sustainability

MDPI

Review

Genetic Traits of Relevance to Sustainability of Smallholder Sheep Farming Systems in South Africa

Annelin Molotsi [1,*], Bekezela Dube [2], Simon Oosting [3], Tawanda Marandure [1], Cletos Mapiye [1], Schalk Cloete [1,4] and Kennedy Dzama [1]

1 Department of Animal Sciences, University of Stellenbosch, Stellenbosch, Private bag X1, Matieland, Stellenbosch 7606, South Africa; tawanda@sun.ac.za (T.M.); cmapiye@sun.ac.za (C.M.); schalkc@elsenburg.com (S.C.); kdzama@sun.ac.za (K.D.)
2 Animal Production Institute, Agricultural Research Council, Private Bag X2, Irene 0062, South Africa; bee.dube@gmail.com
3 Animal Sciences Group, Animal Production Systems, Wageningen University, P.O. Box 338, 6700AH Wageningen, The Netherlands; simon.oosting@wur.nl
4 Directorate Animal Sciences: Elsenburg, Private Bag X1, Elsenburg 7607, South Africa
* Correspondence: annelind@sun.ac.za; Tel.: +27-021-808-3148

Received: 30 May 2017; Accepted: 7 July 2017; Published: 28 July 2017

Abstract: Sustainable livestock production is important to ensure continuous availability of resources for future generations. Most smallholder livestock farming systems in developing countries have been perceived to be environmentally, socially and economically unsustainable. Farming with livestock that is robust and adaptable to harsh environments is important in developing countries especially in semi-arid and arid environments. This review discusses the different sheep farming systems employed by smallholder farmers and associated sustainability problems facing them. The review also gives an overview of sustainability indicators and limitations to the sustainability for the different smallholder sheep production systems in South Africa. It is argued that genetic diversity is important for sustainability and needs to be maintained in sheep for sustainable production and reproduction performance. The application of traditional breeding and genomics to ensure sustainable production is explored. Animal breeding approaches, specifically genomics can be applied to improve areas of environmental sustainability of smallholder sheep farming systems but must be targeted to the specific production environments, challenges, and opportunities of smallholder production. The genetic traits important for sustainability, the role of genomics in improving these traits and linking these genetic traits to different farming systems in South Africa are discussed.

Keywords: social indicators; economic indicators; environmental indicators; robustness; animal breeding; genetic diversity

1. Introduction

Most of the surface area in South Africa is semi-arid, which makes it unsuitable for anything but extensive ruminant livestock farming [1]. In South Africa, the sheep industry is divided into commercial, emerging commercial and smallholder subsistence farmers. There are an estimated 28.8 million sheep in South Africa, of which 21.4 million are owned by commercial farmers [2]. The industry is dominated by the commercial sheep farmers who own more than two thirds of the sheep in the country and supply meat products locally and wool products for export. The emerging and smallholder sheep farmers supply meat and wool products for sale through informal and formal markets and for subsistence. Sheep also play other roles to this sector including, provision of milk and manure, and other religious and cultural roles. The Dohne Merino, Merino and Dorper breeds are the most prominent breeds of sheep in South Africa. Other sheep breeds found in the South African sheep industry include the Dormer, Ile de France, Meatmaster, Namaqua Afrikaner, Afrino, Merino Landsheep and South African Mutton Merino [1]. The number of sheep owned by smallholder farmers is inadequately documented. Sheep used by most smallholder subsistence farmers in South Africa include the Nguni, Damara, Pedi, Namaqua Afrikaner and the Dorper. However, the Dorper is the breed of choice for farmers in the semi-arid and arid environments of South Africa, because of its ability to grow and reproduce in harsh environments. Some of these breeds are indigenous to South Africa and have characteristics that make them well-adapted to local conditions [3–6]. Commercial farmers achieve high production due to selection for improved growth, reproduction, meat and wool traits in exotic breeds [7]. Minimal or no selection took place for any of the abovementioned traits in smallholder sheep production systems resulting in low production performance [8]. Indigenous breeds used in smallholder systems such as the Damara [3] and Namaqua Afrikaner [9], however, outperform commercial breeds for fitness traits, such as survival and tick resistance. Fitness traits can be described as a group of traits enabling animals to adapt and includes several reproduction and survival traits [10]. Selection in commercial flocks has been achieved using traditional breeding methods. However, with the advent of genomics, it is possible to accelerate genetic progress for traits important in smallholder production through more accurate selection, by including molecular markers into traditional breeding values and obtaining genomic breeding values for individuals [11].

Sustainable agriculture implies long-term maintenance of natural systems, to produce in harmony with the available resources without over exploitation of available resources, adequate income per farming unit, fulfillment of basic food needs, as well as provision for both existing and emerging demands and necessities of rural families and communities [12]. The ability of smallholder farmers to exploit the full potential of their livestock is limited by infrastructure, limitations in management, inadequate feed resources, as well as inadequate strategies for genetic improvement of their livestock [13]. These constraints are further aggravated by issues such as climate change, and its impact on the future availability of natural resources, such as water, land, plant and animal species integral to the survival of future generations [14]. It is therefore necessary to have livestock farming systems that are resilient to the effects of climate change. Resilience focus on the adaptive capacity of an ecosystem [15] and therefore in this review we will discuss robustness at animal level.

This calls for adaptation in farming systems and strategies using transdisciplinary and participatory approaches to solve this problem. One such approach is to investigate sustainability on three different pillars, namely, socially, economically and environmentally [16]. Transdisciplinary studies evaluating the sustainability of smallholder livestock farming systems in South Africa are limited. Studies done have covered all three dimensions of sustainability, focusing on sustainability indicators in relation to specific environments and production systems [17,18]. Indicators covered in such studies include education levels, gender roles, cost–benefit analyses, market access, rangeland condition as well as the influence of crop rotation on soil quality [17,18]. Environmental indicators in other literature mainly focus water derived from precipitation, ground water pollution, CH_4 and CO_2 emissions, eutrophication, acidification, change in land use patterns as well as soil erosion [19,20]. Even though biodiversity is mentioned as an indicator, no studies have been done focusing on how to measure biodiversity on a gene level in animals (which will be further referred to as genetic diversity) and its impact on production and reproduction traits. Genetic diversity serves as the raw material to ensure optimum production and reproduction in livestock. The genetic diversity of smallholder sheep populations in Africa is generally unknown, but is directly related to their potential for genetic improvement. Indigenous breeds utilized by smallholder farmers are mostly uncharacterized in terms of their production and reproduction performance. This is due to the absence of recordkeeping and formal breeding strategies in smallholder farming systems. Genetic improvement using traditional breeding strategies thus has limited application and the use of genomic tools can aid in obtaining pedigree information for smallholder sheep flocks. Genomic tools can also be used to determine genetic diversity as well as to identify causal variants for traits related to robustness and important for sustainability through employing genome wide association analyses (GWAS) [21–23].

The objective of this review is to give a brief overview of the sustainability indicators in the ovine resource maintained by smallholder farmers in South Africa and the limitations to sustainable sheep farming in smallholder production systems. The review also provides an overview of the genetic traits important for sustainability, the role of genomics in improving these traits and the linkage of these genetic traits to different farming systems in South Africa.

2. Sustainability Indicators of Sheep Farmers in South Africa

Most sustainability assessment methods follow a hierarchy where dimensions are at the highest level. These dimensions can be classified as social, economic and environmental [16] and indicators can be used to measure them. Sustainability indicators are defined as a variable that provides information on another less accessible variable [24].

2.1. Social Sustainability Indicators

The social dimension of sustainability is often ranked lower than environmental and economic dimensions in sustainability assessment operations [25]. This could be due to the lack of conceptual clarification of social indicators and how to measure it. Omann and Spangenberg [25] reported that "social scientist had bad experiences in the 1960's receiving limited public resonance and been rejected as ideological strait jackets". The social dimension also poses questions to the current European development model which is a fordistic model of society [25]. This dimension has to be considered on the same footing as the other dimensions to avoid bias in assessments. To date, no consensus exists on what constitutes social sustainability. Various studies have derived different social sustainability indicators as based on their research questions. Examples of indicators used to reflect social sustainability in previous studies include; education level, working conditions and quality of life [19]. Social sustainability indicators relevant to South Africa's smallholder livestock production are not known and warrant investigation. The geo-location of most smallholder farmers was influenced by the colonial apartheid regime while, their current socio-economic conditions are a result of policies of both the apartheid government and the new democratic government [26]. Therefore, historic and current events markedly influence the social status of smallholder farmers. Indicators such as food access, family health status, education level, access to information and gender equality in decision making were used to assess the sustainability of the smallholder cattle production system in the Eastern Cape Province of South Africa [18]. It was concluded that the social dimension of the system was partially sustainable. Other indicators relevant to the social dimension of sustainability include household well-being, access to clean water and sanitation, participation to social organizations and animal welfare among other indicators [27]. Certain social indicators will only be applicable to specific farming systems, for instance access to clean water and sanitation might not be a priority in commercial farming systems as this hurdle is already overcome in these systems. In contrast, such indicators would be of greater importance for smallholder farming systems in rural communities. It is thus important to first characterize the farming system before deciding which social indicators are suitable to measure sustainability.

2.2. Economic Sustainability Indicators

Economic sustainability refers to the short-and long-term profitability of a farming system. Indicators used for this includes net farm income, resource use efficiency and productivity [19]. Other studies also used total agricultural offtake as an economic indicator [28,29]. The role of livestock as a direct income source is overridden by socio-cultural roles for most subsistence farmers [30]. For example, to most resource poor subsistence farmers without access to formal financial institutions, livestock are maintained as a form of capital, providing them with savings and offering opportunities for farmers to accumulate wealth [31]. Swanepoel et al. [32] also stated that livestock guarantees financial security and help to finance planned and unplanned expenditure of smallholder farmers. Sustainability indicators based on input–output systems or cost–benefit analyses may thus not directly reflect subsistence livestock production systems as they do in the profit oriented commercial livestock sector [33].

2.3. Environmental Sustainability Indicators

Indicators used to measure environmental sustainability includes CH_4 and CO_2 emissions, eutrophication, acidification, groundwater pollution, dehydration of soil and biodiversity, and the extent of rangeland degradation [19,20]. These indicators are widely covered in literature and will not be explicitly covered in this review. Biodiversity, as mentioned in the literature, is used in the broad sense and includes all components of biological diversity: the variation among animals, plants and microorganisms, including those hosted by livestock species. South Africa's landscape, being mainly suitable for grazing by livestock due to its diverse biomes including grasslands, Nama-Karoo and Karoo vegetation types, among others, is reported as overgrazed [34]. Overgrazing resulted in a decline in biodiversity of the plant species. This resulted in the grazing of all the palatable plant species by livestock and the domination of unpalatable plant species [17,35]. A reduction in palatable grass species will compromise the production of livestock. Low livestock production is linked to reduced income from livestock and thus compromises the livelihood of farmers.

Studies on livestock biodiversity as an indicator of sustainability are limited [33]. A number of studies have however mapped the genetic diversity of major livestock species in South Africa using molecular markers, including work by Halimani et al. [36] on pigs, Mtileni et al. [37] on poultry and Soma et al. [38] on sheep. High levels of genetic diversity have been observed for indigenous sheep genetic resources in South Africa [5,39], thus implicating the potential to use these breeds to develop sustainable breeding programs for smallholders using genomic tools.

The three pillars of sustainability are closely interlinked. The environmental pillar, in this context animal genetic diversity, will influence animal production and thus the economic pillar. The economic pillar will in turn influence the social pillar. If reproduction and production are high, income obtained from sheep will be high. This will positively affect the social pillar of sustainability; where an increased income from livestock will lead to increased food security and well-being of the farmer. There could however be negative tradeoffs between the pillars, for example intensification of sheep production can lead to negative impact on the environment through overgrazing and soil trampling. It is, however, necessary to describe the different sheep farming systems in South Africa and which indicators will be suitable for each system to measure their sustainability. These farming systems have unique problems of sustainability that need to be addressed.

3. Limitations for Sustainability of Sheep Farming Systems in South Africa

The limitations to sustainability for sheep farming systems are driven by the climate, vegetation, topography and husbandry practices and the political dispensation in which it is found, i.e., socialism, communism, capitalism or free-market. In South Africa, smallholder farmers were excluded from supplying food to the market prior to 1980 under the Marketing act 1968 [40]. This has led to commercial farmers dominating the market. The influence of the social dimension on the outcome of the farming system is often overlooked [41].

Due to the political history of South Africa there are different types of smallholder farming enterprises. Prior to colonialism and apartheid most of the land in South Africa belonged to black people. By 1948, eighty seven percent of the land had been redistributed to white people and only 13% to black people staying in the homelands [42]. This had a dramatic effect on agriculture in South Africa, which consists of a small number of commercial farms, co-existing with large numbers of smallholder farms [43]. This system has led to many smallholder farmers ending up with marginal land and resources to farm.

After the 1994 election, black economic empowerment (BEE) actions have been implemented to further/support employment equity. Since then, programs such as the Land Redistribution for Agricultural Development (LRAD) and the Comprehensive Agricultural Support Program (CASP) have been initiated by the Department of Agriculture, Forestry and Fisheries to assist in the agricultural development of underprivileged communities. These programs have been successful in settling 61% of land claims, however problems have occurred in the land redistribution process. These problems are linked to farmers receiving land without adequate training in livestock production, institutional capacity, financial resources and a lack of agricultural support services to allow these farmers to start up viable farming enterprises.

The socio-political situation in South Africa led to the development of the following farming systems: (1) commercial sheep farming system; (2) emerging sheep farming systems; and (3) smallholder farming systems. To measure the sustainability of smallholder sheep farmers in South Africa, it is necessary to determine which indicators are relevant to the specific farming system to address these issues of sustainability.

Sustainability problems of intensive commercial sheep farming systems are related to the effects of intensification. For commercial farmers the economic dimension of sustainability is determined by profitability which depends on income, efficiency and productivity [19]. To achieve high profitability, high input and thus high output system is necessary. Sheep breeds selected for this production system are important, as breeds are required that have high reproduction performance and fast growth rate. Exotic breeds such as the Merino type breeds (Merino, Dohne Merino, South African Mutton Merino and Merino Landsheep) are commonly used in these systems due to their high prolificacy [1,44]. High stocking rates are maintained to achieve high production levels and have resulted in overgrazing of land thus resulting in a decrease of plant and animal biodiversity [45]. The planting of irrigated pastures, have led to the use of pesticides and fertilizers which affected chemical and physical soil quality as well as adding to eutrophication and acidification of soil and water bodies [45]. Social aspects of commercial sheep farming systems can be divided into internal social aspects and external social aspects [19]. The internal social aspects include gender equality and labor inequity, whereas the external social aspects include animal health and welfare. For extensive commercial sheep farmers the economic and social sustainability problems will be similar than for intensive sheep enterprises. The environmental problems will be different in terms of the effects of eutrophication and acidification which will be less in extensive systems due to the use of natural grazing with little additional planted crops or pastures. The problem of overgrazing and resultant decrease in plant biodiversity is, however, more applicable to extensive commercial and smallholder communal sheep farming systems.

Smallholder sheep farmers in South Africa depend on low-input systems. The economic sustainability problems for smallholder farmers include offtake rate and income derived from offtake. Offtake rate can be defined as the proportion of animals sold or consumed within a year [46]. Smallholder farmers also depend on the capital value/insurance value of their sheep as well as offtake. Therefore, owning a large flock of mainly adult sheep may serve as an indicator of wealth and a liquid asset for use to meet family emergencies. Offtake rate for smallholder farmers has been reported to be low [47]. Low offtake rate can be linked to the low reproduction performance observed [8]. Internal social sustainability issues are more important for smallholder farmers. This includes social wellbeing, education levels, health status (including zoonotic diseases risks from affected animals), gender equity, access to food, food safety and access to extension services and information and veterinary services. External social sustainability issues are not a priority as smallholder subsistence farmers are not at the point where their output is marketed to consumers. Environmental sustainability problems include water resources and land available for grazing, sheep resources used (animal biodiversity) and plant biodiversity. Smallholder sheep farmers have sheep genetic resources that are highly genetically diverse [38,39]. Despite high levels of genetic diversity, most smallholder sheep production systems are reported to exhibit low production performance levels and this is mainly attributed to various non-genetic reasons.

Enhancing production performance in commercial sheep flocks have been achieved by altering genetic diversity of the breeding flock using various breeding techniques, including linebreeding (decreasing genetic diversity in a flock) and crossbreeding (increasing genetic diversity in a flock) as well as selection for traits of economic importance. Low production performance of sheep kept by smallholder farmers in low input farming systems can be improved using similar genetic strategies as in the commercial set-up. It is however important to ensure that the accumulation of deleterious loci through the effect of genetic erosion and inbreeding is limited.

4. The Importance of Genetic Diversity for Sustainable Genetic Improvement

4.1. Genetic Variability for Adaptability and Robustness

Genetic diversity can be defined as the genetic variation at neutral or adaptive loci of a population or specie [48]. Neutral genetic diversity is gene variants detected that do not have a direct effect on fitness. This is measured by molecular technique using neutral markers for instance RAPDs, AFLP and microsatellites to estimate parameters such as heterozygosity and homozygosity [48]. Adaptive genetic diversity refers to genes that have an effect on fitness; this can be measured using quantitative genetic experiments to estimate parameters such as heritability (h^2) and genetic variance. In the context of this study genetic diversity studied will focus on using neutral genetic variation in combination with adaptive genetic diversity at breed level.

Genetic diversity within a gene pool determine the fitness/robustness of the animals [10,49] and ultimately adaptability of the animals to the prevailing production environment. Robustness can be defined as the ability of an animal to adapt to challenging environmental conditions [10]. This entails the ability of the animal to survive, reproduce and maintain homeostasis without losing body condition when exposed to adverse conditions [50,51]. Robustness encompass a group of traits enabling animals to adapt and includes several reproduction and survival traits such as disease and parasite resistance, heat tolerance and drought tolerance [50]. Reproduction and survival traits in livestock are known to be lowly heritable and in spite of this, genetic progress has been possible for over 20 years of selection in South African sheep flocks [7]. This indicates the possibility of using adaptive genetic variation to improve robustness traits in South African sheep flocks.

4.2. Genetic Diversity of Indigenous Breeds

Smallholder subsistence sheep farmers make use of indigenous breeds that are more hardy or robust [9,52,53]. Indigenous breeds are sometimes crossed randomly without prior knowledge of pedigree or selection for specific traits. Indigenous Nguni sheep breeds have been shown to have a higher genetic diversity than Merinos using Random Amplified Polymorphic DNA (RAPD) markers [39]. Studies done on the indigenous Namaqua Afrikaner proves them more tick resistant than the South African Mutton Merino (SAMM) and Dorper [8]. The indigenous Namaqua Afrikaner achieved higher survival from birth to weaning (91%) in comparison to the Dorper (88%) [53]. A recent study reported that number of lambs weaned was highest for indigenous Namaqua Afrikaner compared to the Dorper and South African Mutton Merino [52]. These results imply robustness in terms of survival, reproduction and disease/parasite resistance of indigenous breeds. The tradeoff however with indigenous breeds are that their carcass yield is inferior to those of commercial breeds. This was proven true for the indigenous Namaqua Afrikaner breed [54]. Genetic diversity studies have, however, reported low heterozygosity levels within the indigenous Namaqua Afrikaner breed [22,55,56]. The low levels of heterozygosity for this breed could be linked to its small effective population size (Ne). Low levels of heterozygosity has also been reported in other indigenous fat rumped sheep (Black headed Persian and Red head Speckled Persian) whereas indigenous fat tailed sheep such as the Pedi, Swazi and Zulu obtained higher levels of genetic diversity [38]. The reason for these higher levels of diversity could be resultant of some level of crossbreeding in these populations. It is however interesting to note that, even though the Namaqua Afrikaner have high inbreeding levels, their adaptive and fitness traits have not been negatively affected. This could be due to the impact of natural selection on adaptation traits.

4.3. Genetic Diversity of Commercial Breeds in South Africa

Commercial sheep enterprises utilize exotic and synthetic breeds that have been purebred and selected for certain phenotypic traits, such as color and size, for example, in the Dorper breed [57]. These purebreds may accumulate homozygous loci for deleterious genes over time and become inbred, which can result in reduced fitness, poor survival and low reproduction [10]. Commercial breeds are known to have a lower genetic diversity than smallholder populations [56]. Inbreeding in the Danish Texel population has led to a reduction in birth weight, average daily gain and litter size [58]. The use of artificial insemination or the use of one ram of high genetic merit, resulted in a reduced effective population size (Ne), leading to higher inbreeding rates and resulted in a loss of genetic diversity and reproductive fitness. A decrease of genetic diversity through linebreeding and artificial selection have however resulted in increased growth and production traits in exotic sheep breeds [59,60]. Inbreeding percentage should however be kept below 20–25% in sheep flocks to prevent inbreeding depression. Higher inbreeding rates have led to economic losses of $17 per ewe and where inbreeding approached 50% the loss increased to $36 per ewe [61].

4.4. Is Fitness Always Good if Genetic Diversity Is High?

The fact that the Namaqua Afrikaner, Black headed Persian and Red head Speckled Persian have low genetic diversity and still are more robust than exotic breeds [38] is a paradox to the notion that higher levels of genetic diversity are linked to robustness and fitness [10]. The reason for this paradox is unclear and leaves us with the question: "Is fitness always good if genetic diversity is high?" Reed and Frankham [62], however postulates that selection can purge a population of deleterious recessive alleles and in theory can create inbred populations with a higher fitness. This phenomenon of the Namaqua Afrikaner sheep breed could also be explained by the fact that the neutral genetic diversity measures were used to estimate heterozygosity levels within these breeds and thus only refers to gene variants that do not have a direct effect on fitness.

Characterization of traits relevant for sustainability of the specific sheep farming systems is the next step.

5. Genetic Traits Important for Sustainability

Traits of importance for sustainability include reproduction, survival and production traits (Table 1). Reproduction is a composite trait which can be measured by component traits such as number of lambs born per ewe lifetime, or number of lambs weaned per ewe lifetime, litter size, conception rate, lamb survival and mothering ability [63]. The wet–dry phenotype [64] is recorded from an udder examination performed during the marking of recently born lambs or at the weaning of lambs. Wet–dry refers to whether a ewe is lactating or not, and can be used as an indicator of reproductive performance of ewes in low-input farming systems. Heritabilities estimated in Australian Merino flocks range from 0.09 to 0.17 for wet–dry at weaning and 0.04 to 0.11 at lamb marking [65]. The wet–dry phenotype is a composite trait and includes both conception rate and mothering ability. Heritability estimates for the component trait conception rate ranges from 0.01 to 0.30 [66–68]. Estimates for number of lambs born and number of lambs weaned were 0.05 to 0.10 and 0.05 to 0.07, respectively [69,70]. Survival traits in sheep can be measured by survival from birth to weaning. Heritability estimates reported for lamb survival were 0.03 to 0.07 [69,71]. Weaning of lambs occurs at approximately 100 days of age in commercial intensive sheep farming systems. Survival in exotic breeds under harsh conditions is known to be lower than in indigenous breeds. Disease and pathogen resistance are also important traits to consider for sustainability. Studies reported on traits linked to disease resistance in sheep include fecal egg worm count (FEC) as an indicator for resistance to helminth nematodes [69,72], resilience to nematodes, footrot and pneumonia [73] as well as tick resistance [52]. Heritability estimates for FEC were in the range of 0.25 to 0.28 [72] and ranged between 0.07 and 0.59 for tick resistance [52,74].

Estimates depended on the model used to estimate heritability as well as the body location from which ticks were sampled.

Important traits selected for to enhance production are growth traits, such as birth weight, weaning weight, body condition score (BCS), average daily gain, feed conversion efficiency and adult weight [69] as well as carcass traits such as fat depth and eye muscle depth [72]. Heritability estimates for growth and carcass traits are moderate to high, with estimates of 0.30 to 0.41 for adult weight and 0.20 for carcass traits [69]. Heritability estimates for BCS ranged from 0.16 for BCS during mid-pregnancy and 0.18 for BCS two weeks before lambing [75]. Early growth traits such as birth weight and whether or not a lamb was born as single, twin or multiple are important for survival and future growth of an animal, as they are correlated to survival and post-weaning growth performance [76]. Research has shown that birth weight affects survival of lambs, where low birth weight (<3 kg) leads to high mortalities because of starvation and exposure [77] and high birth weight (>6 kg) leads to high mortalities because of dystocia [78]. To obtain maximal survival of lambs, optimum birth weights should be targeted, ranging between 3 and 6 kg. The abovementioned research was done on Coopworth, Romney and Texel sheep breeds. It indicated that birth weight for lambs born as twins or multiples will be lower than single born lambs (0.70 kg and 1.69 kg, respectively) [77]. Feed conversion efficiency is the amount of feed consumed in relation to growth. Feed conversion ratio is highly heritable at 0.26 [79]. Measuring feed intake is difficult in practice and using highly correlated traits such as post weaning weight or yearling weight with feed conversion rate ($r^2 = 0.98$) can be an indication of feed conversion efficiency [79]. This is important where feed scarcity occurs, so the animal will be able to convert low quality feed into growth and production. Growth traits are positively correlated to reproduction traits [69,72]. Selection for growth can thus have an influence on reproduction traits. This is in contrast to the dairy and poultry industry where selection for production traits such as increased milk yield, growth and egg production are negatively correlated with fitness traits [51,80].

Table 1. Heritability estimates for traits important for sustainability.

Trait	Heritability Estimate	Reference
Reproduction		
Wet–dry	0.04–0.17	[65]
Fertility (ewes lambing per ewe joined)	0.05–0.08	[69,70]
Number of lambs born/ewe joined	0.05–0.10	[69,70]
Number of lambs weaned/ewe joined	0.05–0.07	[69,70]
Lamb survival	0.03	[69]
Disease and pathogen resistance		
Fecal egg count	0.27	[69]
Tick Resistance	0.07–0.59	[52,74]
Growth traits		
Birth weight	0.18–0.41	[69,70]
Adult weight	0.30–0.41	[69]
Feed conversion ratio	0.15–0.33	[79]
Carcass weight	0.20	[69]

Quantifying and measuring fitness traits in smallholder production systems can be challenging due to lack of recordkeeping. It is therefore necessary to measure indicator traits that involve minimal recordkeeping and input costs for example wet and dry phenotype as in indicator of reproduction in smallholder sheep farming systems. Smallholder farmers can also implement body condition scoring as a management tool to improve ovulation rate and thus reproduction in their flocks. However, all of the abovementioned traits are important for sustainable sheep production for both smallholder and commercial producers and emphasis of selection for traits would need to be different. Emphasis could be placed according to the input–output of the farming system, as well as the geographical location of the farm. For high input–high output farming systems located in high rainfall geographical regions of South Africa, growth, carcass and reproduction traits could be the main emphasis. In low input–low output farming systems located in drier arid regions of South Africa, survival, disease/pathogen resistance, reproduction and adaptability could be of higher importance. Farmers should include traits important for sustainability of their specific sheep farming system in breeding objectives to enable genetic improvement. Gizaw et al. [81] used a desired-gain selection index to derive relative weights for traits resulting in gains desired by subsistence sheep farmers in Ethiopia. Another means of prioritizing traits of importance could be by adding non market value to the market value of traits [82]. Non market value entails a value given to a trait that is not reflected in the current market economy or that is partly transferred by the market [82]. No studies have been done in South Africa to identify traits of preference for smallholder sheep farmers to include in breeding objectives. The first step will be to start with identifying traits of sustainability for smallholder sheep farmers using participatory approaches, and secondly to set up a recordkeeping system for these traits. Once phenotyping has been established, the use of genomics can be combined with traditional selection and crossbreeding strategies to increase genetic gain. The contribution of indigenous breeds in smallholder sheep farming systems also needs to be investigated.

6. Indigenous Breeds in Smallholder Sheep Farming Systems

Using indigenous breeds in smallholder sheep farming systems can decrease the costs of input related to additional feed or medicine. Meat output and thus income received per kg will be less because of their inferior growth and carcass traits. Thus, the tradeoffs between robustness and carcass traits of indigenous breeds needs to be considered when suggesting these breeds to improve economic sustainability of the smallholder sheep farming systems. Structured breeding programs can be developed where indigenous breeds are crossed with exotic breeds to improve genetic diversity. Examples of this being achieved include composites such as the Meatmaster and Van Rooy, which were derived from crosses between indigenous breeds such as the Damara/Ronderib Afrikaner and exotic breeds such as the Ile de France, Dorper, and SA Mutton Merino [38,83]. A terminal crossbreeding system can be an option, where all the F1 offspring are sold as slaughter lamb [44]. The benefits of an terminal crossbreeding is the effects of F1 hybrid vigor and complementarity, which can lead to an immediate improvement in the desired growth and reproduction traits [84]. This could be of benefit to the smallholder farmer as more carcass yield can be obtained from F1 offspring. This can thus add value in ensuring a higher income to the farmer. Studies of crossbreeding Red Massai (indigenous breed to Kenya) with a Dorper has shown the possible effects of improving resistance to gastro-intestinal parasites [85]. Another option to improve production performance of indigenous breeds would be increase selection for desired traits using genomic selection. Selection for improved robustness or production traits will reduce genetic diversity in a population, however the reduction in diversity will be gradually over a number of generations [7]. This is due to the additive effect of genes using traditional selection methods, where the effect will be cumulative. Crossbreeding on the other hand is using non-additive genetic effects to produce immediate desirable results in terms of production performance.

7. Applying Genomics to Improve Traits Important for Sustainable Farming Systems

Before the advent of high throughput technology, marker assisted selection were explored with the study of markers and their linkage to specific quantitative trait loci (QTL) responsible for phenotypic expression [86]. These markers were used to construct genetic and physical maps of genomes of livestock species [86]. Different genetic markers that were used for marker assisted selection include random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP), microsatellites and single nucleotide polymorphism (SNP). Single nucleotide polymorphisms have become the marker of choice and genotyping platforms are available for ovine species. This includes a 12K SNP chip for parentage determination and genotyping replacements at a low cost, 50K SNP chip [21,87] and recently the 600K SNP chip [88]. The heritability estimates for reproduction and survival traits range from low to medium, whereas estimates for production traits range from medium to high. The use of genomics will be of benefit to the traits that are lowly heritable and expressed later in an animal's life [21]. This will enable the ability to predict a ram/ewes performance for a specific trait at an early age and so increase genetic gain [21]. Genomic tools can help to further elucidate differences between indigenous breeds and exotic breeds in term of reproduction and production traits. This can be done using different methods, for example, studying the genetic diversity and population structure of sheep. This serves as a backbone for genome wide association studies (GWAS) that can be used to associate phenotypes with causal variants [23,89]. Causal variants have been identified for various traits important for sustainability including reproduction [23], gastrointestinal parasite resistance [90,91], growth and meat production [92–94], wool traits [95] and adaptation in extreme environments [96] (Table 2).

Table 2. Examples of causal variants for traits important for sustainability as determined using genomics.

Traits	Causal Variants	Method Used	References
Production traits			
Postweaning gain	MEF2B, RFXANK, CAMKMT, TRHDE and RIPK2	GWAS	[93]
Preweaning gain	PFKFB4, PLA3G6	GWAS	[92]
Body weight	LAP3, NCAPG, LCORL	GWAS	[94]
Carcass quality (Hypertrophy)	Myostatin, Callipyge and Carwell		[97,98]
Shin circumference	ADK and SHISHA9	GWAS	[92]
Fiber diameter	TSPEAR, PIK3R4, KRTCAP3 and YWHAZ	GWAS	[95]
Fiber diameter CV	KIF16B	GWAS	[95]
Fineness dispersion	KIF16B	GWAS	[95]
Crimp	PTPN3, TCF9, GPRC5A, DDX47, EPHA5, TPTE2, NBEA	GWAS	[95]
Disease/pathogen resistance			
Nematodrius average animal effect	S29550.1	GWAS	[90]
Strongyles FEC at 16 weeks	OAR6_40496374.1 SSP1	GWAS	[90]
Gastrointestinal parasite resistance	IFNG, TLR1, TLR6, DYA, TAP1, MUC21, IL18RAP, IL18R1, TAL1, LRP8, PPAP2B		[91]
Adaptation traits			
Adaptation in plateau environments	IFNGR2, MAPK4, NOX4, SLCZA4, PDK1	Whole Genome sequencing	[96]
Adaptation in desert environments	ANXA6, GPX3, GPX7, PTGS2	Whole Genome sequencing	[96]
Adaptation in arid environments	AKR1A1, RAB11FIP2, CPVL and MFSD6	Whole Genome sequencing	[96]
Reproduction traits			
Litter size	GDF9, BMP15, BMPR1B/FecB and B4GALNT2	PCR-RFLP	[89,99]

Causal variants linked to litter size (prolificacy) were growth differential factor (GDF9), bone morphogenetic protein 15 (BMP15), bone morphogenetic protein receptor 1B (BMPR1B) (FecB allele) genes and beta-1,4-N-acetyl-galactosaminyl transferase 2 (B4GALNT2) [99]. GDF 9 is an autosomal gene and is located on chromosome 5 and BMP15 is located on the X-chromosome. BMPR1B is located on chromosome 6 and have six different mutations for this gene, whereas B4GALNT2 is located on chromosome 11. Fecal egg count (FEC) is used to measure resistance to gastrointestinal parasites in sheep, and the causal variants for FEC using a genome wide association study were found on chromosome 14 (linked to *Nematodrius* average animal effect) and chromosome 6 (*Strongyles* FEC at 16 weeks) [90]. Various other genes have been linked to host resistance to different gastrointestinal parasites (*Haemonchus contortus*, *Teladorsagia circumcinta*, *and Trichostrongylus colubriformis*) [91]. These genes were found on ovine chromosome 1, 3, 6 and 20 and are linked to the immune system, mucosal protection and hemostasis [91]. Genes that have been reported to influence carcass traits include callipage, myostatin and carwell genes [97,98]. Another study using three different sheep breeds to determine causal variants for growth and meat traits observed significant loci within chromosome 3, 5 and 9 linked to post weaning gain [92] (Table 2). Causal variants TSPEAR (thrombospondin-type laminin G domain and EAR repeat), KRTCAP3 (expressed in the skin keratinocytes) and KIF16B (kinesin family member 16B) influencing wool traits such as fiber diameter, fiber diameter CV and fineness dispersion were confirmed in Chinese Merino sheep breeds [95]. Whole genome sequencing have been used to identify genes related to adaptation traits in sheep adapted to different environments in Tibetan plateau and Taklimakan desert region in Asia [96]. The abovementioned causal variants are only examples of the abundance of genes already identified in literature.

Sheep can be screened for causal variants using assays consisting of primers of genes related to specific traits of interest [85]. This was done in the study of Liandris et al. [89] using PCR-RFLP to verify the presence of the GDF9 and FecB within two Greek sheep breeds. Following screening for causal variants, introgression of individuals carrying favorable loci into sheep flocks lacking these loci can occur. Successful introgression of FecB mutation into smallholder sheep flocks in India have been reported which resulted in increased number of live born lambs and lamb survival [100].

The issue to bear in mind with GWAS studies is that quantitative traits are most likely to be influenced by many loci of small to medium effect acting on the expression of one trait, than few loci of major effect. Another major issue is that the SNPs included on a chip for GWAS are not the causal variants for the phenotype but are associated with the phenotype because they are in LD with the causal variant [101]. Thus, the variation explained by causal variants are not completely explained by the genotyped SNPs. Causal variants identified will be different in terms of breeds studied and the environment they have adapted to, as seen in a recent study in South African Merino where the major causal variants (GDF9, BMP15, BMPR1B and B4GALNT2) for reproduction have not been confirmed [98] as of yet. Therefore, in attempt to create SNP panels for genetic improvement in smallholder sheep flocks it is important to verify the presence of the causal variants for relevant traits within that flock. Different SNP panels will have to be designed specifically to the farming system and goal of the farmer.

7.1. Genomic Selection

Genomic selection is another tool that can be used to improve genetic gain in sheep flocks. The inclusion of genotypic data based on genetic markers and specifically SNPs can allow the estimation of genomically enhanced estimated breeding values (GEBVs). Genomic selection involves the use of phenotypic and genotype records to derive GEBVs for traits of economic importance. Studies have shown that using genomic best linear unbiased prediction (GBLUP) for the number of lambs weaned in sheep is more accurate than only using best linear unbiased prediction (BLUP) [102]. For this to be possible, an appropriate reference population must be established [102]. A reference population must be fully phenotyped, genotyped, and representative of the population herds/flocks to be predicted. Genomic prediction can be advantageous over pedigree selection when individuals are less related as well as if multi-breed populations are used as reference populations [102]. It was established recently that the use of a multi-breed reference population results in less accurate GEBVs than using smaller single-breed populations [103]. Studies on genomic selection in sheep indicated molecular markers can be used to improve selection accuracy [11,104]. Thus, combining traditional animal breeding and genomics may increase productivity, sustainability and economic viability achieved by animal improvement. There is scope to apply genomic selection to smallholder conditions, where no pedigree information is available; and where reference populations are small. Phenotypic information on the trait of economic importance, whether it be reproduction or growth traits is necessary to successfully achieve this. This could enable the estimation of SNP heritabilities for traits related to sustainability for smallholder farmers such as number of lambs weaned, disease/pathogen resistance, survival, feed conversion efficiency and growth. SNP heritabilities have been estimated for wet–dry trait for smallholder sheep farmers in South Africa [56]. A challenge of implementing this approach for genetic improvement in smallholder systems is the availability of phenotypic data. Obtaining reliable records for traits of economic relevance of an appropriate reference population needs to be addressed. Efforts should be concerted in the development of breeding schemes that allows the recording of traits important for sustainability. Another challenge would be the genotyping costs involved. Genotyping costs per individual using the 50K SNP chip are 73 Euro [105], however these costs have been predicted to decrease in the future [1].

7.2. Willingness and Means for Recording of Phenotypes

Recording of phenotypes to include in selection indices and genomic selection is of vital importance for genetic improvement. This is one of the major challenges for smallholder and even commercial sheep farmers in South Africa due to the extensive nature of sheep farming systems. The availability of the national smallstock improvement scheme (NSIS) makes it possible for registered stud farmers and commercial sheep farmers to participate in genetic improvement programs [1,7]. The question, however, is how do we encourage smallholder farmer to participate in recordkeeping? A study done in Malawi indicated that smallholder farmers' three main reasons for not participating in recordkeeping were: "busy with other activities", "lack of knowledge" and "education" [106]. The study also indicated that recordkeeping was influenced by recording equipment available and herd/flock size. This could be circumvented by the wide available use of smartphones to use as recording equipment. A recent study done in Limpopo, South Africa, indicated that smallholder farmers regularly use smart phones to share information and that a recording application could be developed for the use on smart phones [107]. In addition, recordkeeping systems have been developed using ICT (information and communication technology) technologies in Kenya [108].

8. Conclusions

Addressing sustainability issues of smallholder sheep systems is complex and indicators should be chosen based on the farming goals and the intensity of input–output in the system. A system sustainable for a smallholder subsistence farmer may not be equally sustainable for a commercial smallholder sheep farmer. The type of genetic resources used in a farming system plays an important role in sustainability. Maintaining genetic diversity while selecting for genetic improvement in smallholder flocks is however crucial. Indigenous breeds as an important genetic resource are poorly benchmarked against commercial breeds, thus requiring further research. Choosing the relevant fitness traits to select for is dependent on the geographical location and farming system. Breeding objectives can be developed based on farmers' preference for traits using it as weight to add non market value in the selection index. It is possible to use genomics to improve genetic traits important for sustainability. For commercial sheep farmers, emphasis would be on improving adaptation traits of exotic breeds, whereas for smallholder subsistence farmers the emphasis would be to improve production traits. This can in theory be achieved once successful genotyping or whole genome sequencing has been completed on all sheep resources (both commercial and indigenous) in South Africa. This information can be used to screen both smallholder and commercial sheep flocks for the presence/absence of causal variants related to specific traits of interests for sustainability. Sheep that are positive for the causal variants can then be introgressed into sheep flocks that lack those specific genes necessary to improve both production and robustness through crossbreeding strategies. Genomic selection can also be used to increase genetic gain in smallholder sheep flocks. The limitation, however, is lack of recordkeeping systems and breeding schemes in smallholder sheep farming systems and the costs of genotyping smallholder farming genetic resources. This can potentially be overcome by the collaboration of government, research institutions, higher education and private companies to act as funding bodies for sustainability projects.

Acknowledgments: Hereby we acknowledge all the smallholder farmers of the Western Cape, South Africa for being the inspiration for writing this review. We also acknowledge funding obtained from NUFFIC, and a Thuthuka award from the National Research foundation (NRF).

Author Contributions: A.M. wrote the paper with editorial assistance from T.M., S.O., S.C., B.D., K.D., and C.M.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Cloete, S.W.P.; Olivier, J.J.; Sandenbergh, L.; Snyman, M.A. The Adaption of the South Africa Sheep Industry to New Trends in Animal Breeding and Genetics: A review. *S. Afr. J. Anim. Sci.* **2014**, *44*, 307–321. [CrossRef]
2. Directorate Statistics and Economic Analysis. *Abstract of Agricultural Statistics*; Department of Agriculture, Forestry and Fisheries: Pretoria, South Africa, 2013.
3. Almeida, A.M. The Damara in the Context of Southern Africa Fat-Tailed Sheep Breeds. *Trop. Anim. Health Prod.* **2011**, *43*, 1427–1441. [CrossRef] [PubMed]
4. Snyman, M.A.; van Marle-Koster, E.; Qwabe, S.Q.; Visser, C. Genetic and Phenotypic Profile of Three South African Namaqua Afrikaner Sheep Flocks. *Grootfontein Agric.* **2013**, *13*, 1–10.
5. Gwala, P.E.; Kunene, N.W.; Bezuidenhout, C.C.; Mavule, B.S. Genetic and Phenotypic Variation among Four Nguni Sheep Breeds using Random Amplified Polymorphic DNA (RAPD) and Morphological Features. *Trop. Anim. Health Prod.* **2015**, *47*, 1313–1319. [CrossRef] [PubMed]
6. Kunene, N.; Nesamvuni, E.A.; Fossey, A. Characterisation of Zulu (Nguni) Sheep using Linear Body Measurements and Some Environmental Factors Affecting these Measurements. *S. Afr. J. Anim. Sci.* **2007**, *37*, 11–20.
7. Schoeman, S.J.; Cloete, S.W.P.; Olivier, J.J. Returns on Investment in Sheep and Goat Breeding in South Africa. *Livest. Sci.* **2010**, *130*, 70–82. [CrossRef]
8. Grobler, H. Evaluation Survey at Extensive Farms in the Central Karoo. *Agriprobe* **2010**, *7*, 6–9.
9. Cloete, J.J.E.; Cloete, S.W.P.; Scholtz, A.J.; Matthee, S. The Effect of Breed, Ewe Age and Season on Tick Counts of Indigenous and Commercial Sheep in South Africa. *Proc. Assoc. Adv. Anim. Breed. Genet.* **2013**, *20*, 187–190.
10. Goddard, M. Fitness Traits in Animal Breeding Programs. In *Adaptation and Fitness in Farm Animal Populations*; van der Werf, J.H.J., Graser, H-U., Frankham, R., Gondro, C., Eds.; Springer Science & Business Media: Dordrect, The Netherlands, 2009.
11. Van der Werf, J.H.J. Potential Benefit of Genomic Selection in Sheep. *Proc. Assoc. Adv. Anim. Breed. Genet.* **2009**, *18*, 38–41.
12. Brown, B.; Hanson, M.; Liverman, D.; Merideth, R. Global Sustainability: Toward Definition. *Environ. Manag.* **1987**, *11*, 713–719. [CrossRef]
13. Rege, J.E.O.; Marshall, K.; Notenbaert, A.; Ojango, J.M.K.; Okeyo, A.M. Pro-Poor Animal Improvement and Breeding—What Can Science Do? *Livest. Sci.* **2011**, *136*, 15–28. [CrossRef]
14. World Resources Institute (WRI). *Creating a Sustainable Food Future. A Menu of Solutions to Sustainably Feed More than 9 Billion People by 2050*; World Resources Institute: Washington, DC, USA, 2014.
15. Anderies, J.M.; Folke, C.; Walker, B.; Ostrom, E. Aligning Key Concepts for Global Change Policy: Robustness, Resilience, and Sustainability. *Ecol. Soc.* **2013**, *18*, 8–24. [CrossRef]
16. Oudshoorn, F.W.; Kristensen, T.; Van Der Zijpp, A.J.; de Boer, I.J.M. Sustainability Evaluation of Automatic and Conventional Milking Systems on Organic Dairy Farms in Denmark. *NJAS- Wageningen J. Life Sci.* **2012**, *59*, 25–33. [CrossRef]
17. Mahlobo, B. Multi-Criteria Livestock Assessment for Sustainability of Smallholder Farms in Kwa-Zulu Natal. Masters' Thesis, Stellenbosch University, Stellenbosch, South Africa, 2016.
18. Marandure, T.; Mapiye, C.; Makombe, G.; Dzama, K. Indicator-Based Sustainability Assessment of the Smallholder Beef Cattle Production System in South Africa. *Agroecol. Sustain. Food Syst.* **2016**, *41*, 3–29. [CrossRef]
19. Lebacq, T.; Baret, P.V.; Stilmant, D. Sustainability Indicators for Livestock Farming. A Review. *Agron. Sustain. Dev.* **2013**, *33*, 311–327. [CrossRef]
20. Van Calker, K.J.; Berentsen, P.B.M.; Giesen, G.W.J.; Huirne, R.B.M. Maximising Sustainability of Dutch Dairy Farming Systems for Different Stakeholders: A Modelling Approach. *Ecol. Econ.* **2008**, *65*, 407–419. [CrossRef]
21. Kijas, J.W.; Lenstra, J.A.; Hayes, B.; Boitard, S.; Neto, L.R.; Cristobal, M.S.; Servin, B.; McCulloch, R.; Whan, V.; Gietzen, K.; et al. Genome-Wide Analysis of the World's Sheep Breeds Reveals High Levels of Historic Mixture and Strong Recent Selection. *PLoS Biol.* **2012**, *10*. [CrossRef] [PubMed]
22. Qwabe, S.O.; van Marle-Köster, E.; Visser, C. Genetic Diversity and Population Structure of the Endangered Namaqua Afrikaner Sheep. *Trop. Anim. Health Prod.* **2013**, *45*, 511–516. [CrossRef] [PubMed]

23. Demars, J.; Fabre, S.; Sarry, J.; Rossetti, R.; Gilbert, H.; Persani, L.; Tosser-Klopp, G.; Mulsant, P.; Nowak, Z.; Drobik, W.; et al. Genome-Wide Association Studies Identify Two Novel BMP15 Mutations Responsible for an Atypical Hyperprolificacy Phenotype in Sheep. *PLoS Genet.* **2013**, *9*. [CrossRef] [PubMed]
24. Zahm, F.; Viaux, P.; Vilain, L.; Girardin, P.; Mouchet, C. Farm Sustainability Assessment using the IDEA Method: From the Concept of Farm Sustainability to Case Studies on French Farms. In Proceedings of the International Forum on Assessing Sustainability (INFASA), Bern, Switzerland, 16 March 2006; Volume 14, pp. 77–110.
25. Omann, I.; Spangenberg, J.H. Assessing Social Sustainability: The Social Dimension of Sustainability in a Socio-Economic Scenario. In Proceedings of the 7th Biennial Conference of the International Society for Ecological Economics in Sousse (Tunisia), Köln, Germany, 6–9 March 2002; pp. 1–20.
26. Cousins, B. What is a "Smallholder"? Class Analytic Perspective on Small-Scale Farming and Agrarian Reform in South Africa. In *Reforming Land and Resource Use in South Africa: Impact on Livelihoods*; Routledge: New York, NY, USA, 2010.
27. Vandamme, M.; D'Hease, M.; Speelman, M.; D'Hease, L. Livestock against risk and vulnerability: Multifunctionality of livestock keeping in Burundi. In *The Role of Livestock in Developing Communities: Enhancing Multifunctionality*; Swanepoel, F., Stroebel, A., Moyo, S., Eds.; African Sun Media: Bloemfontein, South Africa, 2010; pp. 107–122.
28. Molotsi, A.H.; Oosting, S.; Cloete, S.W.P.; Dzama, K. Offtake and Genetic Diversity as Indicators of Sustainability for Smallholder Sheep Farming System in the Western Cape, South Africa. In Proceedings of the 6th World Sustainability Forum: Final Press Release, Cape Town, South Africa, 27–28 January 2017.
29. Atanga, N.L.; Treydte, A.C.; Birner, R. Assessing the Sustainability of Different Small-Scale Livestock Production Systems in the Afar Region, Ethiopia. *Land* **2013**, *2*, 726–755. [CrossRef]
30. Musemwa, L.; Mushunje, A.; Chimonyo, M.; Mapiye, C. Low Cattle Market Offtake Rates in Communal Production Systems of South Africa: Causes and Migration Strategies. *J. Sustain. Dev. Afr.* **2010**, *12*, 209–226.
31. Coetzee, L.; Montshwe, B.D.; Jooste, A. The Marketing of Livestock on Communal Lands in the Eastern Cape Province: Constraints, Challenges and Implications for the Extension Services. *S. Afr. J. Agric. Ext.* **2005**, *34*, 81–103.
32. Swanepoel, B.J.; Erasmus, B.J.; Schenk, H.W. *South African Human Resources Management. Theory and Practice*; Juta & Co., Ltd.: Cape Town, South Africa, 2008.
33. Hoffmann, I. Livestock Biodiversity and Sustainability. *Livest. Sci.* **2011**, *139*, 69–79. [CrossRef]
34. Scholtz, M.M.; Bester, J.; Mamabolo, J.M.; Ramsay, K. Results of the National Cattle Survey Undertaken in South Africa, with Emphasis on Beef. *Appl. Anim. Husb. Rural Dev.* **2008**, *1*, 1–9.
35. Herrero, M.; Thornton, P.K.; Gerber, P.; Reid, R.S. Livestock, Livelihoods and the Environment: Understanding the Trade-Offs. *Curr. Opin. Environ. Sustain.* **2009**, *1*, 111–120. [CrossRef]
36. Halimani, T.E.; Muchadeyi, F.C.; Chimonyo, M.; Dzama, K. Some Insights into the Phenotypic and Genetic Diversity of Indigenous Pigs in Southern Africa. *S. Afr. J. Anim. Sci.* **2012**, *42*, 507–510. [CrossRef]
37. Mtileni, B.J.; Muchadeyi, F.C.; Maiwashe, A.; Groeneveld, E.; Groeneveld, L.F.; Dzama, K.; Weigend, S. Genetic Diversity and Conservation of South African Indigenous Chicken Populations. *J. Anim. Breed. Genet.* **2011**, *128*, 209–218. [CrossRef] [PubMed]
38. Soma, P.; Kotze, A.; Grobler, J.P.; van Wyk, J.B. South African Sheep Breeds: Population Genetic Structure and Conservation Implications. *Small Rumin. Res.* **2012**, *103*, 112–119. [CrossRef]
39. Hlophe, S.R. Genetic Variation Between and Within Six Selected South African Sheep Breeds using Random Amplified Polymorphic DNA and Protein Markers. Master's Thesis, University of Zululand, KwaZulu-Natal, South Africa, 2011.
40. Dzivakwi, R. Determinants of Output Prices Formation in Local Sheep Markets. Master's Thesis, University of Western Cape, Cape Town, South Africa, 2010.
41. Boogaard, B.K.; Oosting, S.J.; Bock, B.B.; Wiskerke, J.S.C. The Sociocultural Sustainability of Livestock Farming: An Inquiry into Social Perceptions of Dairy Farming. *Animal* **2011**, *5*, 1458–1466. [CrossRef] [PubMed]
42. Percival, V.; Homer-Dixon, T. Environmental Scarcity and Violent Conflict: The case of South Africa. *J. Peace Res.* **1998**, *35*, 279–298. [CrossRef]

43. Organisation for Economic Co-Operation and Development (OECD). *South Africa, Highlights and Policy Recommendations. OECD Review of Agricultural Policies*; Organisation for Economic Co-Operation and Development: Paris, France, 2006.
44. Cloete, S.W.P.; Cloete, J.J.E.; Durand, A.; Hoffman, L.C. Relative Performance and Efficiency of Five Merino and Merino-type Dam Lines in a Terminal Crossbreeding System with Dormer or Suffolk Sires. *S. Afr. J. Anim. Sci.* **2003**, *33*, 223–232. [CrossRef]
45. Vitousek, P.M.; Mooney, H.A.; Lubchenco, J.; Melillo, J.M. Human Domination of Earth' s Ecosystems. *Science* **1997**, *277*, 494–499. [CrossRef]
46. Otte, M.J.; Chilonde, P. *Cattle and Small Ruminant Production Systems in Sub-Saharan Africa. A Systematic Review*; Food and Agriculture Organisation of the United Nations: Rome, Italy, 2002.
47. Motiang, D.M.; Webb, E.C. Herd Mortality and Cattle Off-Take Rates among Small-Holder Producers in the North West Province of South Africa. *Afr. J. Agric. Res.* **2016**, *11*, 930–934.
48. Holderegger, R.; Kamm, U.; Gugerli, F. Adaptive vs. Neutral Genetic Diversity: Implications for Landscape Genetics. *Landsc. Ecol.* **2006**, *21*, 797–807. [CrossRef]
49. Bijlsma, R.; Loeschcke, V. Genetic Erosion Impedes Adaptive Responses to Stressful Environments. *Evol. Appl.* **2012**, *5*, 117–129. [CrossRef] [PubMed]
50. Knap, P.W. Breeding Robust Pigs. *Aust. J. Exp. Agric.* **2005**, *45*, 763–773. [CrossRef]
51. Star, L.; Ellen, E.D.; Uitdehaag, K.; Brom, F.W.A. A Plea to Implement Robustness into a Breeding Goal: Poultry as an Example. *J. Agric. Environ. Ethics* **2008**, *21*, 109–125. [CrossRef]
52. Cloete, S.W.P.; Cloete, J.J.E.; Scholtz, A.J. Genetic Parameters for Tick Count and Udder Health in Commercial and Indigenous Ewes in South Africa. *Vet. Parasitol.* **2016**, *230*, 33–42. [CrossRef] [PubMed]
53. Snyman, M.A.; Buys, T.; Jonker, M.L. Production and Reproduction Performance of Namaqua Afrikaner Sheep. In Proceedings of the 6th Global Conference on the Conservation of Domestic Animal Genetic Resources, Magalies Park, South Africa, 9–13 October 2005.
54. Burger, A.; Hoffman, L.C.; Cloete, J.J.E.; Muller, M.; Cloete, S.W.P. Carcass Composition of Namaqua Afrikaner, Dorper and SA Mutton Merino Ram Lambs Reared under Extensive Conditions. *S. Afr. J. Anim. Sci.* **2013**, *43*, 27–32. [CrossRef]
55. Sandenbergh, L.; Cloete, S.W.P.; Roodt-Wilding, R.; Snyman, M.A.; van der Merwe, A. Genetic Diversity and Population Structure of Four South African Sheep Breeds. *Proc. Assoc. Adv. Anim. Breed. Genet.* **2015**, 294–297.
56. Molotsi, A.H.; Taylor, J.F.; Cloete, S.W.P.; Muchadeyi, F.; Decker, J.E.; Sandenbergh, L.; Dzama, K. Preliminary Genome-Wide Association Study for Wet-Dry Phenotype in Smallholder Ovine Populations in South Africa. *S. Afr. J. Anim. Sci.* **2017**, *43*, 327–331. [CrossRef]
57. Olivier, J.J.; Cloete, S.W.P. Genetic Analysis of the South African Dorper Sheep. In Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, MG, Brazil, 13–18 August 2006; pp. 26–28.
58. Norberg, E.; Sørensen, A.C. Inbreeding Trend and Inbreeding Depression in the Danish Populations of Texel, Shropshire, and Oxford Down. *J. Anim. Sci.* **2007**, *85*, 299–304. [CrossRef] [PubMed]
59. Swanepoel, J.W.; Van Wyk, J.B.; Cloete, S.W.P.; Delport, G.J. Inbreeding in the Dohne Merino Breed in South Africa. *S. Afr. J. Anim. Sci.* **2007**, *37*, 176–179. [CrossRef]
60. Van Wyk, J.B.; Fair, M.D.; Cloete, S.W.P. Case study: The Effect of Inbreeding on the Production and Reproduction Traits in the Elsenburg Dormer Sheep Stud. *Livest. Sci.* **2009**, *120*, 218–224. [CrossRef]
61. Erkanbrack, S.K.; Knight, A.D. Effects of Inbreeding on Reproduction and Wool Production of Rambouillet, Targhee, and Columbia Ewes. *J. Anim. Sci.* **1991**, *69*, 4734–4744. [CrossRef]
62. Reed, D.H.; Frankham, R. Correlation between Fitness and Genetic Diversity. *Conserv. Biol.* **2003**, *17*, 230–237. [CrossRef]
63. Snowder, G.D.; Fogarty, N.M. Composite Trait Selection to Improve Reproduction and Ewe Productivity: A Review. *Anim. Prod. Sci.* **2009**, *49*, 9–16. [CrossRef]
64. Fourie, A.J.; Cloete, S.W.P. Reproductive Performance of Commercial Merino, Dohne Merino and SA Mutton Merino Flocks in the Southern Cape. *S. Afr. J. Anim. Sci.* **1993**, *23*, 104–110.
65. Lee, G.J.; Sladek, M.A.; Atkins, K.D. *Selection Criteria for within Flock Selection to Improve Reproduction Efficiency*; Sheep CRC: Armidale, Australia, 2010.

66. Tosh, J.J.; Wilton, J.W.; Kennedy, D. Heritability of Fertility in Four Seasons. In Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France, 19–23 August 2002; pp. 23–26.
67. Iniguez, L.C.; Quaas, R.L.; Van Vleck, L.D. Lambing Performance of Morlam and Dorset ewes under Accelerated Lambing Systems. *J. Anim. Sci.* **1986**, *63*, 1769–1778. [CrossRef] [PubMed]
68. Piwczyński, D.; Kowaliszyn, B. Heritability and Breeding Value of Sheep Fertility Estimated by Means of the GIBBS Sampling Method using the Linear and Threshold Models. *J. Cent. Eur. Agric.* **2013**, *14*, 23–32. [CrossRef]
69. Safari, E.; Fogarty, N.M.; Gilmour, A.R. A Review of Genetic Parameter Estimates for Wool, Growth, Meat and Reproduction Traits in Sheep. *Livest. Prod. Sci.* **2005**, *92*, 271–289. [CrossRef]
70. Safari, E.; Fogarty, N.M.; Gilmour, A.R.; Atkins, K.D.; Mortimer, S.I.; Swan, A.A.; Brien, F.D.; Greeff, J.C.; Van Der Werf, J.H.J. Across Population Genetic Parameters for Wool, Growth, and Reproduction Traits in Australian Merino Sheep. 1. Data Structure and Non-Genetic Effects. *Aust. J. Agric. Res.* **2007**, *58*, 169–175. [CrossRef]
71. Bunter, K.L.; Brown, D.J.; Unit, B. Yearling and Adult Expression of Reproduction in Maternal Sheep Breeds are Genetically Diffferent Traits. *Proc. Assoc. Adv. Anim. Breed. Genet.* **2015**, *20*, 82–85.
72. Huisman, A.E.; Brown, D.J. Genetic Parameters for Bodyweight, Wool, and Disease Resistance and Reproduction Traits in Merino Sheep. 3. Genetic Relationships between Ultrasound Scan Traits and other Traits. *Anim. Prod. Sci.* **2009**, *49*, 283–288. [CrossRef]
73. Morris, C.A. Review of Genetic Parameters for Disease Resistance in Sheep in New Zealand and Australia. In Proceedings of the 18th Conference Assocation of Advancement of Animal Breeding and Genetics, Barossa Valley, SA, Australia, 28 September–1 October 2009; pp. 263–271.
74. Grova, L.; Sae-Lim, P.; Olesen, I. Genetic Parameters of Tick-Infestation on lambs of the Norwegian White Sheep. In Proceedings of the 10th World Congress on Genetics Applied to Livestock Production, Vancouver, BC, Canada, 17–22 August 2014.
75. Everett-Hincks, J.M.; Cullen, N.G. Genetic Parameters for Ewe Rearing Performance. *J. Anim. Sci.* **2009**, *87*, 2753–2758. [CrossRef] [PubMed]
76. Matika, O.; van Wyk, J.B.; Erasmus, G.J.; Baker, R.L. Genetic Parameter Estimates in Sabi Sheep. *Livest. Prod. Sci.* **2003**, *79*, 17–28. [CrossRef]
77. Everett-Hincks, J.M.; Dodds, K.G. Management of Maternal-Offspring Behavior to Improve Lamb Survival in Easy Care Sheep Systems. *J. Anim. Sci.* **2008**, *86*, E259–E270. [CrossRef] [PubMed]
78. Brand, A.A.; Cloete, S.W.P.; De Villiers, T.T. Factors that Influence Mortality amongst Lambs in the Elsenburg Dormer and SA Mutton Merino Flocks. *S. Afr. J. Anim. Sci.* **1985**, *15*, 155–161.
79. Snowder, G.D.; van Vleck, L.D. Estimates of Genetic Parameters and Selection Strategies to Improve the Economic Efficiency of Postweaning Growth in Lambs. *J. Anim. Sci.* **2003**, *81*, 2704–2713. [CrossRef] [PubMed]
80. Nielsen, H.M.; Olesen, I.; Navrud, S.; Kolstad, K.; Amer, P. How to Consider the Value of Farm Animals in Breeding Goals. A Review of Current Status and Future Challenges. *J. Agric. Environ. Ethics* **2011**, *24*, 309–330. [CrossRef]
81. Gizaw, S.; Komen, H.; van Arendonk, J.A.M. Participatory Definition of Breeding Objectives and Selection Indexes for Sheep Breeding in Traditional Systems. *Livest. Sci.* **2010**, *128*, 67–74. [CrossRef]
82. Nielsen, H.M.; Christensen, L.G. A Method to Define Breeding Goals for Sustainable Dairy Cattle Produciton. *J. Dairy Sci.* **2006**, *89*, 3615–3625. [CrossRef]
83. Peters, F.W.; Kotze, A.; van der Bank, F.H.; Soma, P.; Grobler, J.P. Genetic Profile of the Locally Developed Meatmaster Sheep Breed in South Africa Based on Microsatellite Analysis. *Small Rumin. Res.* **2010**, *90*, 101–108. [CrossRef]
84. Roux, C.Z. Maximum Herd Efficiency in Meat Production III. Feeder-Breeder Dimorphism. *S. Afr. J. Anim. Sci.* **1992**, *22*, 11–15.
85. Baker, R.; Nagda, S.; Rodriguez-Zas, S.; Southey, B.; Audho, J.; Aduda, E.; Thorpe, W. Resistance and Resilience to Gastro-Intestinal Nematode Parasites and Relationships with Productivity of Red Maasai, Dorper and Red Maasai x Dorper Crossbred Lambs in the Sub-Humid Tropics. *Anim. Sci.* **2003**, *76*, 119–136. [CrossRef]
86. Williams, J.L. The Use of Marker-Assisted Selection in Animal Breeding and Biotechnology. *Rev. Sci. Tech.* **2005**, *24*, 379–391. [CrossRef] [PubMed]

87. Kijas, J.W.; Townley, D.; Dalrymple, B.P.; Heaton, M.P.; Maddox, J.F.; McGrath, A.; Wilson, P.; Ingersoll, R.G.; McCulloch, R.; McWilliam, S.; et al. Genome Wide Survey of SNP Variation Reveals the Genetic Structure of Sheep Breeds. *PLoS ONE* **2009**, *4*. [CrossRef] [PubMed]
88. Anderson, R.; McEwan, J.; Brauning, R.; Kijas, J.; Dalrymple, J.; Worley, K.; Daetwyler, H.; Van Stijn, T.; Clarke, S.; Baird, H.; et al. Development of a High Density (600K) Illumina Ovine SNP Chip and its use to Fine Map the Yellow Fat Locus. In Proceedings of the Plant and Animal Genome XXII Conference, San Diego, CA, USA, 10–15 January 2014.
89. Liandris, E.; Kominakis, A.; Andreadou, M.; Kapeoldassi, K.; Chadio, S.; Tsiligianni, T.; Gazouli, M.; Ikonomopoulos, I. Associations Between Single Nucleotide Polymorphisms of GDF9 and BMP15 Genes and Litter Size in Two Dairy Sheep Breeds of Greece. *Small Rumin. Res.* **2012**, *107*, 16–21. [CrossRef]
90. Riggio, V.; Matika, O.; Pong-Wong, R.; Stear, M.J.; Bishop, S.C. Genome-Wide Association and Regional Heritability Mapping to Identify Loci Underlying Variation in Nematode Resistance and Body Weight in Scottish Blackface Lambs. *Heredity* **2013**, *110*, 420–429. [CrossRef] [PubMed]
91. Benavides, M.V.; Sonstegard, T.S.; Van Tassell, C. Genomic Regions Associated with Sheep Resistance to Gastrointestinal Nematodes. *Trends Parasitol.* **2016**, *32*, 470–480. [CrossRef] [PubMed]
92. Zhang, L.; Liu, J.; Zhao, F.; Ren, H.; Xu, L.; Lu, J.; Zhang, S.; Zhang, X.; Wei, C.; Lu, G.; et al. Genome-Wide Association Studies for Growth and Meat Production Traits in Sheep. *PLoS ONE* **2013**, *8*. [CrossRef] [PubMed]
93. Zhang, L.; Ma, X.; Xuan, J.; Wang, H.; Yuan, Z.; Wu, M.; Liu, R.; Zhu, C.; Wei, C.; Zhao, F.; et al. Identification of MEF2B and TRHDE Gene Polymorphisms Related to Growth Traits in a New Ujumqin Sheep Population. *PLoS ONE* **2016**, *11*, e0159504. [CrossRef] [PubMed]
94. Al-Mamun, H.A.; Clark, S.A.; Kwan, P.; Gondro, C. Genome-Wide Linkage Disequilibrium and Genetic Diversity in Five Populations of Australian Domestic Sheep. *Genet. Sel. Evol.* **2015**, *47*, 90–104. [CrossRef] [PubMed]
95. Wang, Z.; Zhang, H.; Yang, H.; Wang, S.; Rong, E.; Pei, W.; Li, H.; Wang, N. Genome-Wide Association Study for Wool Production Traits in a Chinese Merino Sheep Population. *PLoS ONE* **2014**, *9*, e107101. [CrossRef] [PubMed]
96. Yang, J.; Li, W.R.; Lv, F.H.; He, S.G.; Tian, S.L.; Peng, W.F.; Sun, Y.W.; Zhao, Y.X.; Tu, X.L.; Zhang, M.; et al. Whole-Genome Sequencing of Native Sheep Provides Insights into Rapid Adaptations to Extreme Environments. *Mol. Biol. Evol.* **2016**, *33*, 2576–2592. [CrossRef] [PubMed]
97. Miar, Y.; Salehi, A.; Kolbehdari, D.; Aleyasin, S.A. Application of Myostatin in Sheep Breeding Programs: A review. *Mol. Biol. Res. Commun.* **2014**, *3*, 33–43. [PubMed]
98. Cockett, N.E.; Smit, M.A.; Bidwell, C.A.; Segers, K.; Hadfield, T.L.; Snowder, G.D.; Georges, M.; Charlier, C. The Callipyge Mutation and other Genes that Affect Muscle Hypertrophy in Sheep. *Genet. Sel. Evol.* **2005**, *37*, S65. [CrossRef] [PubMed]
99. Abdoli, R.; Zamani, P.; Mirhoseini, S.Z.; Ghavi Hossein-Zadeh, N.; Nadri, S. A Review on Prolificacy Genes in Sheep. *Reprod. Domest. Anim.* **2016**, *51*, 631–637. [CrossRef] [PubMed]
100. Nimbkar, C.; Kataria, R.S.; Mishra, B.P.; Joshi, B.K.; Ghalsasi, P.M. The FecB Mutation Increases Lamb Production in Smallholder Subsistence Flocks in Maharashtra State of India. *Proc. Assoc. Adv. Anim. Breed. Genet.* **2015**, *20*, 167–170.
101. Wray, N.R.; Yang, J.; Hayes, B.J.; Price, A.L.; Goddard, M.E.; Visscher, P.M. A Commentary on Pitfalls of Predicting Complex Traits from SNPs. *Nat. Rev. Genet.* **2013**, *14*, 894. [CrossRef] [PubMed]
102. Daetwyler, H.D.; Bolormaa, S.; Brown, D.J.; van der Werf, J.H.; Hayes, B.J. A Genomic Prediction Cross-Validation Approach Combining Ewe Repeated Phenotypes and Ram Daughter Trait Deviations. In Proceedings of the Association for the Advancement of Animal Breeding and Genetics, Napier, New Zealand, 20–23 October 2013; pp. 360–363.
103. Legarra, A.; Baloche, G.; Barillet, F.; Astruc, J.M.; Soulas, C.; Aguerre, X.; Arrese, F.; Mintegi, L.; Lasarte, M.; Maeztu, F.; et al. Within- and Across-Breed Genomic Predictions and Genomic Relationships for Western Pyrenees Dairy Sheep Breeds Latxa, Manech, and Basco-Béarnaise. *J. Dairy Sci.* **2014**, *97*, 3200–3212. [CrossRef] [PubMed]
104. Duchemin, S.I.; Colombani, C.; Legarra, A.; Baloche, G.; Larroque, H.; Astruc, J.M.; Barillet, F.; Robert-Granie, C.; Manfredi, E. Genomic Selection in the French Lacaune Dairy Sheep Breed. *J. Dairy Sci.* **2012**, *95*, 2723–2733. [CrossRef] [PubMed]

105. Neogen Corporation. GeneSeek Genomic Sheep (Ovine) and Goat OvineSNP50chip Genotyping Beadchip. 2017. Available online: http://genomics.neogen.com/en/sheep-and-goat#ovinesnp50-genotyping-beadchip (accessed on 3 July 2017).
106. Chagunda, M.G.G.; Msiska, A.C.M.; Wollny, C.B.A.; Tchale, H.; Banda, J.W. An Analysis of Smallholder Farmers' Willingness to Adopt Dairy Performance Recording in Malawi. *Livest. Res. Rural Dev.* **2006**, *18*, 66.
107. Mapiye, O. *Towards a Management Database to Improve the Sustainability of Cattle Production and Its Contribution to Food Security: A Case of Emerging Beef Farmers in Limpopo Province*; Stellenbosch University: Stellenbosch, South Africa, 2017.
108. Irungu, K.R.G.; Mbugua, D.; Muia, J. Information and Communication Technologies (ICTs) Attract Youth into Profitable Agriculture in Kenya. *East Afr. Agric. For. J.* **2015**, *81*, 24–33.

© 2017 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).