dogs.

The loss of genetic diversity in Brazilian German Shepherd dogs is shown in table 2. Approximately 2.34% of genetic diversity was lost from the first generation of founders until 2014. Considering the entire population, approximately 19% of the loss was due to the unequal contribution of founders, and the remaining 81% to genetic drift over generations of non-founders. These results suggested that genetic drift is a common cause of genetic diversity loss in dogs.

The current average inbreeding of the population (FIT) was greater than that expected under random mating (FST). The FIS value, which measures the deviation of causality in mating, was higher than zero, indicating that the inbreeding exceeded the expected level of random mating. This implies that resources were involved among the dogs most closely related to the average, and consequently, the population was distributed into subpopulations. The ratio between NeCi and NeFi allows for the estimation of the equivalent number of subpopulations (S), which was 1.43 in the reference population. Hardy-Weinberg equilibrium deviation in dog breeds can be related to either population subdivision or inbreeding practice, that is, mating between close relatives.

The monitoring of population structure, inbreeding, and other related parameters has excellent potential to prevent major losses of genetic diversity in populations of German Shepherd dogs. The excessive use of ten highly favored ancestors resulted in genetic contributions of 40% to the reference population. Thus, it is recommended that breeders use a more significant number of studs, especially those less genetically related to each other, to at least minimize the loss of genetic diversity and control the level of inbreeding.

CONCLUSION

Evaluation of the data registration histories of German Shepherd dogs showed inbreeding trends over time. The effective population size was relatively small, and the pedigree showed bottlenecks, indicating a loss of genetic diversity in the breed. These results indicated the need to adopt measures against the excessive increase in inbreeding and monitor the effective population size to minimize genetic diversity loss.

ACKNOWLEDGEMENTS

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES)- Finance Code 001. The authors acknowledge the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) by the research grant assigned to Annaiza Braga Bignardi (process number: 305879/2019-7), Mário Luiz Santana Júnior (process number: 305898/2019-1).

DECLARATION OF CONFLICT OF INTEREST

The authors declare that there is no conflict of interest associated with this publication.

AUTHORS' CONTRIBUTIONS

The authors contributed equally to the manuscript.

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