Evaluation of the International Society for Animal Genetics bovine single nucleotide polymorphism parentage panel in South African Bonsmara and Drakensberger cattle

Yandisiwe P. Sanarana[1,2#] · Azwihangwisi Maiwashe[2] · Donagh P. Berry[1,3] · Cuthbert Banga[2] · Este van Marle-Köster[1]

[1]University of Pretoria, Department of Animal and Wildlife Science, Pretoria, Hatfield, 0002, South Africa

[2]Agricultural Research Council-Animal Production, Pretoria, Irene, 0062, South Africa

[3]Teagasc, Animal and Grassland Research, and Innovation Center, Fermoy, Cork, P61 C996, Ireland

Abstract

A panel of 200 single nucleotide polymorphisms (SNPs) have been recommended by the International Society for Animal Genetics (ISAG) for use in parentage verification of cattle. While the SNPs included on the ISAG panel are segregating in European *Bos taurus* and *Bos indicus* breeds, their applicability in South African (SA) Sanga cattle has never been evaluated. This study, therefore, assessed the usefulness of the ISAG panel in SA Bonsmara (BON) and Drakensberger (DRB) cattle. Genotypes of 185 ISAG SNPs from 64 BON and 97 DRB sire-offspring pairs were available, all of which were validated with 119 375 SNPs. Of the 185 ISAG SNPs, 14 and 18 in the BON and DRB, respectively (9 in common to both breeds) were either monomorphic, exhibited at least one discordance between validated sire-offspring pairs, or had poor call rate or clustering issue. The mean minor allele frequency of the 185 ISAG SNPs was 0.331 in the BON and 0.359 in the DRB. The combined probability of parentage exclusion (P_E) was the same (99.46%) for both breeds, while the probability of identity varied from 1.61×10^{-48} (BON) to 1.11×10^{-54} (DRB). Fifteen (23.4%) and 32 (33%) of the already validated sire-offspring pairs for the BON and DRB, respectively, were determined by the ISAG panel to be false-negatives based on a threshold of having at least two discordant SNPs. In comparison to sire discovery using the 119 375 SNPs, sire discovery using only the ISAG panel identified correctly 44 (out of 64 identified using the 119 375 SNPs) unique sire-offspring BON pairs and 62 (out of 97 identified using the 119 375 SNPs) unique sire-offspring DRB when all sires were masked. Five BON and three DRB offspring had >1 sire nominated. This study demonstrated that the use of the ISAG panel may result in incorrect exclusions and multiple candidate sires for a given animal. Selection of more informative SNPs is, therefore, necessary in the pursuit of a low-cost and effective SNP panel for indigenous cattle breeds in SA.

Keywords: Sanga cattle, parentage verification, GenTrain score, false-negative

#Corresponding author: Sanaranay@gmail.com

Introduction

Correct pedigrees form the basis for accurate genetic evaluation using the Best Linear Unbiased Prediction (BLUP) statistical method (Henderson, 1973). Incorrect parentage, however, occurs in practice and has been reported in cattle (Weller et al. 2004; Kios et al. 2012; McClure et al. 2018). Parentage errors are known to negatively affect genetic improvement as well as influence the variance of estimated breeding values (EBVs), thus reducing response to selection (Sanders et al. 2006). Banos et al. (2001) indicated that an 11% paternal error rate in genetic evaluations reduced genetic gain by 11 to 15%. Other studies have predicted that a 10% parentage error, with a heritability of 0.25, would contribute to a 3% (Visscher et al. 2002) to 4.3% (Israel and Weller 2000) reduction in genetic gain. For the same pedigree error and a heritability of 10%, a 7% reduction in genetic gain was observed (García-Ruiz et al. 2019). The application of molecular information to correct pedigree records has improved the precision of parentage assignment (Van Eenennaam., 2016; McClure et al. 2018). This has contributed to more accurate EBVs for traits of economic importance especially those of low heritability such as fertility (Berry et al. 2014) and tick resistance (Junqueira et al. 2017).

Multi-allelic microsatellite markers, also known as short tandem repeats markers, were traditionally the preferred genetic markers for parentage verification, to trace meat through the entire food chain and other applications in a broad range of livestock species (Teneva et al. 2018). Despite high polymorphic content, these markers have limitations including the presence of null alleles, allele drop-outs, and imperfect repeats caused by mutations; hence microsatellite markers require a dedicated platform and skilled interpretation to ensure consistent accuracy (Buchanan et al. 2016). Furthermore, microsatellite genotypes from different laboratories are not always comparable due to the inconsistencies in allele scoring and size determination, with genotyping error rates estimated to 5% per locus (Weller et al. 2004; Fernández et al. 2013).

The discovery of bi-allelic single nucleotide polymorphism (SNP) markers has revolutionized animal breeding with several associated genomic applications for livestock improvement (Georges et al. 2018). Subsequently, SNP-based parentage has become the common practice for parentage validation. The superior performance of SNPs over microsatellite markers in parentage validation has been demonstrated in several studies (Fisher et al. 2009; Fernández et al. 2013; Buchanan et al. 2016). In an effort to expedite the shift from microsatellite markers to SNP-based parentage, the International Society for Animal Genetics (ISAG), together with the International Committee for Animal Recording (ICAR), developed a cattle consensus panel of SNP markers for global application, mainly selected for high minor allelic frequency (ISAG., 2013). The panel consists of a core panel of 100 SNP markers, combined with an additional 100 markers (ISAG200). The core 100 SNP panel, mostly derived from European breeds, have been demonstrated to be insufficient for parentage verification in several breeds,

whereas the ISAG200 panel including SNPs from the *indicine* cattle breeds has been demonstrated to have better resolution power (Strucken et al. 2014; Lyons et al. 2015; Van Doormaal et al. 2016).

In the establishment of SNP-based marker systems, a critical factor to consider is whether the chosen SNPs are informative in multiple cattle populations. This emerges from a non-random selection method that preferentially selects alleles segregating at high frequencies in European *Bos taurus* and *Bos indicus* breeds known as ascertainment bias. The efficiency of the SNP panel varies by breed, depending on the respective minor allele frequency (MAF) (Nielsen and Signorovitch, 2003). The restricted number of breeds used in the establishment of the ISAG panel may consequently influence the applicability of the panel in under-represented breeds. Despite concerns on marker ascertainment bias for the interpretation of parentage results, the quality of the genotype remains the basis for further analysis and accuracy. The applicability of the ISAG SNP panel for parentage testing has not been evaluated in South African Sanga cattle breeds or locally developed composites. Therefore, the aim of this study was to evaluate the effectiveness of the bovine ISAG SNP parentage panel in both SA Bonsmara and Drakensberger beef cattle.

Materials and methods

Genotype data and quality control

Ethical approval was received for the use of external data by the Animal Ethics Committee (AEC) of the University of Pretoria (EC066-16 AEC). Genotypes from 1 567 Bonsmara and 1 022 Drakensberger beef cattle were available from the SA Beef Genomics (BGP) and Red Meat Research Development (RMRD) projects. The South African Stud Book and Animal Improvement Association provided the pedigree data for the genotyped animals. Data edits and calculations were all performed using *R* software (R Development Core Team, 2018). All animals were genotyped with the GeneSeek® Genomic Profiler (GGP) Bovine 150K BeadChip with 138 888 SNP markers in common for both the BON and DRB. A total of 119 375 autosomal SNPs with genomic positions assigned based on UMD3.1 bovine genome build were kept for further analysis. Only 185 SNP markers recommended by ISAG for parentage verification existed in the common dataset. This was satisfactory as 90% of the SNPs were present for the basis of verifying an offspring with one parent (ISAG., 2013). A total of 80 individual samples with more than 10% missing SNP genotypes were not considered further.

Evaluation of the ISAG SNP markers

Mean allele frequency per breed was estimated for each ISAG SNP in the BON and DRB separately. The allele and genotype frequencies were used to estimate different genetic parameters. The call rate, minor allele frequency, Hardy-Weinberg Equilibrium (HWE) *p-value*, the level of heterozygosity (expected and observed) and the polymorphic information content (PIC) per SNP were estimated within

each breed separately. The probability of parentage exclusion (P_E) per SNP for the scenario of one known parent (i.e. sire) was calculated according to Jamieson and Taylor (1997) as:

$$P_E = 1 - 4\sum_{i=1}^{n} p_i^2 + 2\left(\sum_{i=1}^{n} p_i^2\right)^2 + 4\sum_{i=1}^{n} p_i^3 - 3\sum_{i=1}^{n} p_i^4$$

where p_i is the MAF for marker i and n the number of alleles per SNP ($n = 2$ since SNP are biallelic markers). The combined probability of parentage exclusion (P_E) over all the SNPs was calculated as P_{Ej} = 1-(1-P_1) (1-P_2) (1- P_3)….(1-P_k) where j is the probability of exclusion per marker and k is the number of loci. The probability of identity (P_I) that two randomly selected individuals in a population would possess identical SNP genotypes was calculated per SNP. The combined P_I, which is the multiple product of each SNP marker probability, was estimated according to Waits et al. (2001) as follows:

$$P_I = \prod_{i=1}^{N} (p_i^2 + 2p_i^2 q_i^2 + q_i^2)$$

where N is the number of SNPs with p^2, $2pq$, and q^2 as the relative genotype frequencies of AA, AB, and BB respectively, p and q being the A and B allele frequencies.

Pedigree verification and sire-offspring genotype mismatches

Based on the available pedigree information, 50 putative sire-offspring pairs in the BON and 93 in the DRB were available, with the number of offspring per sire ranging from 1 to 21. The (in)validation of these sire-offspring pairs was based on the count of opposing homozygous genotypes between the sire and offspring. This was determined per animal (across all SNPs), using all 119 375 autosomal SNPs. An opposing homozygote was defined as when a sire had a homozygous genotype (AA) and the offspring was also homozygous but for the other allele (BB), and vice versa (Hayes, 2011). Sire parentage exclusion was considered whenever the rate of the mismatches exceeded 1%. A total of 124 male animals (71 BON and 53 DRB) were available in the dataset. In a separate analysis, these were considered as candidate sires where all the known sires of the animals were actually masked and, subsequently, predicted using initially the 119 375 SNPs to identify the true sire-offspring pairs and then using the ISAG panel. This new dataset, comprising of validated 64 BON and 97 DRB sire-offspring pairs, was used to evaluate the ISAG SNP panel for sire discovery. False-negatives were estimated as the proportion of wrongly excluded sire-offspring relationships divided by the total number of true sire-offspring pairs.

Results

Of the 185 ISAG SNPs, 175 had a call rate ≥ of 0.95 (Fig. 1), with just five and eight SNPs in the BON and DRB, respectively, exhibiting a call rate < 0.95.

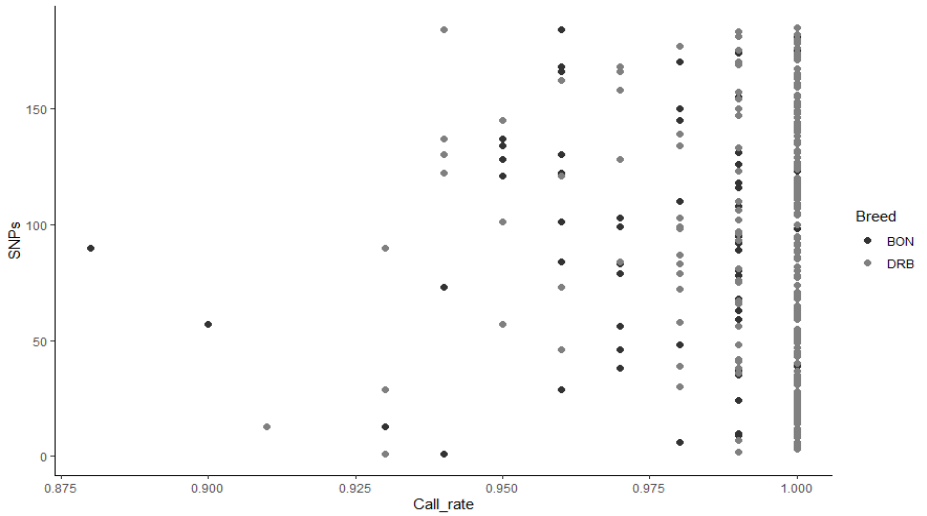


Figure 1. A scatter-plot depicting the call rate of the 185 International Society for Animal Genetics single nucleotide polymorphisms (SNPs) in Bonsmara (BON) and Drakensberger (DRB) cattle breeds

There were two SNPs, ARS-BFGL-NGS-11383 (rs110577061) and ARS-USMARC-Parent-DQ786762 (rs29010772), with a low GenTrain (GT) score of < 0.55 (Fig. 2), one in the BON and both in the DRB. The GT score of the 185 SNPs ranged between 0.49 and 0.90 with a mean of 0.78.

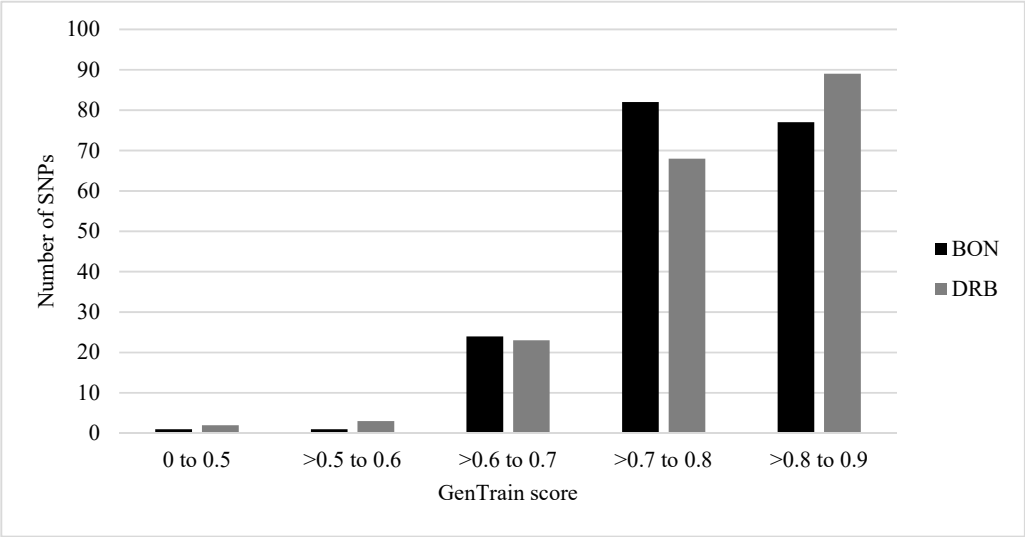


Figure 2. GenTrain score distributions for the 185 International Society for Animal Genetics single nucleotide polymorphisms (SNPs) for the Bonsmara (BON) and Drakensberger (DRB) cattle breeds

The majority of the 185 SNPs had a MAF between 0.1 and 0.5 (Fig. 3) with just three monomorphic SNPs per breed. Of the 185 ISAG markers, 135 and 115 SNPs had a MAF ≥ 0.3 in the DRB and BON, respectively.

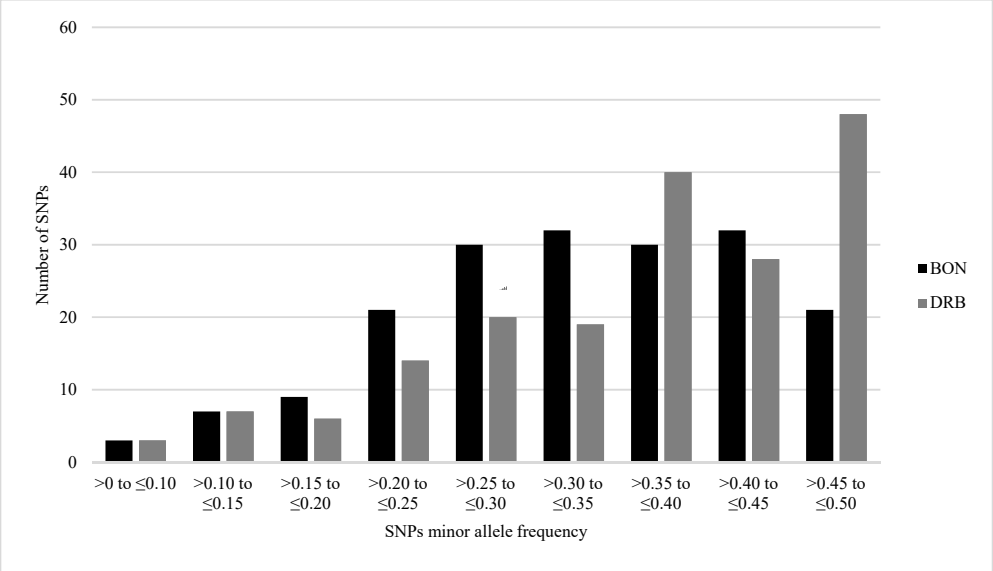
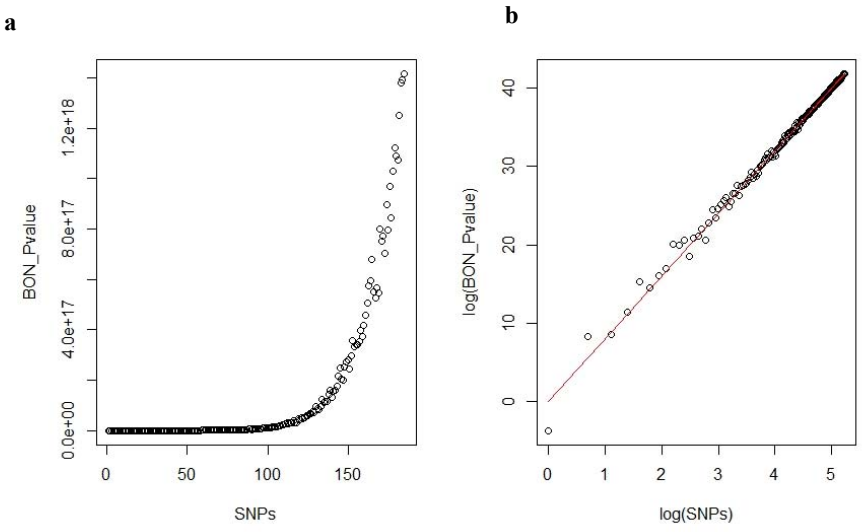


Figure 3. Minor allele frequency distributions for the 185 International Society for Animal Genetics single nucleotide polymorphisms (SNPs) for the Bonsmara (BON) and Drakensberger (DRB) cattle breeds

The distribution of the HWE *p-values* for the ISAG SNPs is represented by quantile-quantile (Q-Q) plots in Fig. 4. Eight and twelve SNPs in the BON and DRB, respectively, deviated (P<0.001) from a uniform distribution.



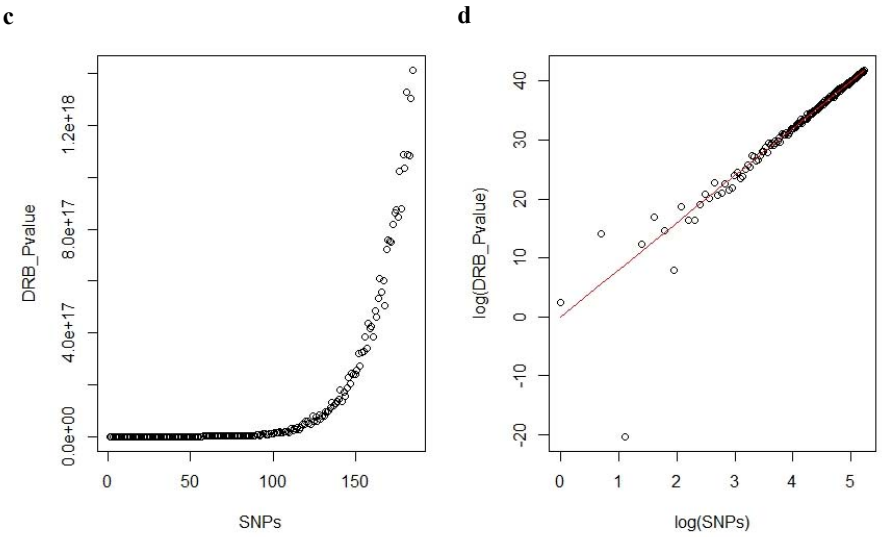


Figure 4. Q-Q plots of HWE *p-values* for 185 International Society for Animal Genetics single nucleotide polymorphism (SNP) panel. **a,b** Bonsmara (BON) and **c,d** Drakensberger (DRB) cattle breeds

The average MAF, H_E and PIC in the two breeds are summarised in Table 1. Each parameter was similar in each breed, except for a slightly higher MAF and H_E in the DRB. The P_E was 99.46% in both breeds and, based on the genotype frequencies, the estimated P_I values ranged from 1.61×10^{-48} to 1.11×10^{-54} in the BON and DRB, respectively.

Table 1. Descriptive statistics for the SA Bonsmara and Drakensberger breeds using the ISAG markers

Populations	MAF	H_O	H_E	PIC	P_E	P_I
BON	0.331	0.212	0.423	0.330	0.9946	1.61E-48
DRB	0.359	0.214	0.437	0.338	0.9946	1.11E-54

MAF, minor allele frequency; H_E, expected heterozygosity; H_O, observed heterozygosity, PIC, polymorphic information content; P_E, the combined probability of parentage exclusion for the scenario of one known parent; P_I, probability of identity

The number of discordant SNPs between sires and their validated offspring is in Fig.5. These discordances occurred in 13 SNPs with two SNPs in common for both breeds. The frequency of discordances per SNP ranged from one to five in the BON and up to 14 in the DRB.

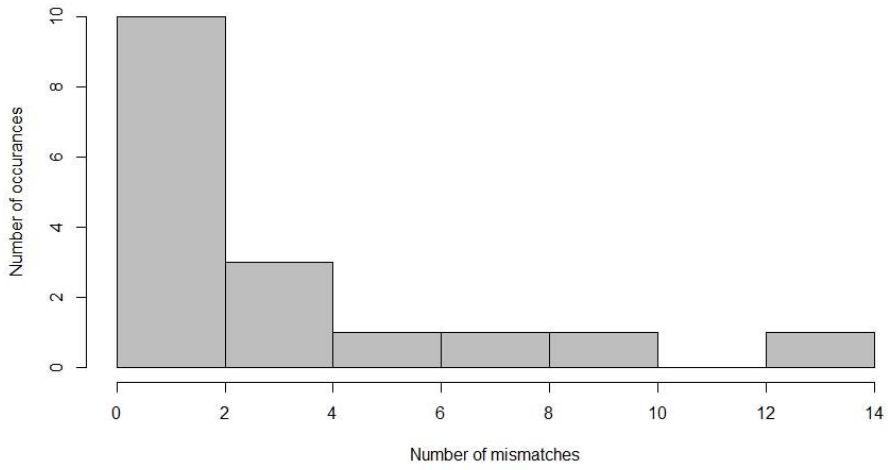


Figure 5. Frequency distribution of the number of mismatches between animals and the sires

Of the 50 BON and 93 DRB sire-offspring pairs recorded in the pedigree and verified with 119 375 SNPs, 5 (10.0%) and 16 (17.2%) parentages, respectively, were inconsistent with that reported in the pedigree. In addition, 19 and 20 additional sire-offspring pairs in the BON and DRB, respectively, were discovered when all the sires were masked and predicted using the 119 375 SNPs. Of the total 64 and 97 sire-offspring pairs in the BON and DRB, respectively, detected with the 119 375 SNP panel, the ISAG panel indicated 15 (23.4%) BON and 32 (33%) DRB sire-offspring pairs as false-negatives. Accurate sire discovery with only one candidate sire was possible for 44 BON and 62 DRB animals using the ISAG 185 SNP genotypes. The ISAG panel assigned multiple sires for a further 5 BON and 3 DRB animals all of which also contained the true sire as determined by the 119 375 SNP panel; a single unique sire was identified for these 8 animals when using the 119 375 SNPs.

Discussion

The value of accurate parentage verification for effective selection and breeding has been demonstrated in several studies (Banos et al. 2001; Visscher et al. 2002; Weller et al. 2004). In developing countries such as SA, routine genotyping is not feasible for all cattle breeds and the adoption of genomic evaluations remains limited. Lower density SNP panels hold the potential for exploiting genomic information at a lower cost. A measure of the applicability or informativeness of a SNP is the extent to which the SNP is segregating in the population within which it will be used. The International Society of Animal Genetics (ISAG) took the initiative to propose a 200-SNP panel that could be used internationally for parentage verification. The present study is the first study to evaluate the effectiveness of these SNPs in SA Bonsmara and Drakensberger beef cattle. In the development of the ISAG panel, SNPs specific to African *Bos taurus* (Sanga) cattle breeds were not included and, thus, this evaluation is crucial prior to recommending the use of this panel in these breeds.

While not all Sanga breeds were included in the present study, a representative sample of a composite and an indigenous cattle of the BON and DRB originated from 22 and 10 herds, respectively, were included to evaluate the efficiency of the ISAG panel. Due to variation in the number of SNP genotypes created during the genotyping process, genotypes on only 185 of the 200 ISAG markers panel were available. The call rate, minor allele frequency, and extent of Hardy-Weinberg equilibrium deviations have been the most commonly used measures to define the integrity of the genotype (Chan et al. 2008). In the pursuit of improving the genotype quality for parentage tests, others (McClure et al. 2015; Berry et al. 2019) have also considered the SNP GenTrain score and the number of discordant SNPs between validated parent-offspring.

The value of a SNP for parentage verification highly depends on the MAF within a population of animals that are being compared. Since only homozygous genotypes in both the parent and offspring are informative, a SNP with low MAF has a limited value for parentage verification (Van Doormaal et al. 2016). A total of 62.2% and 73.0% of the ISAG markers in BON and DRB cattle, respectively, were segregating strongly (i.e., MAF > 0.3) with a mean minor allele frequency of the ISAG SNP panel of 0.331 and 0.359 in the BON and DRB, respectively. This was supported with heterozygosity and polymorphic information content values that were close to 0.5. Of the six monomorphic SNPs identified in the present study, two i.e. ARS-USMARC-Parent-DQ786764 (rs109943112) and ARS-USMARC-Parent-EF034087 (rs110665639) were already reported by McClure *et al.* (2015) to be monomorphic in an Irish multi-breed cattle population. The GenTrain score calculated from the GenomeStudio for each SNP provides a measure that takes into account the quality and shape of the genotype clusters and the relative distance from one another. Both the ARS-BFGL-NGS-11383 (rs110577061) and ARS-USMARC-Parent-DQ786762 (rs29010772) SNPs exhibited poor genotype clustering with a GenTrain score of 0.50 and 0.52, respectively, as well as suffering from low call rates (i.e. <0.93). A total of 13 SNPs had at least one discordant genotype between the validated sire-offspring pairs. SNPs exhibiting some parent-offspring discordances, as well as those with low call rates or poor GenTrain score < 0.55 are often discarded prior to the downstream genomic analyses (Zhao et al. 2015; Judge et al. 2016; Berry et al. 2019). Some SNPs also deviated from HWE indicating either the occurrence of genotype errors or the loss of heterozygotes (Chan et al. 2008). There was no difference in the power of probability of parentage exclusion (P_E) (99.46%) between the two breeds. The P_E value observed in this study corresponds with that reported for Hanwoo and Wagyu cattle in Australia (0.99) using 195 and 199 ISAG SNP markers, respectively (Strucken et al. 2014). The probability of identity was, however, lower in the DRB (1.11×10^{-54}) compared to the BON (1.61×10^{-48}) and suggests that the ISAG SNP panel differed in applicability between the two SA breeds. The values observed in the 185 ISAG SNPs were low compared to those reported in purebred American Angus (2.0×10^{-13}) and multi-breed composite populations (1.9×10^{-10}) with only 32 SNPs (Heaton et al. 2002), in Black Japanese cattle (2.7×10^{-34}) based on 87 SNPs (Hara et al. 2010) and 10^{-44} reported in purebred Angus population in

Argentina with 116 SNPs (Fernández et al. 2013). Given the difference in the number of SNPs tested, a lower probability of identity value would be expected in the present study.

DNA-based parentage verification is used to improve the quality of pedigrees and, consequently, of genetic evaluations. Parent-offspring mismatches between the genotypes of the animal and putative sires provide means to detect errors in pedigree records. Pedigree errors can occur for several reasons including incorrect recording on-farm, multi-sire breeding, mistakes in genotyping laboratories, or even from the genotype format (Weller et al. 2004; McClure et al. 2018). The parentage errors of 10% and 17.2% reported in the present study based on 119 375 SNP genotypes for the BON and DRB, respectively, does indicate issues with recording at the farms.

It is, therefore, imperative that the markers used to assign parentage should be consistently accurate, in order to minimize pedigree errors. The 13 SNPs with some discordances between validated sire-offspring pairs within the ISAG SNP markers suggests that they may in fact not be informative, and could actually be counter-informative within a parentage panel. The false-negative parentages, and failure to exclude parentages that were already validated with the 119 375 SNP genotypes, demonstrated that the use of the ISAG panel in Sanga breeds may lead to parentage errors. This may also mean that, at times, it might not be possible to conclude parentage when closely related candidate sires are linked. These results show the need for the selection of additional informative SNP markers for parentage testing in Sanga breeds.

Acknowledgments

The authors would like to acknowledge funding given by the Technology Innovation Agency (TIA) for the Beef Genomics Project (BGP). We wish to thank the South African Bonsmara and Drakensberger Cattle Breeders Societies for providing access to their genotype and pedigree databases available at the Agricultural Research Council (ARC) and South African Studbook. Authors express their gratitude to projects funded by the Red Meat Research Development (RMRD) under the University of Pretoria (UP) that donated the genotypes. This research project was also financially supported by the ARC, National Research Foundation (NRF), and UP.

Conflict of interest: The authors declare no conflict of interest.

References

Banos, G., Wiggans, G.R. and Powell, R.L., 2001. Impact of paternity errors in cow identification on genetic evaluations and international comparisons. Journal of Dairy Science, 84, 2523-2529.

Berry, D.P., Wall, E. and Pryce, J., 2014. Genetics and genomics of reproductive performance in dairy and beef cattle. Animal, 8(S1), 105-121.

Berry, D.P., McHugh, N., Wall, E., McDermott, K. and O'Brien, A.C., 2019. Low-density genotype panel for both parentage verification and discovery in a multi-breed sheep population. Ireland Journal of Agricultural and Food Research, 58, 1-12.

Buchanan, J.W., Woronuk, G.N., Marquess, F.L., Lang, K., James, S.T., Deobald, H., Welly, B.T. and Van Eenennaam, A.L., 2016. Analysis of validated and population specific SNP parentage panels in pedigreed and commercial beef cattle populations. Canadian Journal of Animal Science, 97, 231-240.

Chan, E.K.F., Hawken, R. and Reverter, A., 2008. The combined effect of SNP-marker and phenotype attributes in genome-wide association studies. Animal Genetics, 40, 149-156.

Fernández, M.E., Goszczynski, D.E., Lirón, J.P., Villegas-Castagnasso, E.E., Carino, M.H., Ripoli, M.V., Rogberg-Muñoz, A., Posik, M.D., Peral-García, P. and Giovambattista, G., 2013. Comparison of the effectiveness of microsatellites and SNP panels for genetic identification, traceability and assessment of parentage in an inbred Angus herd. Journal of Genetics and Molecular Biology, 36, 185-191.

Fisher, P.J., Malthus, B., Walker, M.C., Corbett, G. and Spelman, R.J., 2009. The number of single nucleotide polymorphisms and on-farm data required for whole-herd parentage testing in dairy cattle herds. Journal of Dairy Science, 92, 369-374.

García-Ruiz, A., Wiggans, G.R. and Ruiz-López, F.J., 2019. Pedigree verification and parentage assignment using genomic information in the Mexican Holstein population. Journal of Dairy Science, 102, 1806-1810.

Georges, M., Charlier, C. and Hayes, B., 2018. Harnessing genomic information for livestock improvement. Nature Reviews Genetics, 20, 135-156.

Hara, K., Watabe, H., Sasazaki, S., Mukai, F. and Mannen, H., 2010. Development of SNP markers for individual identification and parentage test in a Japanese black cattle population. Journal of Animal Science, 81, 152-157.

Hayes, B.J., 2011. Technical note: Efficient parentage assignment and pedigree reconstruction with dense single nucleotide polymorphism data. Journal of Dairy Science, 94, 2114-2117

Heaton, M.P., Harhay, G.P., Bennett, G.L., Stone, R.T., Grosse, W.M., Casas, E., Keele, J.W., Smith, T.P.L., Chitko-McKown, G.C. and Laegreid, W.W., 2002. Selection and use of SNP markers for animal identification and paternity analysis in U.S. beef cattle. Mammalian Genome, 13, 272-281

Henderson, C.R., 1973. Sire evaluation and genetic trends. Animal Breeding and Genetics Symposium in Honor of Dr. Jay L. Lush. Champaign, IL., American Society of Animal Science and American Dairy Science Association, 10-41.

International Society for Animal Genetics (ISAG)., 2013. ISAG cattle core and additional SNP panel.www.isag.us/ Docs/Cattle-SNP-ISAG-core-additional-panel-2013.xlsx

Israel, C. and Weller, J.I., 2000. Effect of misidentification on genetic gain and estimation of breeding values in dairy cattle populations. Journal of Dairy Science, 83, 181-187.

Jamieson, A. and Taylor C.S., 1997. Comparison of three probability formulae for parentage exclusion. Animal Genetics, 28, 397-400.

Judge, M.M., Kearney, J.F., McClure, M.C., Sleator, R.D. and Berry, D.P., 2016. Evaluation of developed low-density genotype panels for imputation to higher density in independent dairy and beef cattle populations. Journal of Animal Science, 94 (3), 949-962.

Junqueira, V.S., Cardoso, F.F., Oliveira, M.M., Sollero, B.P., Silva, F.F. and Lopes, P.S., 2017. Use of molecular markers to improve relationship information in the genetic evaluation of beef cattle tick resistance under pedigree-based models. Journal of Animal Breeding and Genetics, 133, 1-13.

Kios, D., van Marle-Köster, E. and Visser, C., 2012. Application of DNA markers in parentage verification of Boran cattle in Kenya. Tropical Animal Health Production, 44, 471-476

Lyons, R.E., Buttsworth, S., Waine, D. and Kelly, M., 2015. SNP-based parentage in an Australian cattle industry context: Does one size fit all? Proc. Association for Advancement of Animal Breeding and Genetics, 21, 249-252.

McClure, M.C.., McCarthy, J., Flynn, P., Weld, R., Keanne, M., O'Connell, K., Mullen, M.P., Waters, S. and Kearney, J.F., 2015. SNP selection for nationwide parentage verification in beef and dairy cattle. International Committee of Animal Recording (ICAR) Technical series. No 19. www.icar.org/wp-content/uploads/2015/11/ICARTechnical-Series-19-Krakow-2015-Proceedings.pdf. (Accessed 20 January 2020)

McClure, M.C., McCarthy, J., Flynn, P., McClure, J. C., Dair, E., O'Connell, D. K. and Kearney, J. F., 2018. SNP data quality control in a national beef and dairy Cattle system and highly accurate SNP based parentage verification and identification. Frontiers in Genetics, 9, 84.

Nielsen, R. and Signorovitch, J., 2003. Correcting for ascertainment biases when analyzing SNP data: applications to the estimation of linkage disequilibrium. Theory Population Biology, 63, 245-255.

R Core Team., 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org

Sanders K., Bennewitz J. and Kalm E., 2006. Wrong and missing sire information affects genetic gain in the Angeln dairy cattle population. Journal of Dairy Science, 89, 315-321.

Strucken, E.M., Gudex, B., Ferdosi, M.H., Lee, H.K., Song, K.D., Gibson, J.P., Kelly, M., Piper, E.K., Porto-Neto, L.R., Lee, S.H. and Gondro, C., 2014. Performance of different SNP panels for parentage testing in two East Asian cattle breeds. Animal Genetics, 45, 572-575.

Teneva, A., Todorovska, E., Petrović, M.P., Kusza, S., Perriassamy, K., Petrović, V.C., Andrić, D.O. and Gadjev, D., 2018. Short tandem repeats (STR) in cattle genomics and breeding. Biotechnology in Animal Husbandry, 34, 127-147.

Van Doormaal, B.J., Kistemaker, G.J. and Johnston, J., 2016. Parentage Analysis Services for Dairy Cattle in Canada. Interbull Bulletin no. 50. Puerto Varas, Chile, October 24-28. www.icar.org/Documents/DNA-WG/Docs/2017-02-20%20Meeting%20Package.pdf. (Accessed 12 October 2019)

Van Eenennaam, A.L., 2016. Use of genetic marker information in beef cattle selection. Applied Reproductive Strategies in Beef Cattle-Des Moines, Iowa, 7-8 September.

Visscher, P.M., Woolliams, J.A., Smith, D. and Williams, J.L., 2002. Estimation of pedigree errors in the UK dairy population using microsatellite markers and the impact on selection. Journal of Dairy Science, 85, 2368-2375.

Waits, LP., Luikart, G. and Taberlet, P., 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Molecular Ecology, 10 (1), 249-256.

Weller, J.I., Feldmesser, E., Golik, M., Tager-Cohen, I., Domochovsky, R., Alus, O. and Ron M., 2004. Factors affecting incorrect paternity assignment in the Israeli Holstein population. Journal of Dairy Science, 87 (8), 2627-2640.

Zhao, F., McParland, S., Kearney, F., Du, L. and Berry, D.P. 2015. Detection of selection signatures in dairy and beef cattle using high-density genomic information. Genetics Selection Evolution, 47, 49.