

# Pedigree analysis of the Afrikaner cattle breed

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## Summary

The reduction of genetic variability in beef cattle has been extensively researched on a global scale. However, the genetic variability and inbreeding of indigenous cattle breeds of Southern Africa, referred to as Sanga cattle, has been less well characterized. Breeds of Sanga cattle include Afrikaner, Drakensberger and Nguni breeds. In recent years, the number of Afrikaner cattle and herds has decreased. Our objective was to determine the mean level of inbreeding ( $F$ ), effective population size ( $N_e$ ) and generation intervals of Afrikaner cattle using their recorded pedigree. A total of 244 718 records extending from 1940 until 2011 were analysed. The average inbreeding coefficient was 1.83 percent and the effective population size was 167.54. The average generation interval was calculated as  $6.6 \pm 3.9$  years. Pedigree analysis on the Afrikaner cattle population yielded levels of inbreeding that appear to be both acceptable and manageable. By implication, the large  $N_e$  results in a low rate of change in  $F$ . Current results study can be utilized by farmers and the breeders' society to conserve the Afrikaner and utilize the breed to its full potential in the era of climate change.

**Keywords:** *Bos taurus africanus*, effective population size, inbreeding coefficient, Sanga

## Résumé

La réduction de la variabilité génétique chez les bovins à viande a fait l'objet de nombreux travaux de recherche à l'échelle mondiale. Pourtant, la variabilité génétique et la consanguinité ont à peine été étudiées chez les races autochtones de bovins à viande du Sud de l'Afrique, regroupés sous le nom de Sanga. Parmi les races du rameau bovin Sanga, se trouvent les races Afrikaner, Drakensberger et Nguni. Ces dernières années, l'effectif de bovins Afrikaners et le nombre d'éleveurs de cette race ont diminué. Notre objectif a été de déterminer le niveau moyen de consanguinité ( $F$ ), la taille effective de la population ( $N_e$ ) et les intervalles générationnels des bovins Afrikaners, en se servant pour cela du registre généalogique de la race. Un total de 244 714 inscriptions faites de 1940 à 2011 ont été analysées. Le coefficient moyen de consanguinité et la taille effective de la population ont été respectivement de 1.83 pour cent et 167.54. L'intervalle générationnel moyen a été de  $6.6 \pm 3.9$  ans, d'après les calculs. Les niveaux de consanguinité décelés par l'analyse généalogique de la population bovine Afrikaner semblent acceptables et maîtrisables. En fait, la grande taille  $N_e$  entraîne un faible taux de changement pour le coefficient  $F$ . Les résultats de cette étude peuvent être utiles à l'association d'éleveurs dans le but de conserver la race Afrikaner et de l'utiliser jusqu'à son plein potentiel à l'ère du changement climatique.

**Mots-clés:** *Bos taurus africanus*, taille effective de population, coefficient de consanguinité, Sanga

## Resumen

La reducción de la variabilidad genética en el ganado vacuno de carne ha sido investigada ampliamente a nivel mundial. Sin embargo, la variabilidad genética y la endogamia de las razas autóctonas del ganado vacuno de carne del Sur de África, conocido como ganado Sanga, han sido estudiadas en mucha menor medida. Entre las razas de ganado bovino Sanga, se encuentran las razas Afrikáner, Drakensberger y Nguni. En los últimos años, el censo de ganado Afrikáner y el número de explotaciones que lo crían han disminuido. Nuestro objetivo fue el de determinar el nivel medio de endogamia ( $F$ ), el tamaño efectivo de la población ( $N_e$ ) y los intervalos generacionales del ganado Afrikáner, empleando para ello su registro genealógico. Se analizaron un total de 244 714 registros, que iban de 1940 a 2011. El coeficiente medio de endogamia fue de 1.83 por ciento y el tamaño efectivo de población fue de 167.54. El intervalo generacional medio ascendió, según los cálculos, a  $6.6 \pm 3.9$  años. Los niveles de endogamia arrojados por el análisis genealógico de la población bovina Afrikáner parecen aceptables y manejables. En consonancia, el gran tamaño  $N_e$  conlleva una baja tasa de cambio en el coeficiente  $F$ . Los resultados del estudio actual pueden ser utilizados por los ganaderos y por la asociación de criadores para conservar la raza Afrikáner y emplearla hasta su pleno potencial en la era del cambio climático.

**Palabras clave:** *Bos taurus africanus*, tamaño efectivo de población, coeficiente de endogamia, Sanga

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## Introduction

Inbreeding occurs when mating of individuals that are more closely related than random individuals from a population (Falconer and Mackay, 1996). Inbreeding causes a

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reduction in genetic variability which in return is the basis of inbreeding depression which affects fitness-related traits such as fertility when recessive alleles are deleterious (Falconer and Mackay, 1996; Croquet *et al.*, 2007; Panetto *et al.*, 2010). In addition, genetic variation will ensure a capacity for long-term response to selection pressures, either through artificial or natural selection (Frankham, Ballou and Briscoe, 2002). Additionally, Vahlsten, Mäntysaari and Strandén (2004) emphasized the importance of monitoring the level and rate of inbreeding within a population across time. The reduction of genetic variability in beef cattle has been researched extensively (e.g. Cleveland *et al.*, 2005; Santana *et al.*, 2010; Piccoli *et al.*, 2014). Further, there have been numerous genetic analyses based on pedigree information in livestock species including dairy cattle (Maiwashe *et al.*, 2006; Mc Parland *et al.*, 2007), beef cattle (Gutiérrez *et al.*, 2003; Bouquet *et al.*, 2011; Steyn *et al.*, 2012a, 2012b), horses (Moureaux *et al.*, 1996; Vicente, Carolino and Gama, 2012) and sheep (Huby *et al.*, 2003; Maiwashe and Blackburn, 2004).

Relatively little work has been conducted to assess the degree of inbreeding in indigenous (Sanga) cattle of Southern Africa. These are breeds with unique characteristics and differ from the *Bos taurus* breeds. Meyer (1984) concluded that Sanga type cattle, with specific reference to the Afrikaner, have distinct genetic markers inherited from both *Bos indicus* and *B. taurus* cattle. The species name, *B. taurus africanus*, was proposed to show that Southern African Sanga cattle such as the Afrikaner and Nguni are distinct from other African taurine cattle (Meyer, 1984; Frisch *et al.*, 1997). Furthermore, Sanga cattle is known for its hardiness, adaptability to extreme environmental conditions, heat tolerance, disease- and external parasite resistance (Scholtz, 2010). The number of the Afrikaner cattle breed has decreased drastically over the past three decades from more than 27 000 seed stock females in 1980 (Bosman, 1994) to 6 000 in 2010 (Bergh and Havenga, 2011), mainly due to the increased popularity of composite breeds. Similarly, the number of registered herds has decreased from 355 to 66.

One method to ensure the future existence of the Afrikaner breed is through the maintenance of genetic variability. Therefore, it was imperative that a pedigree analysis be conducted on the Afrikaner to ensure the sustainable conservation (through avoiding inbreeding between close relatives and sourcing of genetic material from commercial herds) of this indigenous South African breed. Genetic variation is important for the adaptive potential of a population and can be utilized when faced with extreme environmental changes such as global warming.

Quantitative genetics based on pedigree analysis is an alternative measurement to the use of molecular genetic markers to determine the level of genetic variability and inbreeding within a livestock breed. Thus, the aim of the current study was to use pedigree data from the Afrikaner cattle breed to examine the pedigree structure

of the breed, to determine the levels of inbreeding, effective population size ( $N_e$ ), average relatedness ( $AR$ ) and generation intervals. Parameters derived from the probability of gene origin, i.e. effective number of founders ( $f_c$ ) and effective number of ancestors ( $f_a$ ) were also investigated.

## Materials and methods

Pedigree analysis was conducted using ENDOG v4.8 software (Gutiérrez and Goyache, 2005). A total of 244 718 individuals were used in this analysis, which included records from 1940 until 2011. Several analyses were carried out to determine the probability of gene origin, average coefficient of inbreeding, effective population size,  $AR$  coefficient and generation interval (Gutiérrez, Cervantes and Goyache, 2010).

Rates of inbreeding ( $F$ ) were calculated using the regression of applicable values on the year of birth (Meuwissen and Lou, 1992). The individual increase in inbreeding ( $\Delta F_i$ ) was estimated using the individual inbreeding coefficient ( $F_i$ ) as described by Gonzalez-Recio *et al.* (2007) and modified by Gutiérrez, Cervantes and Goyache (2009). Effective population size ( $N_e$ ) can be defined as the number of animals used for breeding which would lead to an increase in inbreeding if the contribution of all breeding animals were equal. The “realized effective size” was calculated according to Cervantes *et al.* (2008).  $AR$  is the probability that an allele belongs to a specific animal when it was randomly selected from the total population within the pedigree. The interpretation of  $AR$  consequently is the depiction of animal in the whole of pedigree, irrespective of the information provided for its individual pedigree (Gutiérrez, Cervantes and Goyache, 2010). The generation interval was calculated as the average age of the parents at the birth of their offspring that replaced them (Falconer and MacKay, 1996). The parameter  $f_c$  can be defined as the number of contributing founders that would be expected to produce the same level of genetic diversity as the population under investigation. For a given number of founders, the more equal the genetic contribution of each founder, the greater the number of effective founders that will be identified. Boichard, Maignel and Verrier (1997) defined  $f_a$  as the minimum number of ancestors (including both founders and non-founders) which demonstrates the complete diversity of the population being studied. The information provided by  $f_c$  is complemented by  $f_a$  given that these parameters account for the losses of the genetic variation that was produced by the uneven number of reproductive animals which produced bottlenecks (Gutiérrez and Goyache, 2005). This parameter, pedigree completeness, indicates the degree of depth of the pedigree. It was measured in complete generation equivalents (CGE). CGE can be defined as the degree of pedigree information of an animal. Three traced generations are computed by ENDOG for each animal in the pedigree: (i) fully traced generations – defined as the individuals separating the progeny of the furthest generation, which is where the second generation of ancestors of the specific individual

are identified. Generation 0 are the founders of the population, which are the ancestors whose parents are both unknown; (ii) maximum amount of generations traced – defined as the amount of generations which separate the individual from its outermost ancestor; (iii) equivalent complete generations – estimates the pedigree of each individual as the sum over all known ancestors of the terms  $(1/2)^n$ . The amount of generations which separates the individual from each identified ancestor is represented by  $n$  (Maignel, Boichard and Verrier, 1996; Boichard *et al.*, 1997).

## Results

Parameters characterizing the genetic variability of the Afrikaner breed are presented in Table 1. The original dataset contained 244 718 animals. The reference population, where both parents are known for an animal, contained 203 821 animals. The effective population size of the founder animals was 396.16 animals.

The effective numbers of founders ( $f_e$ ) and ancestors ( $f_a$ ) were 288 and 226, respectively. The fact that a gap that exists between  $f_e$  (288) and  $f_a$  (226) implies the existence of a bottleneck. Furthermore, when the ratio between  $f_e$  and  $f_a$  ( $f_e/f_a$ ) is 1.27. The ideal ratio should be one. The larger the ratio, the more severe the effect of the bottleneck is (Boichard *et al.*, 1997; Mokhtari *et al.*, 2013). The results from the current study thus do indicate a bottleneck, but the bottleneck was not large enough to have a big effect on the Afrikaner population. The fact that the value of  $N_e$  for the current study is still 167.54, also indicates that the effect of the bottleneck was not severe. The effective population size ( $N_e$ ) was also calculated via two other methods using the ENDOG software, namely complete generations and equivalent generations and values of 61.67 and 87.48 were obtained. Although the latter two

**Table 1.** Parameters characterizing the probability of gene origin in the Afrikaner cattle breed.

Item	Total
Original dataset	244 718
Reference population (animal with both parents known)	203 821
Effective population size of founder animals	396.16
Number of ancestors contributing to reference population	21 263
Effective number of founders ( $f_e$ )	288
Effective number of ancestors ( $f_a$ )	226
Number of ancestors explaining 50 percent of genetic variability	201
Number of founder herds in reference population ( $f_h$ )	528
Effective number of founder herds for the reference population	35.2
Mean $AR$ (%)	0.44
Maximum number of generations	4.42
Number of complete generations	1.86
Number of equivalent generations	2.81
Effective population size ( $N_e$ )	167.54
Mean inbreeding (%)	1.83

**Table 2.** Levels of inbreeding in the Afrikaner breed.

Number of animals ( $N$ )	Level of inbreeding (%)
4	>40
230	30–39.9
3 144	20–29.9
11 666	10–19.9
13 140	6–9.9
35 820	1–5.9
20 134	<1.0

$N_e$ 's are smaller, they are still within the acceptable limits as indicated in the discussion below.

A total of 21 263 ancestors were recorded which contributed to the reference population. A total of 201 ancestors explained 50 percent of the genetic variability of the reference group. The mean inbreeding value was calculated as 1.83 percent with an  $AR$  of 0.44.

The number of animals at each level of inbreeding was calculated (Table 2). There are only four animals which are more than 40 percent inbred. A total of 84 138 animals were inbred to some degree, implying that 160 576 animals showed no levels of inbreeding. Matings between the close relatives were also observed in the study where a total of 67 matings between full sibs (brother and sister) were recorded, which presents 0.03 percent of the population under study. Furthermore, mating between half sibs (half-brother and sister or brother and half-sister) was recorded in a total of 8 607 cases, which amounts to 3.52 percent. Finally, mating between parent and offspring (mother and son or father and daughter) was recorded in 1.17 percent of the records within the dataset, accounting for 2 856 animals.

The increase in inbreeding and the  $AR$  per generation are illustrated in Figure 1. A maximum of 14 generations was detected. Generations 0–2 showed no levels of inbreeding. From generations 2 to 6, there was a steady increase in inbreeding of  $\pm 1$  percentage unit per generation. Until generation 12, inbreeding levels were constant with minimal to no increase of inbreeding for the six generations. From generations 12 to 14, a sharp increase in inbreeding was observed. One explanation for this may be the drastic decrease in the number animals and herds.  $AR$  per generation followed a similar trend compared with the levels of inbreeding. Generations 0–3 displayed a minimum to no increase in relatedness. From generations 3 to 6, a gradual increase was observed. From there on, a constant relatedness level was observed with a slight increase from generations 13 to 14.

The most recent ancestral generation, calculated from all the animals in the dataset, were 87 percent complete. The second ancestral generations for dam and sire lines were on average 69.9 and 73.9 percent complete, respectively. For the third generation, the pedigree completeness decreased to the lowest percentage, at 48.4 percent.

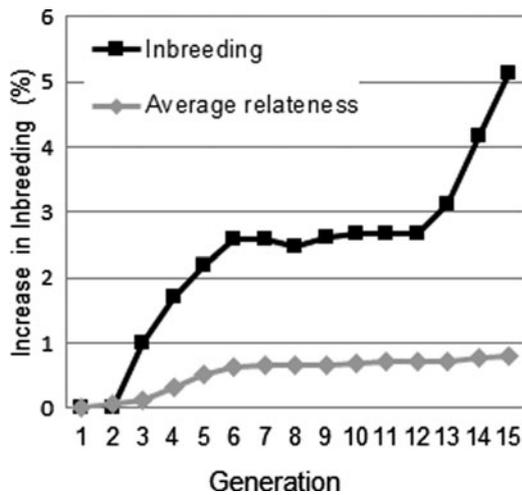


Figure 1. Increase in inbreeding and *AR* for each generation.

The average generation interval for the whole population was calculated as  $6.6 \pm 3.9$  years. Furthermore, the generation interval estimated for the four different gametic pathways was as follows: dam to son:  $6.712 \pm 3.653$  years; dam to daughter:  $6.615 \pm 3.514$  years; sire to son:  $6.507 \pm 4.704$  years and sire to daughter:  $6.489 \pm 4.146$  years.

The numbers of animals used to calculate the level of inbreeding per year for the whole pedigree data and inbred animals are presented in Figure 2. In 1981, there was a sharp increase in the number of animals used in the analysis for both inbred animals and all pedigree data used. The reason for this sharp rise in the number of animals was driven by the society to register more animals.

The mean inbreeding level per year for the whole pedigree data and the mean inbreeding level per year for inbred animals are presented in Figure 3. The proportion of animals that were inbred in 1970 was very low; therefore their

average inbreeding level was high. The opposite happened in 2011, where a larger proportion of animals were inbred, translating into a lower level of inbreeding. From 1970 to 1979, the inbreeding level for all animals showed an increase of 0.94 percent; onwards from 1980 until 2011 all inbreeding levels were above 1 percent. A stable increase in inbreeding levels was visible from 1978 to 1988 and from there on constant levels followed. The year with the highest inbreeding level was 1996, with an average of 2.79 percent. Along with the number of inbred animals increasing, the number of generations of inbred animals also increased; therefore, the level of inbreeding effectively decreased over time. Consequently, the level of inbreeding for the inbred animals showed a constant decrease as the number of generations used in analysis increased.

## Discussion

When the entire dataset was considered, a total of 34.4 percent of animals were, to some degree, inbred. The average inbreeding coefficient for the whole population was 1.83 percent. The value of  $N_e$  for the current study is 167.54. The observed high  $N_e$  of the Afrikaner may be the result of a project involving introgression of Bonsmara genes into the Afrikaner breed by a number of breeders to improve its performance. Following the introgression, line breeding was implemented to a certain degree. This project allowed the *AR* to also stay constant over generations since line breeding was used to breed pure Afrikaner animals, but however caused an increase in inbreeding since a smaller number of pure Afrikaner animals were available. This estimate  $N_e$  of the Afrikaner is similar to that of the Nguni cattle that was estimated to be 168 (Matjuda, 2012). The  $N_e$  reported here is greater than the minimum of 50–100 recommended by the FAO

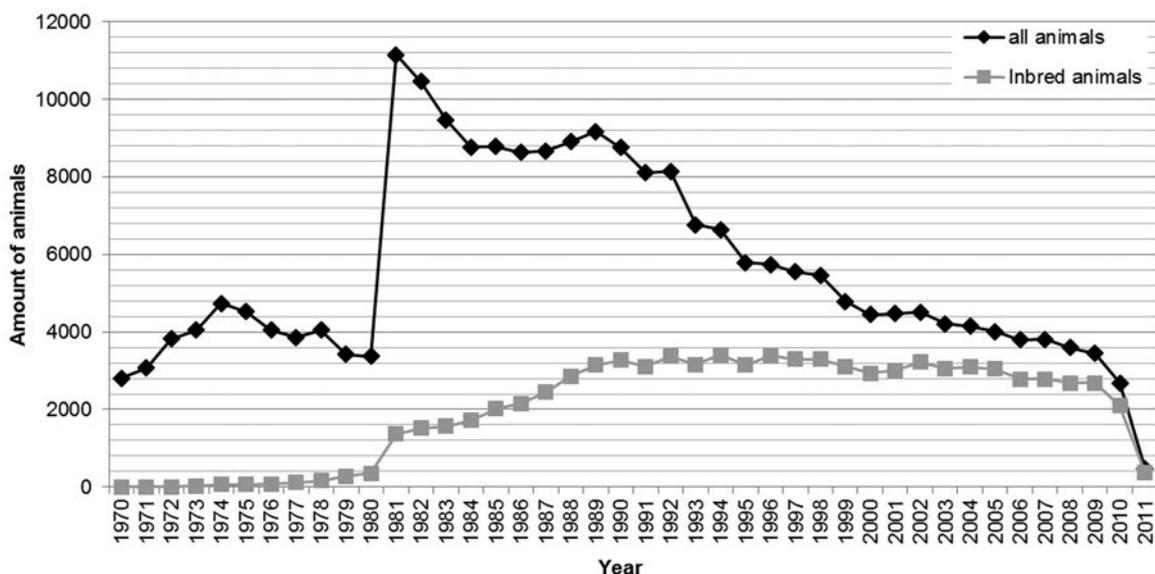
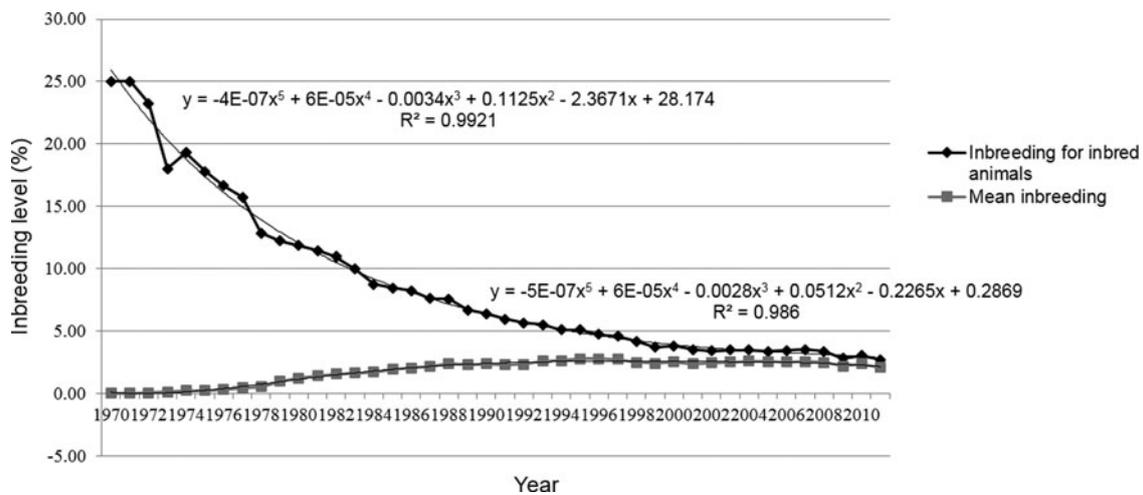


Figure 2. Number of animals used to calculate the level of inbreeding per year for the whole pedigree data and inbred animals.



**Figure 3.** Mean inbreeding level per year for whole pedigree data and mean inbreeding level per year for inbred animals

(1998) and within the 25–255 range of effective population size that was suggested as being critical for maintaining fitness by Meuwissen and Woolliams (1994). The  $N_e$  estimate of the Afrikaner was large when compared with some international breeds. Mc Parland *et al.* (2007) estimated  $N_e$  sizes of 64, 127 and 75 for Irish Herefords-, Simmental- and Holstein-Friesian breeds, respectively, whereas that of Italian beef cattle breeds were in the range from 122 to 138 (Bozzi *et al.*, 2006). Estimates of  $N_e$  for Danish dairy cattle populations ranged from 49 to 157 (Sørensen, Sørensen and Berg, 2004). Pedigree analysis on the Afrikaner cattle population yielded levels of inbreeding that appear to be at acceptable and manageable levels, especially when compared with international breeds such as the Holstein-Friesian.

The comparatively low levels of inbreeding observed in Afrikaner cattle could be due to random mating processes or outcrossing that were induced within the herds. The introgression project may have contributed to keep inbreeding in the Afrikaner population at low levels. As an additional consequence, the relatedness between the animals decreased. The Afrikaner cattle population in study has an acceptable level for the estimated effective population size. The low inbreeding levels confirm the relatively high effective population size. The implication of a high effective population size is that more animals are available for the selection, whereas inbreeding can be contained.

## Conclusions

Pedigree analysis on the Afrikaner cattle population yielded levels of inbreeding that appear to be at acceptable and manageable levels. The inbreeding of the Afrikaner breed has been low even though the number of animals has decreased due to the popularity of exotic and

composite breeds found in South Africa. The current study provided useful results that can be utilized by farmers and the Afrikaner Breeders' Society. The results of this study indicate that there is sufficient variation within the Afrikaner breed of cattle that will allow it to expand into the diverse markets that exist both within and beyond the boundaries of South Africa, especially in the era of climate change. The results also indicate that the breed is in a favourable position to continue countering the undesirable effects of inbreeding.

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