

Strategies for the genetic improvement of South African Angora goats

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Abstract

Selection of Angora goats over the past decades has focused on traits related to fitness, body weight and fiber production. Research for genetic improvement of the Angora has been based on quantitative selection and more recently molecular technology has been applied. Although considerable progress has been made at increasing fine mohair production, the inability of Angora goats to survive sub-optimum conditions has become a concern. Selection emphasis on fibre production resulted in unthrifty animals and the South African (SA) Angora industry is still hampered by the loss of young goats. DNA marker information assists conventional selection by increasing selection accuracy, improving the rate of genetic improvement and leading to a better understanding of the physiological background of traits. The genetic diversity of the SA Angora goat breed was estimated and an improved linkage map was recently developed. The extensive production systems in South Africa pose a challenge for pedigree integrity, and a microsatellite panel was constructed for parentage verification. Selection for quantitative trait loci (QTL) will lead to increased genetic progress and offers the opportunity to improve understanding of and exploit phenotypic variation. Putative QTL associated with fleece and growth traits have been identified in the South African Angora goat population. The current goat SNP chip does not include any fibre-producing goat breed, and this chip is currently being verified in the SA Angora goat population, in conjunction with the sequencing of certain keratin genes.

Keywords: breeding objective, molecular technology, selection criteria, selection index

Introduction

The Angora goat was domesticated in Turkey, from where they were exported to Europe during the sixteenth century in an attempt to establish a mohair industry. The European climate was however not suited to these goats and South Africa (a British colony at the time) presented a favourable region for Angora goat production. The first Angora goats were imported to South Africa during 1838, followed by another 3000 goats between 1856 and 1896 (Friedrich, 2009). The Karoo and semi-arid Eastern Cape region proved to be well-suited to the Angora goats, and a successful industry evolved from this. Today the mohair industry in South Africa consist of approximately 644 000 Angora goats (www.mohair.co.za), most of which are still farmed with in the Eastern Cape.

The Angora goat serves a small, niche industry by producing a lustrous and specialized fibre. Mohair is admired for its superior lustre, handle and high quality and is marketed and promoted by a well-organized international mohair industry. South Africa is the major role player, producing almost 50% of the world product. Mohair is also produced in several other countries, in climatic areas as diverse as the arid areas of southern and south-western USA (Texas, Arizona and New Mexico) and Patagonia in Argentina, to the colder highlands of Lesotho, Great Britain and New Zealand. Most of the world mohair production are imported to South Africa for further processing, and exported with the locally produced mohair (DAFF, 2011). World production of mohair decreased sharply between 1988 and 2003, with a drop of 70% to 6.6 million kg (Van der Westhuysen, 2005) owing mostly to a shift towards synthetic fibres in the fashion industry. Global production has decreased further over the past seven years, primarily due to the global financial crises. Goat-produced fibres make up about 0.04% of the world textile fibre production (Lupton, 2004), to which the total mohair production contribute less than 0.02%.

South Africa is widely considered as the most reliable producer of a good quality clip of mohair worldwide, and produces approximately 48% of the world product annually (DAFF, 2011). Early processing (e.g. scouring and combing) of the mohair is performed in South Africa and then sold as “tops”, while raw (unprocessed) mohair is also sold. Mohair in either of these forms is mainly sold at orderly “open-cry” auctions, although a few companies market their product exclusively under

brand names (e.g. Camdeboo) (Van der Westhuysen, 2005; DAFF, 2011). Mohair production in South Africa has decreased by almost 30% from 3.7 million kg in 2004 to 2.3 million kg in 2010. This decrease has been attributed to a continuing drought in large parts of the production region (Eastern Cape Province), as well as the global financial crises (DAFF, 2011). South African producers are facing challenges to remain productive and competitive and breeders have to adapt to demands for finer fibres, decreasing profit margins, a challenging production environment and changed land-use patterns. Therefore, the continuous evaluation and improvement of selection criteria and breeding goals are of the utmost importance to maintain the world-renowned quality clip and efficient production of South African mohair.

The aim of this review was to provide an overview of the genetic improvement of the South African Angora by discussing (i) selection criteria and genetic parameters, ii) selection programs based on quantitative selection, and (iii) molecular approaches to genetic improvement.

Selection criteria: Fibre traits

Mohair traits include both physical and quality traits with fibre diameter (FD) still being the most important economically, determining both the price and the processing of the fibre. Fibre diameter is moderate heritable, with estimates varying between 0.30 and 0.45 for the SA Angora goat population, and fleece weight (FW) being lowly to moderately heritable (Table 1). Genetic parameters have been estimated for fleece weight and fibre diameter in French (Allain and Roguet, 2003), Argentinean (Taddeo et al., 1998), Australian (Gifford et al., 1991) and South African (Snyman and Olivier, 1996; 1999; Visser et al., 2009) Angora goats. Staple length and subjective fleece traits such as the general appearance and the style, character and evenness of the fleece have a smaller influence on the price. Very few reliable variance estimates are available for these traits (Snyman, 2002; McGregor and Butler, 2004). Breeders tend to place emphasis on the subjective traits despite the low heritability and repeatability estimates, and this is currently discouraged.

Table 1 Heritability and repeatability estimates for mohair traits in South African Angora goats

Trait	Heritability	Repeatability
Greasy fleece weight (FW)	0.19 ¹	0.41 ¹
	0.24 ²	
Fiber diameter (FD)	0.30 ¹	0.68 ¹
	0.45 ²	
Coefficient of variation of fibre diameter (CVFD)	0.37 ²	
Standard deviation of fiber diameter (SDFD)	0.32 ²	
Comfort factor (CF)	0.63 ²	
Spinning fineness (SF)	0.61 ²	
Standard deviation of fibre diameter along the length of staple (SDA)	0.14 ²	
Softness	0.07 ¹	0.32 ¹
Face cover	0.33 ¹	0.37 ¹
Style	0.13 ¹	0.24 ¹
Evenness	0.26 ¹	0.23 ¹
Character	0.14 ¹	0.35 ¹
Kemp	0.01 ¹	0.29 ¹
Pigmentation	0.43 ¹	0.62 ¹

¹ Snyman and Olivier (1999), ² Visser et al. (2009)

An important contribution in recent years was the addition of quality traits in selection programs; especially those measured using Optical Fibre Diameter Analyser (OFDA) technology. OFDA2000 technology is currently routinely used for fleece measurement in most animal fibre producing countries, including South Africa. The measurement of fibre diameter, as well as other important quality traits has offered the inclusion of new criteria in the selection objective. The quality traits are associated with the full diameter profile, and include coefficient of variation of fibre diameter (CVFD), standard deviation of fiber diameter (SDFD), comfort factor (CF), spinning fineness (SF) and standard deviation of fiber diameter along the length of the staple (SDA). These

traits have however largely been ignored by the mohair industry, and there is a dearth of information on genetic parameters for them, with estimates only for French and South African Angora goats (Allain and Roguet, 2006; Visser et al., 2009). In Table 1 a summary is provided of the heritability estimates that have been estimated for some quality traits in SA Angora goats.

In the selection for fine mohair, breeders have been challenged with unfavourable correlations between fibre diameter and fleece weight. Medium to strong positive correlations of 0.35 (Allain and Roguet, 2003) to 0.55 (Snyman and Olivier, 1996) have been reported, while lower positive (0.08, Visser et al., 2009) and even negative values (-0.29, Pattie et al., 1990) have also been published. General consensus is that fibre diameter and fleece weight should both be selected on by making use of a selection index. Quality traits should also receive consideration for inclusion in a selection index, but the economic weighting factors of these should first be determined.

Selection criteria: Growth and reproduction traits

From the early 1970s until 1990, SA Angora goats have been intensely selected for increased mohair production, with no selection directed towards weaning weight. Body weight was compromised leading to smaller, unthrifty animals with an inability to survive sub-optimum conditions. Since then, animals have become larger but body weight is still of concern to breeders.

Body weight is not only important as a factor influencing mohair production, but is directly related to the survivability of young goats, and the reproductive ability of young does. Survivability is directly correlated to birth and weaning weights and the poor growth rate of the Angora goat breed has been well-documented (Snyman, 2007, 2010; Goosen et al., 2010). Approximately 19% of pre-weaning mortalities in SA Angora goats can be attributed to small, unthrifty kids that could not suckle without assistance, with a clear correlation between survival rate and birth weight (Snyman, 2010). Pre-weaning kid mortality has also been shown to be influenced significantly by different management systems in combination with genetics, mothering ability and milk production of the mothers (Snyman, 2010). Evaluation of post-weaning growth rate of kids without supplementary feeding was found to be unacceptably low (Snyman, 2007). The harsh climatic conditions in South

Africa necessitate supplementation up to eight month of age for mohair production and to ensure growth of the young does. Most of the farmers do not supplement ewe kids after weaning, due to direct costs that results in many young does not reaching the target weight of 25kg at 18 months and a low conception rate at first mating. Inadequate nutrition also affects weaning percentage, kid mortality and survival rates. This problem could be moderated by management practices, but selection for genetic improvement of pre- and post-weaning growth should result in a long-term solution. Mortality rates of South African Angora goats have been poorly documented, making it very difficult to improve reproduction efficiency on a genetic level.

Several studies since the early 1960s suggested a genetic basis for the negative association observed between selection for fine hair production and fitness traits (Van Heerden, 1963; Wentzel et al., 1979, Herselman, 1990; Herselman and Van Loggenberg, 1995). Over many decades it was suggested that the focus should be on an increased body weight of does associated with offspring with higher survivability. The high abortion rates in Angora does could be attributed to endocrine failure that was caused either by nutritional or other stress factors. An alternative cause for abortion documented by Wentzel et al. (1979) was chronic hyperadrenocorticism that interferes with the water and electrolyte balance resulting in placental dysfunction, foetal oedema and intra uterine death. Limited evidence for this was found and the major stressor for abortion remains high energy demands during pregnancy and adverse climatic conditions.

It has been shown that young animals are more prone to cold stress and measurements of their adrenal and thyroid function showed an acute drop in blood glucose, a lower response to increasing their energy and an inability to maintain body temperature (Cronje, 1992). Angora goats were compared to Boer Goat and Merino sheep with regard to insulin- induced stress and ACTH and CRH stimulation, showing that plasma cortisol increased in both the Boer goat and Merino sheep while the absence of a response in the Angora indicated hypocortisolism (Engelbrecht et al., 2000). The potential cause was investigated by Storbeck et al., (2007, 2008, 2009) on a mitochondrial level who identified two cytochrome isoforms (CYP17) as the primary cause of hypocortisolism in the South African Angora goat. 3Beta HSD has been identified as a contributing factor to the reduction of cortisol precursors (Goosen et al., 2010). As high quality mohair traits have been found to be

negatively related to fitness traits (Snyman and Olivier, 1999; Webb and Casey, 2010), it was postulated by Goossen et al. (2010) that the selection for fleece traits have resulted in a reduced adrenal function, characterized by a decrease in cortisol production.

Body weight is included in the selection index used by Angora farmers, both because of its importance in reproduction and adaptability and to counteract the unfavourable correlated response when selecting for decreased fibre diameter. Selection for increased weight should have an additional benefit of higher mature weight and improved reproduction rates of young does. As the CYP 17 isoforms observed seem to be under the control of two separate CYP17 genes (Storbeck et al., 2009), specific breeding programs need to be implemented to study variation in the SA Angora goat in order to identify favourable genotypes.

Selection programs

Selection of Angora goats over the past four decades were primarily based on conventional selection. The registration system for all seed stock animals in South Africa dates back to 1904 (Schoeman et al., 2010) and made provision for storage of pedigree information and official performance recording. A pilot study for animal recording in Angora goats was only implemented in 1983, with the approval of the Angora Stud Breeders' Society (Delpont and Erasmus, 1984). It was followed by the closure of the Angora herd book in 1984 and in 1999 animal recording for the Angora goat became operational within the National Small Stock Information Scheme (NSIS) of South Africa (Olivier, 2002). The aim of the NSIS was the recording of traits of economic importance and genetic analyses thereof that would benefit farmers in selection programs. Participation of breeders in the NSIS was not compulsory and poor participation in the NSIS resulted in a lack of comprehensive and complete data for South African Angora breeders, which lead to limited application of Estimated Breeding Values in the wider Angora goat industry in South Africa.

Research flock

A fine-hair resource flock was established in 1988 at the Jansenville Experimental Station in the Eastern Cape Province with the aim of breeding fine-hair producing Angora goats, without sacrificing body weight (Snyman, 2002; Schoeman et al., 2010). Two lines were maintained, a control herd and a fine hair herd. Research showed that body weight could be maintained while reducing fibre diameter. Currently selection indices are available to the breeders where emphasis is placed on fibre diameter, fleece weight and body weight in varying ratios (Snyman et al., 1996; Snyman and Olivier, 1996). In 2002 the selection strategy followed by the industry was evaluated, and Snyman (2002) concluded that selection for decreased fibre diameter, while maintaining or increasing body weight and fleece weight leads to the genetic improvement of SA Angora goats.

Quantitative selection has had a major impact on the genetic progress realized to date, especially with regard to mohair traits. The availability of OFDA technology has contributed to the objective evaluation of quality related traits, but there is still room for improvement. The Angora industry is faced with challenges for improving reproduction and survivability and molecular tools holds potential for future genetic improvement in this regard.

Molecular research

Since the advent of molecular genetics, livestock breeding has entered a new era. The application of biotechnology in farm animals has become the focus of many research groups and institutes. Molecular studies on the goat have however remained limited, with the goat genome sequencing project completed only as recently as 2012. Genomics do however hold promise for the goat industry in a number of ways, including pedigree verification, traceability of products, diagnostic tests and marker assisted or gene assisted selection (MAS or GAS).

The goat linkage map is relatively underdeveloped (Maddox and Cockett, 2007) when compared to most other livestock species. A low-resolution genetic map was published by Vaiman et al. (1996), followed by a more densely populated map on the male chromosome by Schibler et al. (1998), both using microsatellites. Although several QTL studies have been performed on small-stock

species and partial linkage maps were created as by-products of these studies, these maps are mostly not publicly available (Maddox and Cockett, 2007) and did not contribute towards an advanced linkage map. Despite the generally good alignment between the caprine and ovine linkage maps a relatively large number of discrepancies between the species were reported (Maddox, 2005), including many inversions in locus orders between the two maps. The accuracy and coverage of these maps were improved upon by Visser et al. (2010) by adding microsatellite markers and correcting previously reported inversions, based on an Angora goat population. It resulted in a shorter, more accurate caprine map which was used in the molecular studies performed on South African Angora goats.

Genetic variation

Estimating genetic variation of populations is crucial as knowledge of with-in breed variation is the first step towards responsible exploitation of domestic animal biodiversity (Iamartino et al., 2005). Genetic diversity studies on South African goats include a study on commercial meat goat breeds (Visser et al., 2004) and a broader phylogenetic study that included Angora goats, three meat goat breeds and indigenous populations (Pieters, 2007). An in-depth genetic diversity study was conducted on an Angora goat reference population which included more than 1000 individuals of stud farmers, and which was deemed representative of the South African Angora goat industry. It was found that the level of genetic diversity compared favourably with that of other goat breeds, with an observed heterozygosity value of 63.5% over 94 loci (Table 2) and a gene diversity estimate of 61.5% (Visser and Van Marle-Köster, 2009). The levels of heterozygosity indicated that there was sufficient diversity to exploit natural variation on a molecular level for improved production.

Parentage verification

The improvement of pedigree integrity using DNA technology has been shown to be a viable option in Angora goats. SA Angora goats are primarily farmed under extensive production systems and herd sizes may vary from 1000 to 2500 goats per herd. Stud breeders taking part in the NSIS firstly make use of individual mating, either via Artificial insemination or single-sire group mating,

where each sire is run with its allocated group of ewes for at least two oestrus cycles. This is followed by over-mating in the form of flock mating, where all the rams are put together with all the ewes for a further oestrus cycle. This mating practice limits accurate pedigree recording. Commercial breeders only make use of flock-mating by putting all the male and female animals together, making pedigree recording impossible. Pedigree recording thus only takes place in stud herds, experimental herds and in certain group breeding schemes. Approximately 23% of SA Angora goat kids born in both commercial and stud herds between 2000 and 2004 had incomplete or inaccurate pedigree records (Friedrich, 2009). Angora ewes are known to abandon kids if they feel threatened during parturition (Hafez and Hafez, 2000), leading to incorrect maternal allocation. Inaccurate parentage recording over time results in lower selection efficiency due to mating based on incorrect pedigree data (Pollak, 2005).

In order to maintain a high quality clip it is essential for breeders to be able to select the best parents for mating from accurate pedigree data and breeding value information. Correct pedigrees are essential for accurate genetic parameter estimation, which has an impact on rate of genetic progress (Visscher et al., 2002; Bolormaa et al., 2008). A microsatellite marker panel consisting of 14 markers with a Combined Probability of Exclusion (CPE) of 0.997 was created for use in the SA Angora goat industry (Visser et al., 2011a). This panel is currently applied locally and should lead to increased selection accuracy and an improved rate of genetic gain.

Selection

The genetic improvement of production and quality mohair traits of Angora goats in South Africa has been based on phenotypic information for the past two decades. The identification of QTL explaining significant fractions of the genetic variance in these traits should however lead to increased accuracy of Estimated Breeding Values (EBVs) with a corresponding faster rate of genetic improvement (Van der Werf, 2007; Purvis and Jeffery, 2007). Eighteen QTL for mohair traits (including fleece weight (FW), fibre diameter (FD), coefficient of variation of fibre diameter (CVFD), comfort factor (CF), spinning fineness (SF) and variation along the length of the fibre (SDA)) were identified on thirteen chromosomes (Visser et al., 2011b).

A few of the putative QTL hold specific promise. The unfavourable positive genetic correlation between FD and FW has posed a challenge in Angora goat breeding strategies. The detection of a QTL for FD on a separate chromosome (CHI 4) as for FW (CHI 2, 5 and 24), might pose an opportunity to decrease or maintain fibre diameter using marker assisted selection, while increasing fleece weight. In addition, processing and fabric properties are influenced significantly by fibre diameter distribution (Qi et al., 1994; Smith et al., 2006). The use of marker assisted selection to directly improve traits correlated with more uniform production (CVFD, SDFD, SDA) can contribute to a higher quality clip and improved attributes when compared to synthetic fibres. Quantitative selection for decreased variation in fibre diameter along the staple has not been successful and MAS can make a significant contribution to this trait. Fibre-associated QTL were detected on chromosomes where the *KRT* and *KAP* genes have been assigned to (mainly CHI 1 and 5). The putative QTL detected support the suggestion that *KRT* and *KAP* could be possible candidate genes for fibre yield and quality and should receive further attention in fibre-producing goats.

In a separate QTL identification study focusing on pre-weaning growth traits, four chromosomal regions of interest with an influence on birth weight (BW) were identified on CHI 4, 8, 18 and 27 (Visser et al., 2013). Analyses indicated two candidate regions for weaning weight (WW) on CHI 16 and 19 respectively. The growth hormone gene (*GH1*) has been mapped to BTA 19 (corresponding to CHI 19, on which a putative QTL for WW was identified), indicating that this chromosome should be associated with growth traits (Hediger et al., 1990; Taylor et al., 1998). Chromosomal fragments influencing various growth traits have been detected on this chromosome, i.e. birth weight and post-weaning average daily gain (ADG) in cattle (Kneeland et al., 2004) and weight at first shearing in sheep (Roldan et al., 2010). After validation, the putative QTL identified in this study could be used to manipulate early growth and due to a strong positive genetic correlation, also yearling weight in Angora goats.

SNP genotyping now provides the opportunity to track the total genetic variance for a trait with a marker panel via genomic selection. Assembly of the goat genome was performed at the Beijing genome institute and SNP data from different international projects were collated with the aim of developing a 50k SNP chip for goats (Tosser-Klopp et al., 2012). This consortium chip is currently

available at a commercial level through Illumina and will present the opportunity of genomic selection in goats. Setting up a training population and estimating prediction equations will however be a long-term project, and its applicability in the South African goat industry will depend on overcoming financial and resource constraints. Until such a time, increasing the rate of genetic gain via MAS will be a more feasible option.

The way forward

The impact of DNA-verified parentage on the accuracy of EBV estimation and re-ranking of sires, and thus the value of routine testing to farmers is currently being quantified. Participation in the NSIS is relatively low, but if breeders have the option to include DNA-verified parents, receive more accurate EBVs and obtain visible results, national recording should improve. This should lead to an increased rate of genetic improvement and assist the national flock in maintaining its superior mohair production.

Genes that have been investigated in cashmere-producing goats and wool sheep include keratin-associated proteins (*KAP1* to *KAP9*) and intermediate filament proteins (*KRT* genes). Variations in these genes is thought to play a functional role in the expression of fibre quality, but very little evidence of this have been found in goats. Sequencing of individuals with extreme phenotypes (very coarse vs. very fine mohair etc.) should indicate whether variation in these genes is responsible for phenotypic variation. This should lead to the identification of candidate genes that affect the economically important traits and could lead to Gene Assisted Selection. *KAP1* and *KAP8* are currently being investigated in the SA population.

The International Goat Genome Consortium (IGGC) has recently developed a 50k goat SNP chip, which is available through Illumina (Tosser-Klopp et al., 2012). Although six different milk and meat goat breeds were used for sequencing when developing the chip, no fibre-producing breeds were included in the project. It is well-known that polymorphic loci differ greatly between breeds (Garrick, 2011) as was shown in Illumina's Bovine SNP50 content validation study, where the polymorphic loci ranged between 23 567 for Nellore cattle to 43 723 for the Charolais breed.

Before the 50k chip can be applied in the South African Angora goat population, it is necessary to verify the polymorphisms. This will empower applications such as identification of QTL via genome-wide association studies (GWAS), selection signatures and genomic selection. A reduced panel of highly informative markers could also possibly be produced to be used as a diagnostic tool.

Conclusion

In order to maximise selection accuracy and rate of genetic improvement, DNA-based parentage verification should be incorporated as a routine molecular tool for all South African stud (and where possible commercial) Angora goat breeders. These breeders must maintain the superior quality clip for which the country is known, while facing various challenges. The use of the current selection indices has yielded favourable results. However, quality traits that contribute to both the processing performance and consumer satisfaction should be included in the selection strategy. Furthermore, the use of MAS for fleece and growth traits in combination with accurate EBV information could lead to a rapid genetic improvement, especially for traits that are difficult or expensive to measure. In this way the reproductive inefficiency of the Angora goat might be addressed. After identification of genes and their expression patterns, specific loci might be targeted to increase favourable allele frequencies in the population.

The genetic improvement of South African Angora goats should be based on a comprehensive, integrated approach where both quantitative and molecular tools should be applied.

Conflict of Interest

None of the authors (C Visser, E van Marle-Köster) has a financial or personal relationship with other people or organisations that could inappropriately influence or bias the paper entitled “Strategies for the genetic improvement of South African Angora goats”.

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