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Genetic diversity of Afrikaner cattle in southern Africa

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Abstract The Afrikaner is an indigenous South African breed of “Sanga” type beef cattle along with breeds such as the Drakensberger and Nguni. Six composite breeds have been developed from crosses with the Afrikaner. Additionally, Afrikaner has been the base from which exotic breeds were established in South Africa through backcrossing. The study examined genetic diversity of Afrikaner cattle by genotyping 1257 animals from 27 herds in different geographic areas of South Africa and Namibia using 11 microsatellite markers. Multiple-locus assignment, performed using the Bayesian clustering algorithm of STRUCTURE, revealed three underlying genotypic groups. These groups were not geographically localized. Across herds and markers, the proportion of unbiased heterozygosity ranged from 0.49 to 0.72 averaging 0.57; mean number of alleles per locus ranged from 3.18 to 7.09, averaging 4.81; and allelic richness ranged from 2.35 to 3.38, averaging 2.67. It is concluded that a low inbreeding level of 2.7% and a moderate to high degree of variation still persists within the Afrikaner cattle breed, despite the recent decline in numbers of animals.

Keywords *Bos taurus africanus* · Inbreeding · Heterozygosity · Microsatellite markers · Sanga

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Introduction

The Afrikaner is an indigenous South African breed of “Sanga” type cattle (*Bos taurus africanus*). Sanga cattle result from admixture of *Bos indicus* and *Bos taurus* (Payne and Wilson 1999; Makina et al. 2016). The Sanga breeds are well adapted and widely dispersed throughout Southern Africa. Afrikaner cattle, in particular, are characterized by resistance to heat and ticks, quiet temperament, and satisfactory fertility under harsh conditions (www.thecattlesite.com/breeds/beef/25/africander/overview).

Until the 1970s, Afrikaner was South Africa’s most abundant breed of cattle. However, the overemphasis on show standards and the neglect of performance led to a decline in its popularity and consequent reduction in numbers of pure-bred animals (Steenkamp and Tissier 2016). It was hypothesized that these problems resulted from inbreeding depression following a severe bottleneck due to a Rinderpest epidemic and the South African War at approximately the turn of the twentieth century (Coetzer and Van Marle 1972). Afrikaner cattle were also diverted to alternative uses in the livestock sector, such as crossbreeding. Six other composite breeds (i.e., Afrigus, Afrisim, Bonsmara, Hugenoot, SA Braford, and Sanganer) have been developed from crosses with the Afrikaner (Scholtz 2010).

The specific goals were to (i) determine levels of heterozygosity and inbreeding of Afrikaner cattle across a broad sample of herds and thus identify reservoirs of genetic diversity and (ii) determine the genetic structure of the breed and elucidate patterns of differentiation across herds. In fulfilling these goals, genetic differences between seedstock and commercial herds were discerned.

Genetic diversity, as quantified by genetic variance, is essential to ensure viability of breeds and for them to respond to selection pressures. Climate change is predicted to cause

extreme environmental conditions in South Africa (Scholtz et al. 2013) with the potential for adverse impacts on livestock (Schlenker and Lobell 2010) that may not be as readily mitigated by selection, if genetic variance has been reduced by inbreeding. These issues combined with the otherwise generally favorable characterization of Afrikaner cattle motivated this study.

Materials and methods

Samples were collected from different geographical areas in South Africa and further afield in Namibia and were accumulated at the Animal Production Institute of the Agricultural Research Council (ARC, Irene) and at Unistel Medical Laboratories (UML, Cape Town). Originally, there were samples from 1374 animals. Editing consisted of the removal of samples from herds of less than 10 animals and animals whose genotypes were not scored at two or more loci. After editing there were 1091 animals from 18 seedstock herds and 166 animals from nine commercial herds, which were represented in the data.

The samples were genotyped at either ARC or UML. Both laboratories used standard methods for DNA extraction of hair samples, genotyping, and allele calling. Genotypes were generated for the 11 microsatellite markers (BM1824, BM2113, SPS115, ETH3, ETH10, ETH225, INRA23, TGLA53, TGLA122, TGLA126, and TGLA127) recommended by the International Society of Animal Genetics (ISAG) for parentage testing. Concordance of the scoring of genotypes across laboratories was assured by the redundant genotyping and scoring five randomly selected Afrikaner cattle at both laboratories.

Mean number of alleles per locus (MNA) and unbiased heterozygosity (Hz) (Nei 1987) were calculated using the Microsatellite Toolkit (MS Toolkit) for Excel (Park 2001). MS Toolkit was also used to create input files for the statistical analysis programs which include, ARLEQUIN (Excoffier et al. 2005), FSTAT v2.9.3 (Goudet 2002), and STRUCTURE (Pritchard et al. 2000). Allelic richness (Rs) and unbiased *F*-statistics (Wright 1951; Weir and Cockerham 1984) were calculated using FSTAT. Genetic differentiation between seedstock and commercial herds (groups) and among herds within groups were assessed by Analysis of Molecular Variance (AMOVA) using ARLEQUIN. A neighbor-joining (NJ) relationship tree constructed from the F_{ST} -statistics using MEGA6 (Tamura et al. 2013).

To further describe the genetic diversity within Afrikaner, a Bayesian-based assignment approach for analysis of genotypes across multiple loci was conducted using STRUCTURE (Pritchard et al. 2000). Individuals were probabilistically assigned to one or more of *K* clusters. Values of *K*

evaluated ranged from 1 to 10 with 15 replicate analyses conducted for each. All runs consisted of a burn-in period of 100,000 iterations followed 20,000 additional Markov Chain Monte Carlo (MCMC) iterations for estimation. Structure Harvester v0.6.93 (Earl and vonHoldt 2012) was used to determine the most likely value of *K* given the data by the ΔK method of Evanno et al. (2005).

Results

The number of alleles per locus ranged from eight at locus BM1824 to 19 at locus TGLA53. Unbiased estimates of heterozygosity (Hz) ranged from 0.494 ± 0.053 (Hz \pm SD) to 0.723 ± 0.037 (Table 1). The averages within herds, thus, mean Hz was 0.570 ± 0.057 , with an average of 4.81 ± 1.74 alleles per locus. Also within herds, allelic richness (Rs) estimates ranged from 2.348 ± 0.614 to 3.376 ± 0.645 and averaged 2.666 ± 0.667 .

Averages of MNA, Hz, and Rs were similar for commercial and seedstock herds. The genetic similarity of seedstock and commercial herds of Afrikaner cattle was likewise supported by the AMOVA with the difference between groups only explaining 0.34% of the genetic diversity (Table 2). The individual herds within groups were more diverse, explaining approximately 4.48% of the molecular variance. Thus, animals within herds were heterogeneous with differences among them explaining the vast majority of genetic variation that was present in these data. Unbiased estimates of Wright's *F*-statistics (Wright 1951) were 0.027, for within breed inbreeding (F_{IT}) and -0.022 , for within herd inbreeding (F_{IS}).

Assignment of all animals to one or more of three genetic clusters was sufficient to describe the structure of Afrikaner (i.e., $K = 3$). The relationship of ΔK to *K*, which Evanno et al. (2005) suggested aid in appropriately identifying the number of genetic clusters (Fig. 1). Twelve of the 18 seedstock herds were characterized by a majority of membership (i.e., $p > 0.50$) in a single cluster (Table 3). However, only one of the nine commercial herds was characterized similarly.

Unbiased genetic distances between herds were also estimated (Fig. 2). As with the assignment to genetic clusters, three main groups also appear evident in the neighbor-joining tree. Both seedstock and commercial herds are present in each group.

Discussion

Costs of experiments, such as this one, are determined by numbers of animals and numbers of loci. These costs are particularly relevant to work supported by developing countries. Here, an existing database of genotypes, created by a breed society in verifying parentage, was used. Its liability is the

Table 1 Genetic diversity results of Afrikaner seedstock and commercial herds based on 11 microsatellite markers. The parameters are type = seedstock (SS) and commercial (COM)

Herd area	Type	<i>N</i>	<i>H_z</i> ± <i>SD</i>	<i>MNA</i> ± <i>SD</i>	<i>Rs</i> ± <i>SD</i>	<i>F_{IS}</i>
Marblehall	SS	15	0.510 ± 0.062	3.27 ± 1.19	2.353 ± 0.640	- 0.091
Kameel	SS	16	0.494 ± 0.053	3.82 ± 0.98	2.412 ± 0.543	0.055
Bothaville	SS	20	0.658 ± 0.032	5.18 ± 1.60	2.995 ± 0.446	0.001
Olifantshoek	SS	12	0.514 ± 0.057	3.36 ± 1.50	2.348 ± 0.614	- 0.095
Thabazimbi	SS	23	0.592 ± 0.064	4.91 ± 2.07	2.765 ± 0.704	- 0.041
Standerton	SS	18	0.561 ± 0.063	4.00 ± 1.41	2.591 ± 0.705	- 0.021
Otjiwarongo	SS	13	0.627 ± 0.062	5.18 ± 2.18	2.976 ± 0.808	- 0.064
Ladybrand	SS	10	0.577 ± 0.070	4.27 ± 1.68	2.741 ± 0.767	- 0.115
Theunissen1	SS	12	0.526 ± 0.059	3.18 ± 1.17	2.379 ± 0.596	- 0.006
Theunissen2	SS	99	0.569 ± 0.064	4.64 ± 2.25	2.593 ± 0.742	- 0.053
Komatiepoort	SS	48	0.560 ± 0.060	4.91 ± 2.63	2.571 ± 0.669	0.022
Potchefstroom	SS	234	0.549 ± 0.052	7.45 ± 1.92	2.554 ± 0.566	- 0.003
Bloemfontein	SS	163	0.599 ± 0.061	6.27 ± 2.05	2.756 ± 0.697	- 0.005
Fochville1	SS	23	0.723 ± 0.037	6.36 ± 1.91	3.376 ± 0.645	- 0.051
Fochville2	SS	35	0.649 ± 0.037	6.27 ± 2.10	3.000 ± 0.574	- 0.007
Koppies	SS	14	0.525 ± 0.069	3.55 ± 1.29	2.448 ± 0.714	- 0.092
Laersdrif	SS	69	0.582 ± 0.051	5.91 ± 1.92	2.702 ± 0.587	- 0.092
Bloemhof	SS	267	0.557 ± 0.060	7.09 ± 2.07	2.625 ± 0.684	- 0.028
Theunissen	COM	18	0.598 ± 0.057	5.09 ± 1.87	2.794 ± 0.756	- 0.014
Dannhauser	COM	14	0.549 ± 0.050	4.82 ± 1.78	2.639 ± 0.662	- 0.018
Dordrecht	COM	20	0.544 ± 0.040	4.45 ± 1.13	2.503 ± 0.429	- 0.079
Ficksburg	COM	20	0.558 ± 0.065	4.18 ± 1.78	2.611 ± 0.758	0.032
Stoffberg	COM	19	0.574 ± 0.063	4.73 ± 2.00	2.713 ± 0.761	0.008
Rustenburg	COM	18	0.576 ± 0.060	4.18 ± 1.40	2.638 ± 0.726	0.000
Superbia	COM	17	0.524 ± 0.063	3.27 ± 1.35	2.405 ± 0.648	- 0.031
Delareyville	COM	20	0.520 ± 0.061	5.18 ± 2.14	2.496 ± 0.705	- 0.058
Winburg	COM	20	0.566 ± 0.065	4.36 ± 1.63	2.695 ± 0.860	0.005

N herd sample size, *H_z* unbiased heterozygosity, *SD* standard deviation, *MNA* mean number of alleles, *Rs* allelic richness, *F_{IS}* within herd inbreeding coefficient

limited number of microsatellite markers that have been historically recommended by the International Society for Animal Genetics for use in parentage verification. However, individual polymorphic microsatellite loci have considerably greater information content than bi-allelic loci (e.g., Schaid et al. 2004; Fernández et al. 2013). Further, Pritchard et al. (2000), Rosenberg et al. (2001), Fan et al. (2005) and others have demonstrated the utility and accuracy of fewer microsatellite loci than were used here for similar purposes. Important advantages of parentage databases arise from the number

Table 2 Analysis of molecular variance for seedstock and commercial herds

Source of variation	Sum of squares	Variance components	% variation
Among groups	18.732	0.0102	0.34
Among populations within groups	361.624	0.13498	4.48
Within herds	3680	2.92761	97.1

of animals contained therein and the breath of sampling they represent.

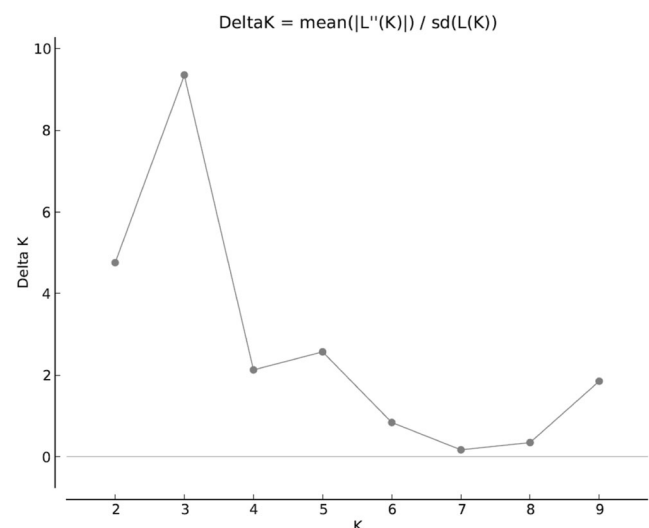
**Fig. 1** Plot of Delta*K* showing that the animals from 27 herds had the highest probability of representing three genetic clusters (*K* = 3)

Table 3 Proportion of membership of each herd to each of three identified clusters ($K = 3$). A significance level of $p > 0.050$ was applied when assigning herds into clusters

Predefined populations	Type	Inferred clusters		
		1	2	3
Marblehall	SS	0.101	0.111	0.788
Kameel	SS	0.193	0.405	0.402
Bothaville	SS	0.737	0.077	0.185
Olifantshoek	SS	0.208	0.578	0.214
Thabazimbi	SS	0.429	0.163	0.408
Standerton	SS	0.292	0.120	0.588
Otjiwarongo	SS	0.593	0.088	0.319
Ladybrand	SS	0.593	0.128	0.279
Theunissen1	SS	0.109	0.145	0.746
Theunissen2	SS	0.100	0.108	0.791
Komatiepoort	SS	0.155	0.164	0.680
Potchefstroom	SS	0.127	0.179	0.694
Bloemfontein	SS	0.478	0.383	0.139
Fochville1	SS	0.722	0.168	0.111
Fochville2	SS	0.561	0.302	0.137
Koppies	SS	0.311	0.478	0.211
Laersdrif	SS	0.356	0.432	0.212
Bloemhof	SS	0.148	0.755	0.097
Theunissen	COM	0.387	0.489	0.124
Dannhauser	COM	0.355	0.367	0.278
Dordrecht	COM	0.557	0.356	0.087
Ficksburg	COM	0.280	0.414	0.306
Stoffberg	COM	0.287	0.318	0.395
Rustenburg	COM	0.366	0.318	0.316
Superbia	COM	0.241	0.277	0.482
Delareyville	COM	0.390	0.206	0.404
Winburg	COM	0.445	0.230	0.325

Genetic variation is required for response to selection and hence for adaptation to different environmental pressures (FAO 1998; Frankham et al. 2002). Thus, sufficient genetic variation will ensure a breed has the ability to improve in its ability to meet consumer preferences and to respond to changing environmental conditions including climate and exposure to new disease vectors. Concern for the loss of genetic variation in Afrikaner has been raised previously (Coetzer and Van Marle 1972). This concern motivated the present investigation into genetic diversity of Afrikaner cattle in South Africa. The 57% average level of heterozygosity observed in Afrikaner was intermediate in comparison to cattle breeds: Senegalese breeds (Ndiaye et al. 2015), Creole cattle breeds (Delgado et al. 2011), Hallikar breed (Hepsibha et al. 2014), Chinese indigenous breeds (Zhang et al. 2007), Mozambican cattle breeds (Bessa et al. 2009), and Canadian Angus (Carruthers

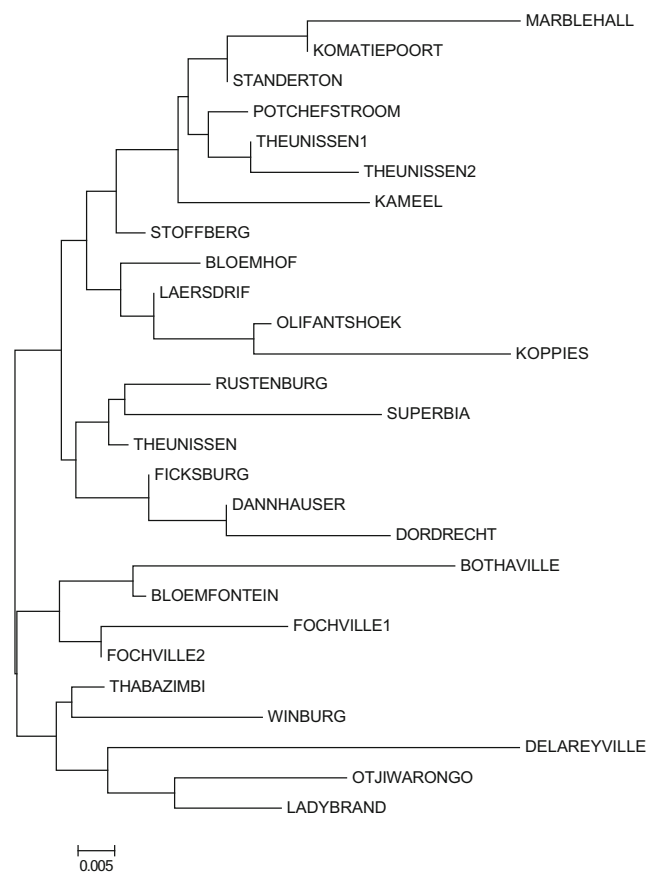


Fig. 2 Neighbor-joining tree illustrating genetic distances between herds of Afrikaner cattle

et al. 2011). Inbreeding estimates were generally small. F_{IS} was slightly negative indicating a small surplus of heterozygotes within herds whereas, F_{IT} was slightly positive indicating a small general surplus of homozygotes across the entire population. A total of seven herds from both groups, seedstock, and commercial, had F_{IS} values that were greater than zero. These herds possibly used different mating strategies, such as linebreeding, which caused inbreeding to increase. A comprehensive review of the consequences of inbreeding in cattle found performance generally reduced by inbreeding across a host of growth, reproduction, and carcass traits (Burrow 1993). Average inbreeding coefficient levels of less than 5% within a breeding program may be considered low, with effects that are perhaps unable to be detected in all but the most powerful experiments. Inbreeding levels of 5 to 10% being considered more moderate and having effects that are likely to be perceived, thus warranting more careful management. The inbreeding level of the Afrikaner population calculated by the microsatellite markers are 2.7%. With the use of pedigree data, Pienaar et al. (2015) estimated the inbreeding coefficient as 1.83%. Therefore, the perception of inbreeding having seriously compromised performance that was alluded to by Coetzer and van Marle (1972) seems

unsupported in current data. Pienaar et al. (2015) also concluded that the Afrikaner has gone through a bottleneck, however, it was not large enough to have a severe impact on the breed. However, it is entirely possible that is exactly what took place in the past with the less successful herds either adopting mating systems that reduced their level of inbreeding or ceasing to exist. The industry perception of Afrikaner would plausibly be affected by experiences from herds with naive strategies mate allocation given the attendant risks associated with inbreeding. In any case, it appears important to restrict inbreeding to acceptable levels in order to mitigate the associated risks and thereby ensure viability (Fernández et al. 2005). Individual breeders can offset past inbreeding and thus increase the average level of heterozygosity in their herds by outcrossing guided by genetic distances. Such outcrossing would be expected to increase genetic variability and thus provide greater opportunity for selection to effectively offset changing environmental conditions.

The genetic similarity of seedstock and commercial herds is noteworthy; here, they were indistinguishable. It could be hypothesized that differences between seedstock and commercial Afrikaner herds would have arisen from differences in breeding objectives. Commercial breeders might tend to focus largely on economically relevant traits; whereas seedstock breeders may tend to also give attention to breed standards (Scholtz 2005). The present data do not support this hypothesis. Granted, the present data arise from assays of selectively neutral alleles and any effect of selection on them would depend on linkage disequilibrium. It is more likely that frequent movement of seedstock bulls to commercial herds as might be expected from the typical pyramidal structure of the beef industry (Newman 2011) would contribute to this circumstance, as would conversion of seedstock herds to commercial production. This latter phenomenon is a trend that has been observed over time in Afrikaner as the number of seedstock animals decreased (Jordaan 2015).

Conclusions

The decline in numbers of purebred Afrikaner cattle that has occurred in recent years has not affected their variability and inbreeding as may have been expected. The presence of moderate to high degree of variation within Afrikaner positions the population to respond favorably in genetic improvement programs and to arising environmental challenges.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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