

Genomic technologies for food security: A review of challenges and opportunities in Southern Africa

Esté van Marle-Köster¹, Carina Visser¹, Mahlako Makgahlela², Schalk WP Cloete^{3,4}

¹Department of Animal & Wildlife Sciences, University of Pretoria, Private Bag x20, Hatfield, 0028, South Africa (evm.koster@up.ac.za; carina.visser@up.ac.za)

²Agricultural Research Council-Animal Production Institute, Private Bag X2, Irene, 0062, South Africa (MMakgahlela@arc.agric.za)

³Department of Animal Sciences, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

⁴Directorate Animal Sciences: Elsenburg, Western Cape Department of Agriculture, Elsenburg 7607, South Africa (SchalkC@elsenburg.com)

Corresponding author:

Esté van Marle-Köster

E-mail: Evm.koster@up.ac.za

Phone: +27 12 420 3612

Private Bag x 20, Hatfield, Pretoria, 0028, South Africa

Abstract

The Southern African Development Community (SADC) region includes 15 member states which all face growing population numbers and a possible protein shortage within the next 20 years. Although these countries have a wealth of livestock genetic resources and mostly are quite agriculturally dependent, there exist clear limitations and challenges regarding animal recording, genetic improvement, production efficiency and the implementation of new technologies, such as genomic selection (GS). Genomic selection incorporates genomic information with phenotypic information (breeding values) to derive genomic estimated breeding values (GEBV) and leads to an increased rate of genetic improvement. The countries within the SADC region are in several stages of development with regard to agriculture and infrastructural development and this limits the implementation of advanced technologies. The establishing of reference populations seems beyond the capacity of most of these countries at present, mainly in terms of financial viability, infrastructural support and national cohesion. Genomic technology however holds potential for the introgression of favourable genes in resource-poor livestock production systems and traceability of livestock products. Furthermore,

identification of traits associated with adaptability and disease resistance and unique products would contribute to food security on various levels. This review discusses interventions that may mitigate constraints, and proposes key research areas needed for addressing the limitations mentioned.

Keywords: Genetic improvement; genotyping platforms; hard-to-measure traits; indigenous livestock; reference population

1. Introduction

The growing demand for protein originating from livestock has been widely discussed and is well documented (Kahi & Rewe, 2008; Pica-Ciamarra et al., 2010; Van Marle-Köster & Webb, 2014). The world population is expected to grow to approximately 9 billion by 2050 (United Nations, 2011), with approximately 8 billion of the world population living in developing countries (Thornton, 2010; Capper, 2013). In sub-Saharan Africa alone, the human population is expected to grow at a rate of 1.2 % per year with a two-fold increase in the demand for meat and milk. Southern Africa is facing palpable challenges to meet these demands considering the large number of constraints that these countries are already subjected to. These constraints vary from biological and environmental effects including periodic drought, shortage of grazing as well as ecto- and endo-parasites (Gwaze et al., 2009) to a range of socio-economic and political factors (Iñiguez, 2011). In most of the literature on livestock development in Africa (Wurzinger et al., 2011; Herrero et al., 2013; Rothschild & Plastow, 2014), these limitations have been highlighted as major issues in preventing the countries to increase productivity and produce much needed protein. Livestock production is also under pressure due to the envisaged effects of climate change which is foreseen to impact upon its sustainability (Nardone et al., 2010; Rust & Rust, 2013).

Over the past few decades, developments in the field of molecular genetics and animal breeding have opened new avenues for accelerating genetic progress and increasing the accuracy of selection of superior genetic stock (Rothschild & Plastow, 2007). For most livestock species, whole genome sequences have been completed and deoxyribonucleic acid (DNA) markers have been commercialized in useful diagnostic applications such as DNA-based parentage testing (Van Marle-Köster et al., 2013), the identification of genetic defects and marker assisted selection (Blasco & Toro, 2014). Commercial single nucleotide polymorphism (SNP) chips have recently been developed for use in genomic selection (Blasco & Toro, 2014). As these genomic developments have mainly been used in the developed world the question could be raised if it will contribute to increased production in developing countries.

Africa is a diverse continent with an agricultural sector that has to function within certain limitations that will remain relevant and real for some time to come (Van Marle-Köster & Webb, 2014). Therefore, this review focuses on Southern African countries to provide a perspective on the

alternative approaches for application of genomic tools. In the process, attention is given to indigenous resources, livestock recording and structures already in place as well as advances in developed countries and the feasibility of applying these advances locally. Finally, the review suggests a few ideas on the research and development required to ensure the future sustainability of ruminant livestock production in the SADC region.

2. The SADC region

2.1 Member states, demographics and economics

The SADC is an inter-governmental organization that consists of 15 member states (Figure 1).

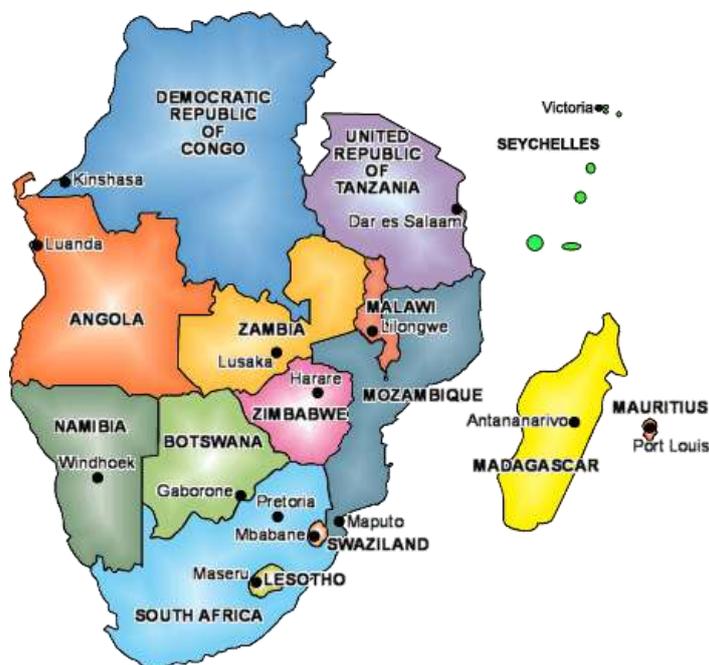


Figure 1 Countries forming part of the Southern African Development Community (SADC) region

The region had approximately 281 million inhabitants in 2011 (SADC, 2013), with more than 60% of the total population resident in the Democratic Republic of the Congo (DRC – 27%), South Africa (18%) and Tanzania (16%). The gross regional product of SADC amounted to 650935 million US\$ in 2011 (SADC, 2013). The bulk of this regional product (63%) was generated in South Africa, followed by Angola at 15%. Agricultural activities contributed between 4% and 27% of national GDP of the individual member states (Directorate of Food, Agriculture and Natural Resources, 2011). According to this source, agricultural products are also important for earning foreign revenue, averaging 13% of export earnings across the region. Agricultural products furthermore contribute 66% to inter-regional trade.

The various countries within the SADC region are in several stages of development with regard to agriculture and infrastructural development (SADC, 2013). Despite these differences, the member states aim to further socio-economic cooperation and integration as well as political and security cooperation among them. The Livestock Unit (LU) within the Food, Agriculture and Natural Resource Directorate aims to address common challenges and to coordinate livestock development activities. The identification, diagnosis and control of trans-boundary diseases (such as foot and mouth disease and Rift Valley Fever) is one area that receives special attention (SADC, 2013).

2.2 Topography, climate and environment

In total, the size of the SADC region comprises nearly 10 million km², with approximately 25% arable land (SADC, 2010). The size of the individual countries making up the SADC region range from more than 1 million km² in the DRC (2.3 million km²), Angola (1.2 million km²) and South Africa (1.2 million km²) to below 0.1 million km² in Lesotho, Mauritius and Swaziland (Directorate of Food, Agriculture and Natural Resources, 2011). Seven terrestrial ecological zones include highly variable habitat types, from mangroves in Mozambique and Tanzania to desert and xeric shrub lands in Angola, Namibia and South Africa (SADC, 2010). Average annual precipitation in the region is highly variable, ranging from below 100 to 300 mm in the arid parts of Namibia and South Africa to in excess of 2000 mm and above in parts of the DRC, Madagascar, Mauritius and the Seychelles (Directorate of Food, Agriculture and Natural Resources, 2011).

2.3 Livestock species and diversity

Despite the huge diversity between these countries, some unique aspects are shared with regard to the availability of livestock genetic resources and their development. Cattle, sheep and goats play a major role in the livelihood of the population in all these countries. According to Rischkowsky et al. (2007), 19% of 990 cattle breeds, 18% of 559 goat breeds and 12% of 1129 sheep breeds in the world can be found in Africa. A wealth of breed diversity can thus be expected in the broader African region. The total ruminant livestock populations in SADC member countries are estimated at 64 million cattle, 39 million sheep and 38 million goats (SADC, 2013). These species contribute to food security, socio-economic and cultural needs. Approximately 75% of animals constituting these livestock populations are maintained within small farming operations or kept by small holders (Moyo & Swanepoel, 2010). The presence of a large variety of indigenous livestock breeds within the SADC region is a major asset for this region. It is estimated that there are approximately a hundred different livestock breeds that include cattle, sheep and goats. The list compiled by the FAO (2007) however includes composite breeds as well as a number of ecotypes which have not yet been classified as individual breeds. The concept of breed as defined by the FAO (1999) may include a group of animals that can be defined based on external characteristics or defined by its geographical/cultural separation that resulted in a phenotypically similar group. It is expected that there may be many more ecotypes that would qualify

as individual breeds but they have either not been investigated or the data to substantiate their status as a breed is not publically available. It is also possible that a number of breeds have not been included in the Domestic Animal Diversity Information System (DAD-IS) of the FAO as they have been lost due to arbitrary cross-breeding between populations. Furthermore, it is estimated that about 700 local livestock breeds of all species worldwide may have become extinct over the past few centuries (Hoffman, 2011). The data completeness for indigenous breeds varies from 34% to 50% across continents according to DAD-IS (Tixier-Boichard, 2014). Despite the apparently rich diversity in terms of breeds on the African continent (Rischkowsky et al. 2007), there is still no clarity on the number of indigenous breeds vs. composites and ecotypes in Southern Africa. This emphasises the importance of breed characterization, both on a phenotypic and genetic level, of indigenous farm animal resources.

Genomic tools are useful for genetic characterization of breeds and a number of Southern African indigenous sheep, goat and cattle breeds have been investigated on a molecular level. Mitochondrial DNA, microsatellite markers and more recently SNP technology have been widely applied for this purpose (Bhargava & Fuentes, 2010; Lenstra et al., 2012). Studies on genetic characterization of livestock in the SADC region have focused on indigenous goats. These countries include Tanzania (Muema et al., 2009), Mozambique (Garrine et al 2007), South Africa (Visser et al., 2004; Pieters et al., 2009; Mdladla et al., 2014), Namibia (Els et al., 2004) and Botswana (Maletsanake et al., 2013). In South Africa genetic characterization studies were also done on both sheep (Kunene et al., 2009; Soma et al., 2012; Qwabe et al., 2012) and cattle populations (Makina et al., 2014) while in Malawi one study on cattle has been reported (Changadeya et al., 2012).

Genetic characterization of indigenous livestock is often performed with conservation in mind and the focus tends to be on ecotypes and populations that are not well defined or adequately phenotyped. Unfortunately the populations subjected to research are mostly not included in selection for improved production or utilization. Indigenous livestock species are a valuable genetic resource to contribute to food security in a number of ways (Hoffmann, 2011), but they are generally not included in commercial production value chains to the marketplace.

Studies of genetic characterization have contributed to knowledge of genetic relationships, diversity and population structure of indigenous stock and may have assisted in conservation of some breeds (Tixier-Boichard, 2014). A dearth of knowledge remains with regard to traits that make these breeds unique and can be exploited in selection for increasing their productivity and contribution to food security. Indigenous breeds are often praised for their adaptive traits and low susceptibility to diseases, but scientific studies to confirm and exploit these characteristics have been limited (FAO, 2007). Only a few Southern African indigenous cattle and sheep breeds have been reported to the DAD-IS as having high resistance/resilience to tick-borne diseases and gastro-intestinal parasites (Table 1).

Table 1. Adaptive characteristics of indigenous cattle and sheep breeds in the SADC region

Species	Country	Breeds	Quality	Reference
Cattle	South Africa	Nguni, Pedi, Shangaan, Tswana	High tolerance to tick-burdens	FAO (2007)
		Nguni	Lower tick counts	Marufu et al., (2011, 2014)
Sheep	South Africa	Damara	High tolerance to Heart-water disease	FAO (2007)
		Namaqua Afrikaner	Low tick counts	Cloete et al. (2013)
	Mozambique	Landim	High tolerance to tick-burdens	FAO (2007)

It is expected that there are more local breeds in the SADC region with similar advantages, but these breeds probably have not yet been recognised as a valuable genetic resource or included in research efforts.

2.4 Livestock recording and evaluation infrastructure

The backbone for successful application of quantitative animal breeding has always been recording of accurate phenotypes as an essential component of genetic evaluation. In an evaluation by Thieme (2007) it was evident that the basic tools required for animal improvement was only applied in a small percentage of livestock breeds in Africa (Table 2). It is evident that the basic prerequisites for carrying out structured animal improvement programmes are lacking for most African breeds. It is not foreseen that this situation will be vastly different in the SADC region. Indeed, Brockhaus (2007) reported that the bulk of Southern African countries have a limited capacity for managing genetic resources for food production. The infrastructure for carrying out basic animal improvement operations are severely constrained in Africa in general. These constraints are present at all levels, namely physical infrastructure, human capacity as well as at the level of policy development.

New and improved technologies have the potential of making recording easier and far more cost effective for stud breeders and even commercial farmers. In the SADC region, countries such as South Africa and Namibia have well established animal recording systems. In South Africa animal recording was established as early as 1917 and 1959 for dairy and beef cattle respectively (Bergh, 2010). Fleece testing in sheep has been conducted since 1934, while the formal South African Small Stock Improvement Scheme dated back to 1964 (Cloete et al., 2014). The 1981/82 production year is

Table 2. Basic breeding tools applied in Africa for livestock improvement (Source: adapted from Thieme, 2007)

Percentage of breeds with a:	Cattle	Sheep	Goats
Breeding goal	18	14	21
Strategy implemented	13	9	15
Individual identification	11	9	18
Performance recording	12	8	21
Artificial insemination	23	2	5
Genetic evaluation	9	5	16

formally considered as the operational start for dairy goat recording in South Africa (Olivier et al., 2005). Namibian animal recording systems are very similar to those in South Africa, and farmers make use of either Breedplan® (www.nsba.iway.na) or SA Studbook (www.studbook.co.za) as service providers for routine genetic evaluations. Botswana is the only SADC country with a well-established traceability system as they are major exporters of beef to the European Union where traceability for all animals is a pre-requisite (Department of Animal Health and Production, 2007). Farmers make use of the “Livestock Identification and Trace-back system” (LITS) which is based on a reticular bolus with a microchip containing data for collection by the extension officers at herd level. In the remaining SADC countries animal recording systems have not been well developed and there is a lack of both phenotypic and pedigree data.

3. Livestock genomics in context

Genomics include a number of genetic applications such as diagnostic testing for genetic defects (Gholap et al., 2014), major genes (Rothschild & Plastow, 2014) and parentage verification (Van Eenennaam & Drake, 2012). These tools have been proved to be useful in selection programs for various livestock species in the developed world. Research done in developing countries has shown the usefulness of tools such as diagnostic and parentage testing (Kios et al., 2011). The uptake on farmer level is limited due to costs, a lack of phenotypic information and poor information dissemination (Cloete, 2012).

In countries that have effective, operational phenotypic recording systems, traditional quantitative animal breeding has been successful in improving quantitative traits measured in farm animals of both sexes. However, selection responses at an industry level for economic traits that are lowly heritable, expensive or difficult to measure, and measured late in life are more difficult to achieve. It is expected that selection for these traits will benefit the most from the application of genomic tools as reviewed for cattle by Van Marle-Köster et al. (2013) and for sheep by Cloete et al. (2014). In the developing

countries, traits that would fall into this category include disease resistance, reproduction efficiency and carcass traits, all of which are essential for food security in the region.

In animal breeding, the latest molecular innovation was the application of genomic selection (GS) methodology, which incorporates genomic information into existing tools to derive genomic estimated breeding values (GEBV) (Meuwissen et al., 2001). The GEBV are derived from SNP effects estimated from a large group of predictor animals, termed the reference population, that have SNP genotypes and accurate phenotypes for numerous traits and trait complexes (Goddard, 2009).

These reference populations are used to develop prediction equations for associating phenotypes and SNP markers in the estimation of GEBV, and generally consist of at least 1000 high-impact animals. The reference population forms the basis for implementation of GS, as its accuracy depends on the size of the reference population, extent of linkage disequilibrium (LD), marker density and effective population size (Daetwyler et al., 2008; Goddard, 2009). Rapid uptake of GS in over 15 developed countries such as the United States (US), Canada, the Netherlands, Australia, New Zealand, France and the Nordic countries (Hayes et al., 2009; Reinhardt et al., 2009; Su et al., 2010; Rowe et al., 2013; Auvray et al., 2014) was facilitated by automated cutting edge next-generation sequencing and genotyping technologies (Illumina 2011a; 2011b; 2012) that enabled rapid and cost-effective genotyping of large numbers of animals.

In the SADC context, the generating of such reference populations faces various challenges and limitations, as discussed by Scholtz et al. (2013). Practical challenges include small population sizes, the absence of a large number of (accurately) phenotyped animals and EBV information and the lack of both genotyping infrastructure and a national / regional cohesive strategy. The prohibitive cost of SNP Chip genotyping also poses a major financial challenge.

Indigenous breeds are known for their small population sizes per country, as many breed classifications are performed based on geographical location. Many “breeds” are of the same ecotype, and could be clustered into one grouping. A possible way of circumventing the problem regarding small population sizes would be to establish across-breed reference populations. Accuracies of GEBV derived from reference populations that combines animals from multiple breeds or populations are often higher than achieved with small individual breeds (Hayes et al., 2009; Brøndum et al., 2011) or pedigree-based parental averages (Makgahlela et al., 2013; Dodds et al., 2014). It is however crucial that the breeds are closely related or of the same production type, otherwise the prediction equations derived from one breed will not accurately predict GEBV for another breed (Garrick, 2011). Such phenomena could occur because the LD phase tends to be different in different breeds and hence, SNP markers associate with different QTL (Kizilkaya et al., 2010). Accordingly, combining populations with different genetic architectures in terms of allele frequencies tends to reduce the marker-QTL LD, which in turn could reduce prediction accuracy (de Roos et al., 2009; Hayes et al., 2011). It was suggested that these shortcomings could be overcome by increasing the marker density such that the phase of LD persist across breeds (de Roos et al., 2009; Daetwyler et al., 2010), and by using

ancestral haplotype segments instead of single markers, which increases LD and prediction accuracy (de Roos et al., 2011).

In situations where pedigree data are incomplete or unreliably recorded, genomic data obtained using BovineSNP50 or BovineHD arrays (Illumina, 2011a; Illumina, 2012) can be used to assign parentage, reconstruct individual genealogical information, and validate incorrect pedigrees (Wiggans et al., 2009; Gorbach et al., 2010; Toro et al., 2011a; VanRaden et al., 2013). Pedigree correction, construction, and discovery of unknown parents is presently performed as a routine service for dairy animals in the US (Wiggans et al., 2009). Genealogical information is useful to monitor inbreeding and avoid loss of genetic diversity in conservation and breeding strategies, where population parameters are used as indicators (Meuwissen, 1997; Toro et al., 2011b). In the absence of pedigree data, genomic data can be used directly to estimate genealogical co-ancestry, monitor inbreeding and genetic diversity within and across populations (Eding and Meuwissen, 2001; Toro et al., 2011a & b).

4. Potential of genomic selection to the SADC region

Encouraging reports from developed countries show the potential of integrating genomic technology into animal breeding, with the primary beneficiaries being large-scale commercial producers. However, it is disturbing that it is yet unclear if this innovation will benefit those African countries needing it the most. Although at various intensities, these countries have the most disadvantaged commercial farmers, and substantial numbers of subsistence farmers with high levels of food insecurity. South Africa has a quite vibrant commercial agricultural livestock sector, while small-scale farming is also commonly practiced on commonages and tribal land with communal land use. Cloete (2012) compared literature reporting on these farming systems for beef cattle, dairy cattle, meat and dairy goats as well as sheep where it was emphasized that production efficiency was appreciably higher in the commercial sector. However, communal farmers in particular often had markedly different usage patterns for the livestock under their control compared to their commercial counterparts. Guidelines are available to allow communal farmers to partake in the National Beef Recording and Improvement Scheme in South Africa (Nengovhela et al., 2010), but uptake is low. Cloete (2012) argued that the lack of phenotypic information is a major constraint in efforts to improve the stock farmed by resource-poor farmers on a genetic level, since all interventions would require basic performance information. On a positive note, Gizaw et al. (2014) recently reported that information on pedigrees and live weights of Menz sheep in Ethiopia could be used in animal improvement programs resulting in genetic gains for smallholder farms. The recording system in the latter study hinged on observations by young boys caring for the flocks and being recorded by one of the participating farmers acting as an enumerator. Successes such as this ought to be possible to replicate in the SADC region, ensuring an enabling environment for the possible future uptake of initially breeding principles and eventually GS in the region.

So far, there are no reported experiences in the application of full-scale GS in the SADC region, only arbitrary plans. Therefore, the primary focus in this section is to articulate directions and alternatives for implementing GS for livestock genetic improvement in the food-deficient SADC region, which is often in a disadvantaged position in terms of technological expertise and infrastructure when compared to the food-surplus countries in the Northern hemisphere (Cloete et al. 2014). The foundation to accurately estimated EBVs for economic traits, subsequently used for decision-making in breeding programmes is decades of pedigree and animal performance records. The limitations to increased food production in several SADC states include the absence of programmes for recording standardized phenotypes, and lack of or inaccurately recorded pedigrees, due to costs associated with maintaining such schemes (Rege et al., 2011). These challenges are followed by a lack of national genetic evaluations, programmes for monitoring genetic diversity within populations and optimum breeding schemes, needed to identify productive and adapted individuals for breeding purposes (Brockhaus 2007; Thieme 2007). Genomic selection offers several alternatives to fast-track livestock genetic progress in SADC states with available phenotypes and pedigrees, even in the absence of pedigree information. However, recording of the most pertinent phenotypes (e.g. fertility, disease resistance, meat quality) will remain a critical challenge to take full advantage of this technique, as advocated by Cloete (2012) and Henryon et al. (2014).

Generating large reference populations remains a challenge in SADC, pertaining to start-up capital and often numerically small and discrete populations which tend to limit the accuracy of GEBV's (Rius-Vilarrasa et al., 2011; Thomassen et al., 2012), therefore species and breed-specific strategies will be required. In dairy cattle, primarily males were genotyped, but females could also be included to increase the size of the reference population. In addition, strategies that combine genotypes of animals from different breeds into the same reference population could be valuable, especially in South Africa with many beef cattle and sheep breeds of smaller sizes.

Genotyping costs could be reduced by firstly exploring pedigree information to identify influential animals within a population, and then determining the costs of SNP genotyping relative to animal value. It is prudent to ensure that the most expensive SNP genotyping arrays (i.e. Cattle: BovineSNP50v2 and BovineHD; Sheep: OvineSNP50 and OvineHD; Goats: CaprineSNP50) are used to genotype high impact genetically informative animals, while cheaper lower density SNP chips (Illumina, 2011b) could be used to genotype animals contributing less information or selection candidates. Finally, algorithms could be used to impute missing genotypes from lower density to higher density SNP-chips for such animals (Browning and Browning, 2009). Accuracies of imputing missing genotypes from BovineLD to BovineSNP50 to BovineHD by any method are generally greater than 90% (Dassonneville et al., 2011; Brøndum et al., 2012; Weng et al., 2012). Similar results have been reported by Hayes et al. (2011) in sheep, showing that the imputation accuracy of Merinos from a 5K SNP chip (71%) was substantially reduced relative to breeds with a smaller effective population size, such as the Border Leicester, Polled Dorset and White Suffolk which

exceeded 80%. In dairy cattle, proven bulls with an EBV accuracy of close to 100% can be defined as genetically highly informative whereas cows and heifers will be less informative. In beef cattle and small ruminants pedigree information can be examined to determine key animals as defined by their marginal genetic contribution (Boichard et al., 1997). These key animals are necessary to explain the complete genetic diversity of the entire population, and could form a very good reference population for imputation.

An alternative method that could assist in the reduction of genotyping costs in the SADC region could be the pooling of DNA. Bell et al. (2014) genotyped pooled DNA representing a range of dag score phenotypes in commercial Merino sheep as well as the rams used to sire these progeny. It was feasible to compute the contribution of individual sires to each pool, providing information on the genotypic make-up of each sire for dag scores. As rams were genotyped individually, they could be entered in a reference population, along with information pertaining to their ability to transfer alleles desired for a quantitative trait of economic importance. Serious thought should be put into the possibility of using such a technique to obtain genomic information on traits of economic importance (such as reproduction and disease resistance) in the unpedigreed flocks/herds of small-scale and communal farmers. Carefully thought-out strategies involving pooled DNA may be a cost-effective alternative to the capital-intensive prediction of GEBVs.

Developments in the application of genome-based technologies in SADC will more closely follow success stories from developed world but challenges, which will be discussed in the following section, will hinder the rate of progress. SADC farmers would benefit from these but for example, are unable to afford the technology, and existing animal breeding infrastructures are inadequate. Regardless of the flexibility in adopting these technologies, critical gaps such as traditional animal breeding infrastructure will need to be addressed first for most countries. Optimal benefits from GS can only be realised once an efficient processing pipeline has been established by all stakeholders.

5. Challenges to consider in creating a framework for GS in SADC countries

Although the benefits of genomic tools are numerous, the delivery of these modern techniques are heavily dependent on the presence of recording systems, infrastructure and transportation services (Rothschild & Plastow, 2014). These factors are in various stages of development and implementation in different SADC countries. The success of application of genomic technologies in any breeding scheme will hinge on careful design and planning. Henryon et al. (2014) questions whether GS would ensure long term genetic gains and therefore stresses the importance of well-planned breeding programs with clear objectives. International support organizations (e.g. Heifer International, Bill and Melinda Gates Foundation) may play a crucial role in the improvement of resources to facilitate the possibility of GS in the region.

Ascertainment bias poses a challenge in applying the available SNP chips for searching for regions under selection for adaptive traits in local and indigenous livestock breeds. The absence of such

breeds in the design of the SNP chips lead to fewer polymorphic loci available. A study including Nguni and Afrikaner cattle yielded fewer informative SNP compared to breeds such as the Angus and Holstein that were included in the original development of the BovineSNP50 bead chip (Qwabe et al., 2013). Sandenbergh (2015) similarly inferred that, at ~34000, the indigenous Namaqua Afrikaner sheep breed had substantially fewer informative SNP-loci compared to the Merino (~45000), when using the Ovine 50K genotyping array. Other South African sheep breeds partially or completely descended from European germplasm, like the Dorper and SAMM, were intermediate at respectively ~41400 and ~41900 in terms of the number of informative SNP.

Cloete et al. (2014) noted challenges in terms of budgetary constraints and suitably trained analysts to genotype animals for a reference population followed by implementing a system of GS in South African sheep. The dominant position of South Africa to the SADC gross regional product (63%) has already been mentioned. According to the recent South African National Survey of Research and Experimental Development for 2012-13, South Africa invests 0.76% of its GDP in Research and Development (Statistical Report, 2014). This figure is down from ~0.9% for the period from 2004/05 to 2009/10 and does not compare favourably with other countries in the Brazilian, Russian, India and China (BRIC) grouping (China – 1.84% and the Russian Federation – 1.09%) as well as the Organisation for Economic Development and Cooperation's (OECD) average of 2.4% (OECD StatExtracts, 2014). The number of researchers per 1000 fulltime equivalents (FTE) in South Africa remained quite stable at 1.4 to 1.6 over the past decade (Statistical Report, 2014). This figure also does not compare favourably with an OECD average of 7.7 researchers per 1000 FTE. Based on these figures, Cloete et al. (2014) contended that South Africa need to work upon its capacity to conduct high-level research such as creating an environment to implement GS. It would not be unreasonable to assume that the same basic situation exists throughout the SADC region.

Another potential challenge to the implementation of genomic tools in the SADC region, is resistance to genetic engineering and the perception that enhancing pedigree-based EBV with genomic tools fall into this category. Many African countries have policies to prevent genetically modified organisms (GMOs) to be produced in or even entering their countries. Improved communication will be key to ensure acceptance of the potential advantages of genomic tools.

At present, most genomic tools are perceived to be expensive and beyond the realm of developing countries (Cloete, 2012). It would however be unwise to ignore these technologies as the benefits of more accurate selection and an accelerated rate of genetic improvement would have a significantly positive effect on production and food security. A low-risk strategy for countries that are currently not able to afford genomic technologies would be to follow the developments and pitfalls that developed countries are highlighting and position themselves in such a way that implementation and uptake of methodologies could follow quickly once it is accepted. Indeed, a recent study in the United Kingdom indicated that the best economic gains should be achievable using genomic selection tools in terminal traits of beef bulls and meat sheep whereas reduced benefits would accrue for maternal traits (Todd,

2013). The latter study defined novel traits for predicting carcass excellence to demonstrate the potential of these technologies. When Table 2 is considered, it is clear that interventions like using computer tomography for sheep, as indicated by Todd (2013), are not realistic options for small-scale farmers in the SADC region. In fact, Cloete (2012) and Gizaw et al. (2014) contended that major steps towards a sustainable small-scale production system could be taken by merely applying well-known and extensively tested quantitative genetics principles already implemented for commercial agriculture. Given the environmental constraints of the region, both Cloete (2012) and Cloete et al. (2014) stressed the importance of hard-to-measure adaptability traits as candidates for GS. A lack of commercial and communal phenotypes may complicate this quest but may be compensated for by using well-phenotyped resource flocks under constitutional control in reference populations (Cloete et al., 2014). The information nucleus flock fulfils a similar role in Australia (Rowe et al., 2013).

For new technologies to be successful and effective in small-holder systems, it needs to fit into the existing system and be seen as a priority intervention (Marshall et al., 2011). It will probably be difficult to convince upcoming farmers of the benefits of MAS or GS as opposed to the immediate positive effect that crossbreeding poses. Nonetheless, it was stressed by Cloete (2012) that interventions to the benefit of small-scale production systems should take place with the cooperation and support of all roleplayers. The lack of active community involvement has often led to the failure of livestock breeding projects in developing countries like those in the SADC region (Kosgey et al., 2006). In contrast, successful projects were generally characterised by stakeholder involvement (Kahi et al., 2010). The multifunctional role of livestock in communities in the developing world stems from the importance of close involvement of livestock with the entire community (Moyo & Swanepoel, 2010). Close interaction of local committees, researchers and development practitioners is suggested to be beneficial for project success (Pell et al., 2010). Nesamvuni et al. (2010) stressed the importance of participatory development approaches. The latter authors contended that integrated research and development programs are highly preferable to research and development programs operating in isolation. An excellent example of participatory action to reach a common goal is evident from the study by Gizaw et al. (2014), where the recording of information on the flocks used were coordinated and conducted by community members.

6. Shaping the future

Despite the challenges discussed in section 4 and 5, it is apt to consider genomic based selection strategies for future developments that may contribute to food security. Indigenous livestock resources, as pointed out in section 2.3, are seen as an important asset when farming under limiting environmental conditions (Eisler et al., 2014). Efforts should therefore be directed to adequate genetic characterisation and benchmarking against alternative breeds/ecotypes in terms of production, resistance to stressors and reproduction (Cloete, 2012). The current lack of information creates a

distinct opportunity for relatively low-cost research for members of scientific teams. Such studies should be encouraged to ensure that adapted genotypes are maintained under long-term sustainable environmental conditions.

Secondly, there seems to be adequate scope for the establishment of adapted recording schemes involving flocks/herds of resource-poor farmers. The need for the acquisition of phenotypic records from this sector is paramount, seeing that animals performing under sometimes severely limited conditions are truly well adapted (Eisler et al., 2014). Modern technology, such as storing data on a centralised database using cell phone technology, facilitates such recording enterprises (Gizaw et al., 2014). It ought to be feasible to adopt these principles within the SADC region. In this way, a comprehensive service can be rendered to resource-poor farmers, even in the absence of infrastructure to record data. This can be combined with an open-nucleus system, which has been advocated as a means to accelerate genetic progress of flocks/herds in developing countries (Kosgey et al., 2006). This is the outlay used in the study by Gizaw et al. (2014), where genetic parameters and genetic trends of village Menz sheep were compared with a nucleus flock under institutional control.

The proper characterisation and benchmarking of indigenous breeds should be followed with adapted genotyping strategies to ensure adequate genetic information to enable GS in the major traits and trait complexes of economic importance. Preferably genotyping platforms should be sufficiently dense to allow the identification of genomic regions potentially involved with the ability of indigenous breeds to adapt to adverse conditions. Given that indigenous breeds are often subject to ascertainment bias when the existing genotyping platforms are used, it is important to ensure that genomic information at an adequate number of informative loci is available for this purpose. It is assumed that the adaptive characteristics of indigenous breeds to adverse conditions will justify the investment in genotyping costs.

A major challenge awaits scientists in the SADC region, namely to establish reference populations for all commercial and indigenous breeds of economic interest in the region for the future implementation of GS. It is foreseen that the funds to fulfil this will not be raised easily, since even well-off overseas research and development institutions concede that the cost of such projects is likely to be too much for one organisation to bear (Pollak et al., 2012). Similarly, the expertise to allow a major intervention like this is unlikely to be vested in a single organisation. The success of any enterprise of this nature will hinge upon the ability of organisations to collaborate in a constructive fashion (Cloete et al., 2014). The ability of principal investigators on specific projects to leverage funds from various local and international funding bodies will also be a prerequisite for success. Part of the money needed for these projects may be leveraged from commercial agriculture for projects benefitting this sector. However, funding for research on the flocks/herds of small-scale farmers will need to be funded from external sources. Scientists/sociologists dedicated to the cause of improving the livelihood of this sector will face a challenging situation with reference to the acquisition of funds for such projects. The cutting down on genotyping costs by pooling DNA may have a role to play in delivering services

to this sector, while further reductions in the cost of genotyping may also assist (Cloete, 2012). Considerable research efforts should be undertaken before a comprehensive service will be rendered to all stakeholders. The success of such projects will depend on the support of the broader industry in monetary terms, but also in-kind by the rendering of services or doing in-house data recording. Ideally, regional governments would sense the importance of the proposed interventions and support the efforts of the scientists involved. Project teams involved in this research should also be strengthened by scientists/institutions abroad, as local expertise will be lacking in several skills that are needed to successfully implement projects of this nature at the scale needed (Cloete et al., 2014). Finally, after substantial gains have been made in the local expertise on the subject of GS, other lucrative venues could be investigated to further strengthen local collaboration in the region. Such an opportunity exists in the introgression of favourable genes in resource-poor livestock production systems, possibly using germplasm from commercial stud rams or bulls. This intervention could be applied in nucleus herds and flocks, with subsequent dissemination to the smallholder populations. This solution is pertinent only in cases where a specific production system is already in place. The availability of equipment and techniques for tracing products in the SADC countries, can make important contributions to traceability and proof of origin of animal products could assist in valorising products originating from livestock. Animal-products are often sold through informal channels, such as farmers' markets and food stalls and verification of the food's source of species and origin could be very valuable. Efforts from researchers and funders should be directed towards appropriate available genomic technologies to actively pursue traceability issues in developing countries.

7. Conclusions

Food security will not be ensured by focussing on one discipline, but will require the ability of SADC livestock scientists and their co-workers to integrate genomics, quantitative breeding, nutrition, physiology and management with a careful consideration of the production system and the socio-economic environment. It is envisaged that genomic tools will be applied in future to search for traits associated with adaptation and disease resistance and unique product traits. This is an essential step to provide the knowledge to formulate appropriate breeding objectives and selection criteria for these breeds within the small-holder systems. This may ensure the uptake of these populations also in commercial, low-input systems to contribute to food security.

Acknowledgements

The authors acknowledge the material and intellectual support from their respective institutions, as well as the funding bodies contributing to the research needed in preparation for compiling this contribution (Cape Wools SA, the Western Cape Agricultural Research Trust, the Technology and Human Resources for Industry Programme).

References

- Auvray, B., McEwan, J. C., Newman, S. -A. N., Lee, M., & Dodds, K. G. (2014). Genomic prediction of breeding values in the New Zealand sheep industry using a 50K SNP chip. *Journal of Animal Science*, *92*, 4375-4389.
- Bell, A., Henshall, J., McCulloch, R., & Kijas, J. (2014). Evaluating Sires from Commercial Progeny Data Using Pooled DNA. In *Proceedings of the 10th World Congress on Genetics Applied to Livestock Production*. Accessed from https://asas.org/docs/default-source/wcgalp-proceedings-oral/156_paper_10358_manuscript_1334_0b.pdf?sfvrsn=2 on 15 September 2014.
- Bergh, L. (2010). The national beef recording and improvement scheme. In M. M. Scholtz (Eds.), *Beef breeding in South Africa* (pp. 55-70). South Africa: Agricultural Research Council.
- Bhargava, A. & Fuentes, F.F. (2010). Mutational dynamics of microsatellites. *Molecular Biotechnology*, *44*, 250-266.
- Boichard, D., Maignel, L., & Verrier, E. (1997). The value of using probabilities of gene origin to measure genetic variability in a population. *Genetics Selection Evolution*, *29*(1), 5-23.
- Blasco, A., & Toro, M. A. (2014). A short critical history of the application of genomics to animal breeding. *Livestock Science*, *166*, 4-9.
- Brockhaus, M. (2007). Institutions and stakeholders. In B. Rischkowsky, & D. Pilling (Eds.). *Part 3: The state and capacities in animal resource management – The state of the World's Animal Genetic Resources for Food and Agriculture* (pp. 187-214). Rome: FAO, Commission on Genetic Resources for Food & Agriculture.
- Brøndum, R. F., Rius-Vilarrasa, E., Strandén, I., Su, G., Guldbandsen, B., Fikse, W. F., & Lund, M.S. (2011). Reliabilities of genomic predictions using combined reference data of the Nordic Red cattle populations. *Journal of Dairy Science*, *94*, 4700-4707.
- Brøndum, R. F., Ma, P., Lund, M. S., & Su, G. (2012). Short communication: Genotype imputation within and across Nordic cattle breeds. *Journal of Dairy Science*, *95*, 6795-6800.
- Browning, B. L., & S. R. Browning. (2009). A unified approach to genotype imputation and haplotype-phase inference for large data sets of trios and unrelated individuals. *The American Journal of Human Genetics*, *84*, 210-223.
- Capper, J. L. (2013). Should we reject animal source foods to save the planet? A review of the sustainability of global livestock production. *South African Journal of Animal Science*, *43*(3), 233-246.
- Changadeya, W., Ambali, A. J. D., Nyirenda, J. C., Chagunda, M. G. G., & Kaunda, E. (2012). Genetic diversity and population structure of Malawi Zebu cattle. *International Journal of Physical and Social Sciences*, *2*, 59-81.
- Cloete, J. J. E., Cloete, S. W. P., Scholtz, A. J., & Mathee, S. (2013). The effect of breed, ewe age and season on tick counts of indigenous and commercial sheep in South Africa. *Proceedings of the Association for the Advancement in Animal Breeding and Genetics*, *20*, 187-190.

- Cloete, S. W. P. (2012). Breeding in developing countries and tropics. In R. A., Meyers (Ed.). *Encyclopedia of Sustainability, Science and Technology* (pp. 1740-1795). New York: Springer Science and Business Media. DOI: 10.1007/978-1-4419—0851-3.
- Cloete, S. W. P., Olivier, J. J., Sandenbergh, L., & Snyman, M. A. (2014). The adaptation of the South Africa sheep industry to new trends in animal breeding and genetics: A review. *South African Journal of Animal Science*, *44*, 178-188.
- Daetwyler, H. D., Villanueva, B., & Woolliams, J. A. (2008). Accuracy of predicting the genetic risk of disease using a genome-wide approach. *PLoS ONE*, *3*, e3395.
- Daetwyler, H. D., Hickey, J. M., Henshall, J. M., Dominik, S., Gredler, B., Van der Werf, J. H. J., & Hayes, B. J. (2010). Accuracy of estimated genomic breeding values for wool and meat traits in a multi-breed sheep population. *Animal Production Science*, *50*, 1060-1068.
- Dassonneville, R., Brøndum, R. F., Druet, T., Fritz, S., Guillaume, F., Guldbbrandtsen, B., Lund, M. S., Ducrocq, V., & Su, G. (2011). Effect of imputing markers from a low-density chip on the reliability of genomic breeding values in Holstein populations. *Journal of Dairy Science*, *94*, 3679-3686.
- De Roos, A. P. W., Hayes, B. J., & Goddard, M. E. (2009). Reliability of genomic predictions across multiple populations. *Genetics*, *183*, 1545-1553.
- De Roos, A. P. W., Schrooten, C., & Druet, T. (2011). Genomic breeding value estimation using genetic markers, inferred ancestral haplotypes, and the genomic relationship matrix. *Journal of Dairy Science*, *94*, 4708-4714.
- Department of Animal Health and Production (2007). Livestock Identification and Trace-back System (LITS, Omang wa Dikgomo). Botswana: Gaborone.
- Directorate of Food, Agriculture and Natural Resources (2011). Regional Agricultural Policy (RAP): Country Summary Agricultural Policy Review Reports. Accessed from http://www.sadc.int/files/7113/5293/3509/Regional_Agricultural_Policy_Review_Reports_2011.pdf on 6 January 2015.
- Dodds, K. G., Auvray, B., Lee, M., Newman, S. -A. N., & McEwan, J. C. (2014). Genomic selection in New Zealand dual purpose sheep. In *Proceedings of the 10th World Congress on Genetics Applied to Livestock Production*. Vancouver, BC, Canada, 2014. Accessed from https://asas.org/docs/default-source/wcgalp-proceedings-oral/333_paper_10352_manuscript_1331_0.pdf?sfvrsn=2 on 15 September 2014.
- Eding, H., & Meuwissen, T. H. E. (2001). Marker-based estimates of between and within population kinships for the conservation of genetic diversity. *Journal of Animal Breeding and Genetics*, *118*, 141-159.
- Eisler, M. C., Lee, M. R. F., Tarlton, J. F., Martin, G. B., Beddington, J., Dungait, J. A. J., Greathead, H., Liu, J., Mathew, S., Miller, H., Misselbrook, T., Murray, P., Vinod, V.K., Van Saun, R., & Winter, M. (2014). Steps to sustainable livestock. *Nature*, *507*, 32-34.

- Els, J. F., Kotze, A., & Swart, H. (2004). Genetic diversity of indigenous goats in Namibia using microsatellite markers: preliminary results. *South African Journal of Animal Science*, 34, 65–67.
- FAO (1999). The global strategy for the management of farm animal genetic resources. Rome: Food and Agriculture Organization of the United Nations.
- FAO (2007). The State of the World's Animal Genetic Resources for Food and Agriculture. In B. Rischkowsky, & D. Pilling (Eds.), *Section E: Animal genetic resources and resistance to disease* (pp. 101-110). Rome: FAO, Commission on Genetic Resources for Food & Agriculture.
- Garrick, D.J., (2011). The nature, scope and impact of genomic prediction in beef cattle in the United States. *Genetic Selection Evolution* 43, 17-28.
- Garrine, C. M. L. P. (2007). Genetic characterization of indigenous goat populations of Mozambique. Ph.D. Thesis. Department of Production Animal Studies, Faculty of Veterinary Science, University of Pretoria. Pretoria.
- Gholap, P.N., Kale, D.S. & Sirothia, A.R. (2014). Genetic diseases in cattle: A review. *Research Journal of Animal, Veterinary and Fishery Sciences*, 2, 24-33.
- Gizaw, S., Goshme, S., Getachew, T., Haile, A., Rischkowsky, B., Van Arendonk, J., Valle-Zárate, A., Dessie, T., & Mwai, A. O. (2014). Feasibility of pedigree recording and genetic selection in village sheep flocks of smallholder farmers. *Tropical Animal Health and Production*, 46, 809–814.
- Goddard, M. (2009). Genomic selection: prediction of accuracy and maximization of long term response. *Genetica*, 136, 245-257.
- Gorbach, D. M., Makgahlela, M. L., Reecy, J. M., Kemp, S. J., Baltenweck, I., Ouma, R., Mwai, O., Marshall, K., Murdoch, B., Moore, S., & Rothschild, M. F. (2010). Use of SNP genotyping to determine pedigree and breed composition of dairy cattle in Kenya. *Journal of Animal Breeding and Genetics*, 127, 348-351.
- Gwaze, F. R., Chimonyo, M., & Dzama, K. (2009). Communal goat production in Southern Africa: a review. *Tropical Animal Health and Production*, 41, 1157-1168.
- Hayes, B. J., Bowman, P. J., Chamberlain, A. J., & Goddard, M. E. (2009). Invited review: Genomic selection in dairy cattle: Progress and challenges. *Journal of Dairy Science*, 92, 433-443.
- Hayes, B. J., Bowman, P. J., Daetwyler, H. D., Kijas, J. W., & Van der Werf, J. H. J. (2011). Accuracy of genotype imputation in sheep breeds. *Animal Genetics*, 43, 72-80.
- Henryon, M., Berg, P. & Sørensen, A.C.(2014). Animal-breeding schemes using genomic information need breeding plans designed to maximise long-term genetic gains. *Livestock Science*, 166, 38-47.
- Herrero, M., Grace, D., Njuki, J., Enahoro, D., Silvestri, S., & Rufino, M.C. (2013). The roles of livestock in developing countries. *Animal*, 7, 3-18.
- Hoffman, I. (2011). Livestock biodiversity and sustainability. *Livestock Science*, 139, 69-79.

- Illumina. (2011a). BovineLD Genotyping Beadchip. Accessed 11 April 2014. http://www.illumina.com/Documents/products/datasheets/datasheet_bovineLD.pdf.
- Illumina. (2011b). BovineSNP50 Genotyping BeadChip. Accessed 11 April 2014. http://www.illumina.com/Documents/products/datasheets/datasheet_bovine_snp50.pdf.
- Illumina. (2012). BovineHD Genotyping BeadChip. Accessed 08 May 2014. http://www.illumina.com/Documents/products/datasheets/datasheet_bovine_hd.pdf.
- Iñiguez, L. (2011). The challenges of research and development of small ruminant production in dry areas. *Small Ruminant Research*, 98, 12-20.
- Kahi, A. K., Bett, R. C., & Rewe, T. O. (2010). Socio-economic drivers of successful breeding programs in developing countries. In: *Proceedings of the 9th World Congress on Genetics Applied to Livestock Production*, Leipzig, Germany, August 2010.
- Kahi, A. K. & Rewe, T. O. (2008). Biotechnology in livestock production: Overview of possibilities for Africa. *African Journal of Biotechnology*, 7(25), 4984-4991.
- Kios, D., Van Marle Köster, E. & Visser, C. (2011). Application of DNA markers in parentage verification of Boran cattle in Kenya. *Tropical Animal Health and Production*, 44, 471-476.
- Kizilkaya, K., Fernando, R. L., & Garrick, D. J. (2010). Genomic prediction of simulated multibreed and purebred performance using observed fifty thousand single nucleotide polymorphism genotypes. *Journal of Animal Science*, 88, 544-551.
- Kosgey, I. S., Baker, R. L., Udo, H. M. J., & Van Arendonk, J. A. M. (2006). Successes and failures of small ruminant breeding programmes in the tropics: a review. *Small Ruminant Research*, 61, 13-28.
- Kunene, N. W., Bezuidenhout, C. C., & Nsahlai, I. V. (2009). Genetic and phenotypic diversity in Zulu sheep populations: Implications for exploitation and conservation. *Small Ruminant Research*, 84, 100-107.
- Lenstra, J. A., Groeneveld, L. F., Eding, H., Kantanen, J., Williams, J. L., Taberlet, P., Nicolazzi, E. L., Sölkner, J., Simianer, H., Ciani, E., Garcia, J. F., Bruford, M. W., Ajmone-Marsan, P., & Weigend, S. (2012). Molecular tools and analytical approaches for the characterization of farm animal genetic diversity. *Animal Genetics*, 41, 1-20.
- Makina, S. O., Muchadeyi, F. C., van Marle-Köster, E., MacNeil, M. D., & Maiwashe, A. (2014). Genetic diversity and population structure among six cattle breeds in South Africa using a whole genome SNP panel. *Frontiers in Genetics*, 5, 1-7.
- Makgahlela, M. L., Strandén, L., Nielsen, U. S., Sillanpää, M. J., & Mäntysaari, E. A. (2013). The estimation of genomic relationships using breedwise allele frequencies among animals in multibreed populations. *Journal of Dairy Science*, 96(8), 5364-5375.
- Maletsanake, D., Nsoso, S. J., & Kgwatalala, P. M. (2013). Genetic variations from 12 microsatellite markers in an indigenous Tswana goat flock in South-eastern Botswana. *Livestock Research for*

- Rural Development*, 25(2), Article 21. Accessed from <http://www.lrrd.org/lrrd25/2/male25021.htm> on 3 December 2014.
- Marshall, K., Quiros-Campos, C., van der Werf, J. H. J., & Kinghorn, B. (2011). Marker-based selection within smallholder production systems in developing countries. *Livestock Science*, 136, 45-54.
- Marufu, C. M., Qokweni, L., Chimonyo, M., & Dzama, K. (2011). Relationships between tick counts and coat characteristics in Nguni and Bonsmara cattle reared on semiarid rangelands in South Africa. *Ticks and Tick-Borne Diseases*, 2, 172-177.
- Marufu, C. M., Dzama, K., & Chimonyo, M. (2014). Cellular responses to *Rhipicephalus microplus* infestations in pre-sensitised cattle with differing phenotypes of infestation. *Experimental and Applied Acarology*, 62, 241-252.
- Mdladla, K., Dzomba, E. F., & Muchadeyi, F.C. (2014). Genetic diversity, population structure and relationships of South African indigenous goat populations using genome-wide SNP markers. In *Programme and Abstracts of the SA Genetics Society (SAGS) & SA Society of Bioinformatics (SASBi) Joint Congress*. Kwalata Game Ranch, Hammanskraal, Gauteng, SA, 23-26 September 2014. Oral session, S4-9.
- Meuwissen, T. H. E. (1997). Maximising the response of selection with a predefined rate of inbreeding. *Journal of Animal Science*, 75, 934-940.
- Meuwissen, T.H.E., Hayes, B. & Goddard, M.E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics*, 157, 1819-1829.
- Moyo, S., & Swanepoel, F. J. C. (2010). Multifunctionality of livestock in developing communities. In F., Swanepoel, A., Stroebel, & Moyo, A. (Eds.), *The role of livestock in developing communities: enhancing multifunctionality* (pp. 1-11). Netherlands: Technical Centre for Agricultural and Rural Cooperation.
- Muema, E. K., Wakhungu, J. W., Hanotte, O., & Jianlin, H. (2009). Genetic diversity and relationship of indigenous goats of Sub-saharan Africa using microsatellite DNA markers. *Livestock Research for Rural Development*, 21, Article 28. Accessed from <http://www.lrrd.org/lrrd21/2/muem21028.htm> on 3 December 2014.
- Nardone, A., Ronchi, B., Lactera, N., Ranieri, M. S., & Bernabucci, U. (2010). Effects of climate change on animal production and sustainability of livestock systems. *Livestock Science*, 130, 57-69.
- Nengovhela, N. B., Maiwashe, A., & Matjuda, L. E. (2010). Breeding principles and guidelines for the emerging beef farmer. In M. M., Scholtz (Ed.), *Beef Breeding in South Africa (2nd ed.)* (pp. 139-148). South Africa: Agricultural Research Council.
- Nesamvuni, E. A., Swanepoel, F. J. C., & Stroebel, A. (2010). Interactions between gender, environment, livelihoods, food, nutrition and health. In F., Swanepoel, A., Stroebel, & Moyo,

- A. (Eds.), *The role of livestock in developing communities: enhancing multifunctionality* (pp. 93-105). Netherlands: Technical Centre for Agricultural and Rural Cooperation.
- OECD StatsExtracts (2014). Accessed from <http://stats.oecd.org/> on 6 January 2015.
- Olivier, J. J., Cloete, S. W. P., Schoeman, S. J., & Muller, C. J. C. (2005). Performance testing and recording in meat and dairy goats. *Small Ruminant Research*, *60*, 83-93.
- Pell, A. N., Stroebel, A., & Kristjanson, P. (2010). Livestock development projects that make a difference: what works, what doesn't and why. In F., Swanepoel, A., Stroebel, & Moyo, A. (Eds.), *The role of livestock in developing communities: enhancing multifunctionality* (pp. 13-29). Netherlands: Technical Centre for Agricultural and Rural Cooperation.
- Pica-Ciamarra, U., Baker, D., Bedane, B., Emwanu, T., & Morgan, N. (2010). Integrating Livestock into Agricultural Statistics. *Joint paper of the World Bank, FAO, AU-IBAR, ILRI with support from the Gates Foundation*.
- Pieters, A., Van Marle-Köster, E., Visser, C., & Kotze, A. (2009). South African Developed meat Type Goats: A forgotten animal genetic resource? *AGRI*, *44*, 33-43.
- Pollak, E. J., Bennett, G. L., Snelling, W. M., Thallman, R. M., & Kuehn, L. A. (2012). Genomics and the global beef cattle industry. *Animal Production Science*, *52*, 92-99.
- Qwabe, S. O., Van Marle Köster, E., & Visser, C. (2012). Genetic diversity and population structure of the endangered Namaqua Afrikaner sheep. *Tropical Animal Health and Production*, DOI: 10.1007/s11250-012-0250-x.
- Qwabe, S. O., Van Marle-Köster, E., Maiwashe, A., & Muchadeyi, F. C. (2013). Evaluation of the BovineSNP50 genotyping array in four South African cattle populations. *South African Journal of Animal Science*, *43*, 64-67.
- Rege, J. E. O., Marshall, K., Notenbaert, A., Ojango, J. M. K., & Okeyo, A. M. (2011). Pro-poor animal improvement and breeding – What can science do? *Livestock Science*, *136*, 15-28.
- Reinhardt, F., Liu, Z., Seefried, F., & Thaller, G. (2009). Implementation of genomic evaluation in German Holsteins. *Interbull Bulletin*, *40*, 219-226.
- Rischkowsky, B., Pilling, D., & Scherf, B. (2007). Status of animal genetic resources. In B. Rischkowsky, & D. Pilling (Eds.). *Part 1: The state of agricultural biodiversity in the livestock sector – The state of the World's Animal Genetic Resources for Food and Agriculture* (pp. 23-49). Rome: FAO, Commission on Genetic Resources for Food & Agriculture.
- Rius-Vilarrasa, E., Iso-Touru, T., Strandén, I., Schulman, N., Guldbrandtsen, B., Strandberg, E., Lund, M. S., Vilkki, J., & Fikse, W. F. (2011). Characterization of linkage disequilibrium in a Danish, Swedish and Finnish Red Breed cattle population. In *Proceedings of the 62nd Annual Meeting of the European Federation for Animal Science* (pp.177). Stavanger, Norway. Wageningen Academic Publishers, Wageningen, the Netherlands.
- Rothschild, M.F., & Plastow, G. S. (2007). Impact of genomics on animal agriculture and opportunities for animal health. *Trends in Biotechnology*, *26*(1), 21-25.

- Rothschild, M. F., & Plastow, G. S. (2014). Applications of genomics to improve livestock in the developing world. *Livestock Science*, 166, 76-83.
- Rowe, J. B., Gill, S., Banks, R. G., & Van der Werf, J. H. J. (2013). Genomics for the Australian sheep industry: from design to delivery. *Proceedings of the Association for the Advancement in Animal Breeding and Genetics*, 20, 14-17.
- Rust, J. M., & Rust, T. (2013). Climate change and livestock production: A review with emphasis on Africa. *South African Journal of Animal Science*, 43(3), 255-267.
- SADC (2010). Adaptation and Mitigation Actions, Supported by Enabling Measures of Implementation. In *Southern Africa Sub-Regional Framework of Climate Change Programmes*. Accessed from http://www.sadc.int/files/1313/5293/3533/Regional_Infrastructure_Development_Master_Plan_Meteorology_Sector_Plan.pdf on 6 January 2015.
- SADC (2013). Selected indicators for the SADC region for 2011 with charts. Accessed from http://www.sadc.int/files/6213/6267/6607/Selected_Indicators_2011_with_charts06March2013_FINAL.pdf on 6 January 2015.
- Sandenbergh, L. (2015). Identification of SNPs associated with robustness and greater reproductive success in the South African Merino sheep using SNP chip technology. Ph.D (Genetics). Thesis. Department of Animal Sciences, Faculty of Agricultural and Forestry Sciences, University of Stellenbosch. Stellenbosch.
- Scholtz, M.M., Maiwashe, A., Naser, F.W.C., Theunissen, A., Olivier, W.J., Mokolobate, M.C. & Hendriks, J. (2013). Livestock breeding for sustainability to mitigate global warming, with the emphasis on developing countries. *South African Journal of Animal Science*, 43, 269-281.
- Soma, P., Kotze, A., Grobler, J. P., & van Wyk, J. B. (2012). South African sheep breeds: Population genetic structure and conservation implications. *Small Ruminant Research*, 103, 112-119.
- Statistical Report (2014). South African National Survey of Research and Experimental Development: Statistical report 2012/13. Accessed from <http://www.dst.gov.za/index.php/resource-center/rad-reports> on 6 January 2015.
- Su, G., Guldbbrandtsen, B., Gregersen, V. R., & Lund, M. S. (2010). Preliminary investigation on reliability of genomic estimated breeding values in the Danish Holstein population. *Journal of Dairy Science*, 93, 1175-1183.
- Thieme, O. (2007). Structured breeding programmes. In B. Rischkowsky, & D. Pilling (Eds.). *Part 3: The state and capacities in animal resource management – The state of the World's Animal Genetic Resources for Food and Agriculture* (pp. 215-241). Rome: FAO, Commission on Genetic Resources for Food & Agriculture.
- Thomassen, J. R., Guldbbrandtsen, B., Su, G., Brøndum, R. F., & Lund, M. S. (2012). Reliabilities of genomic estimated breeding values in Danish Jersey. *Animal*, 6(5), 789-796.

- Thornton, P. K. (2010). Livestock production: recent trends, future prospects. *Philosophical Transactions of the Royal Society*, 365, 2853-2867.
- Tixier-Boichard, M. (2014). Status and gaps in characterization of animal genetic resources. In *Proceedings of the 10th World Congress of Genetics Applied to Livestock Production*. 18-22 August, Vancouver, Canada 2014
- Todd, D. (2013). Implementation of genomic selection in UK beef and sheep breeding. Ph.D. thesis, University of Edinburgh, Edinburgh, United Kingdom.
- Toro, M. A., T. H. E. Meuwissen, J. Fernández, I. Shaat and A. Mäki-Tanila. (2011a). Assessing the genetic diversity in small farm animal populations. *Animal* 5, 1-15.
- Toro, M. A., García-Cortés, L. A., & Legarra, A. (2011b). A note on the rationale for estimating genealogical coancestry from molecular markers. *Genetics Selection Evolution*, 43, 27.
- United Nations (2011). World Population Prospects: The 2010 Revision.
- Van Eenennaam, A.L. & Drake, D.J. (2012). Where in the beef cattle supply chain might DNA tests generate value? *Animal Production Science*, 52, 185-196.
- Van Marle-Köster, E., Visser, C., & Berry, D. P. (2013). A review of genomic selection - implications for the South African beef and dairy cattle industries. *South African Journal of Animal Science*, 43, 1-17.
- Van Marle-Köster, E., & Webb, E. C. (2014). A Perspective on the Impact of Reproductive Technologies on Food Production in Africa. *Current and Future Reproductive Technologies and World Food Production Advances in Experimental Medicine and Biology*, 752, 199-211.
- VanRaden, P. M., Null, D. J., Sargolzaei, M., Wiggans, G. R., Tooker, M. E., Cole, J. B., Sonstegard, T. S., Connor, E. E., Winters, M., van Kaam, J. B. C. H. M., Valentini, A., Van Doormaal, B. J., Faust, M. A., & Doak, G. A. (2013). Genomic imputation and evaluation using high-density Holstein genotypes. *Journal of Dairy Science*, 96, 668-678.
- Visser, C., Hefer, C. A., Van Marle-Köster, E. & Kotze, A. (2004). Genetic variation of three commercial and three indigenous goat populations in South Africa. *South African Journal of Animal Science*, 34, 24-27.
- Weng, Z., Zhang, Z., Ding, X., Fu, W., Ma, P., Wang, C., & Zhang, Q. (2012). Application of imputation methods to genomic selection in Chinese Holstein cattle. *Journal of Animal Science and Biotechnology*, 3, 6.
- Wiggans, G. R., Sonstegard, T. S., VanRaden, P. M., Matukumalli, L. K., Schnabel, R. D., Taylor, J. F., Schenkel, F. S., & Van Tassell, C. P. (2009). Selection of single-nucleotide polymorphisms and quality of genotypes used in genomic evaluation of dairy cattle in the United States and Canada. *Journal of Dairy Science*, 92, 3431-3436.
- Wurzinger, M., Sölkner, J., & Iñiguez, L. (2011). Important aspects and limitations in considering community-based breeding programs for low-input smallholder livestock systems. *Small Ruminant Research*, 98, 170-185.