

Evaluation of production and reproduction of three South African Angora goat *CYP17* genotypes

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Abstract

Two *CYP17* genes, located on different loci and expressing enzymes with significantly different activities, have been identified in the South African Angora goat population. Three unique genotypes (named H_e , H_u , and H_o), which differed not only in the genes encoding *CYP17*, but also in copy number were subsequently identified in the Angora goat. The aim of this study was to evaluate the production and reproduction performance of these three genotypes. Bodyweight, fleece and reproduction data, and blood samples from 466 Angora ewes from three flocks were obtained from the GADI-Biobank. Data had been collected on Flock 1 from 2000 to 2015, Flock 2 from 2000 to 2014 and Flock 3 from 2000 to 2010. Bodyweight data included birth weight, weaning weight, 8-, 12-, and 16-month bodyweight, as well as bodyweight recorded annually for the ewe flock before mating. Fleece data included fleece weight and fibre diameter recorded at the second and third shearings at 12 and 18 months old, respectively. Fleece weight, fibre diameter, style and character were also recorded annually for the ewe flocks during the winter shearing. Individual reproduction records included information on whether the ewe had kidded, whether the ewe had aborted, number of kids born, stillborn kids, kids that died soon after birth, kids reared by a foster mother, kids reared as orphans, number of kids weaned and total weight of kids weaned. Total lifetime reproductive performance of genotyped ewes was calculated for number of kids born, number of kids weaned, and total weight of kids weaned. Blood samples were also collected from 100 sexually active Angora rams from four sources. *CYP17* genotyping was carried out using an ARMS-qPCR (amplification refractory mutation system qPCR) assay. Serum testosterone was quantified using high performance liquid chromatography mass spectrometry. The distribution of the ewes across the three *CYP17* genotypes was 36.7% H_e , 51.5% H_u , and 11.8% H_o , and was in accordance with the distribution of the Angora veld rams (38.0% H_e , 46.4% H_u , and 15.6% H_o). In this study, animals of the H_u genotype were heavier from weaning age onwards, although this difference in bodyweight was significant only at 8 months old and in the adult ewes. No differences were observed between the H_e and H_o animals. Adult ewes of the H_e genotype (1.35 kg) produced heavier ($P < 0.05$) fleeces than the H_u (1.27 kg) and H_o (1.24 kg) genotypes. Fibre diameter of the fleeces of the H_o ewes (33.0 μm) was higher than that of the fleeces of the H_e ewes (32.2 μm ; $P < 0.05$) and the H_u ewes (32.7 μm ; $P > 0.05$). No significant differences were recorded in reproductive performance among the genotypes, although the H_o ewes had the lowest (1.03 and 0.89) and the H_e ewes the highest (1.07 and 0.93) number of kids born and weaned per year respectively. Results on the rams indicated that the *CYP17* genotype had no effect on testosterone production by Angora rams. From the results of this study no evidence could be found that selection for any of the three genotypes would adversely affect any growth, mohair production or reproduction function of Angora ewes. A breeding strategy incorporating selection for productive traits and the *CYP17* genotype, aimed at increasing the frequency of the ACS+ gene and thus the H_e genotype in the population, could be followed without having a negative effect on the genetic progress of productive traits.

Keywords: Bodyweight, fleece weight, number of kids weaned, testosterone, weight of kids weaned

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Introduction

One of the continual problems that face the South African mohair industry is the severe loss of Angora goats during cold spells, owing to the inability of the goats to cope with severe stress (Wentzel *et al.*, 1979; Fourie, 1984; Storbeck *et al.*, 2007; Snyman & Van Heerden, 2011; Snyman *et al.*, 2017). Previous research

has shown that the Angora goat is unable to produce sufficient cortisol (the adrenal steroid hormone released in response to physiological stress) in reaction to cold stress (Van Rensburg, 1971; Herselman & Pieterse, 1992; Herselman & Van Loggerenberg, 1995; Engelbrecht *et al.*, 2000; Engelbrecht & Swart, 2000; Storbeck *et al.*, 2008; Storbeck *et al.*, 2009). This deficiency in cortisol production could be attributed to anomalies in the adrenal steroidogenesis of the Angora goat. A single enzyme, namely cytochrome P450 17 α -hydroxylase/17,20 lyase (CYP17), was identified as the probable cause of the problem (Storbeck *et al.*, 2008). Depending on CYP17 activity, the adrenal steroid hormone biosynthesis pathway is either directed to the formation of mineralocorticoids and glucocorticoids or to precursors of sex hormones (Gilep *et al.*, 2011).

Two CYP17 genes have been identified in the South African Angora goat population, namely ACS- (GenBank accession no. EF524063) and ACS+ (GenBank accession no. EF524064) (Storbeck *et al.*, 2008). The sequences of these two CYP17 genes differ by four single nucleotide polymorphisms and express enzymes with significantly different activities (Slabbert, 2003; Storbeck *et al.*, 2007; Storbeck *et al.*, 2008; Storbeck *et al.*, 2009). Research involving copy numbers of these genes indicated that in both the South African Angora goat and the Boer goat, CYP17 ACS- and ACS+ are not two alleles of a single CYP17 gene, as initially indicated by Slabbert (2003) and Storbeck *et al.* (2007), but are separate genes that occur at different loci (Storbeck *et al.*, 2008). To date, the Angora and Boer goats are the only mammals to be reported to possess two CYP17 genes encoding two CYP17 isoforms (Nakajin *et al.*, 1981; Chung *et al.*, 1987; Givens *et al.*, 1994). The product of the CYP17 ACS- was shown to exhibit significantly enhanced 17,20-lyase activity which prevented the accumulation and availability of cortisol precursors during adrenal steroidogenesis (Storbeck *et al.*, 2008). This 'abnormal' enzyme activity is believed to be the leading cause of the observed hypocortisolism in these animals (Storbeck *et al.*, 2009). Interestingly, CYP17 alleles of the same gene have been associated with different physiological cortisol responses in Merino sheep (Hough *et al.*, 2010; Hough, 2012; Qui, 2015).

Three unique genotypes, which differed not only in genes encoding CYP17, but also in copy number, have subsequently been identified in the Angora goat (Storbeck *et al.*, 2008). For the purposes of this study these genotypes were denoted H_e , H_u and H_o . The H_o genotype has only one CYP17 gene, namely ACS-. The H_e genotype has both CYP17 genes (ACS+ and ACS-) at two loci and therefore twice the copy number of H_o with a ACS- : ACS+ ratio of 2 : 2 (Storbeck *et al.*, 2008). Crossing H_o and H_e goats has been shown to yield an intermediate genotype, H_u , which receives both the ACS- and ACS+ genes from the H_e parent, but only the ACS- gene from the H_o parent. Therefore, in this genotype, the ACS- : ACS+ ratio would be 2 : 1, which is supported by the copy number, where the H_u genotype yielded a 1.4-fold greater copy number than the H_o group (Storbeck *et al.*, 2008). Although the location of the ACS- and ACS+ genes has not yet been mapped in the Angora goat, data obtained from preliminary breeding studies have confirmed the existence of these three genotypes (Swart, 2011).

An insulin-induced stress experiment confirmed that there was a significant difference in the ability of the three genotypes to produce cortisol in response to physiological stress (Storbeck *et al.*, 2008; Hough *et al.*, 2010). The H_e genotype was the best cortisol producer during the insulin-induced stress test, and the H_o genotype produced the least cortisol. Subsequent to the insulin-induced stress test, a simulated cold stress test was performed at Grootfontein Agricultural Development Institute (GADI) (Snyman *et al.*, 2017). While the H_o genotype again produced the least cortisol during the cold stress test, the rectal temperature of the H_u genotype dropped significantly more than that of the other two genotypes. The H_e genotype was the best performer in both the insulin-induced and cold stress tests, and therefore represents the hardiest genotype.

In addition to being important in cortisol production, the CYP17 enzyme is vital for the production of oestrogens (female sex hormones) and androgens (male sex hormones) (Payne & Hales, 2004). The effect of the CYP17 genotypes on the reproductive fitness of Angora ewes was thus investigated (Swart, 2012; Swart, 2013). The results indicated that the H_o genotype is a poor reproducer; 62.5% of the H_o group were poor reproducers, while the H_u and H_e groups contained 35% and 42% poor reproducers, respectively. Poor reproducers were defined as ewes that had weaned fewer kids than they had had kidding opportunities in the flock. However, a larger sample group needs to be investigated before final recommendations can be made to the industry.

This study formed part of a bigger project, which investigated the possibility of breeding more hardy Angora goats without negatively affecting the reproductive fitness of the goats or decreasing the quality of mohair, for which South Africa is known. Data gathered to date suggest that the H_e genotype is the hardiest and should be selected for. However, there is a dearth of information of the relative production and reproduction performance of the three genotypes. The aim of this study was therefore to evaluate the production and reproduction performance of the three Angora goat CYP17 genotypes to determine whether selection for the H_e genotype would have a detrimental effect on productive performance and ultimately to be able to make recommendations to the industry about the way forward regarding implementation of selection practices incorporating the CYP17 genotype.

Material and methods

Resources from the GADI-Biobank, including blood samples and phenotypic data, were used for the first part of this study. Reproduction and production data of the Angora ewes from the three flocks in the GADI-Biobank that had the most complete datasets were used. Lifetime reproductive performance of the ewes in each of these flocks was calculated. Ewes with incomplete records for reproduction, bodyweight and hair production and those without available blood samples were omitted. Subsequently, for each flock, ewes from among the good, average and poor reproductive performers were randomly selected to genotype the *CYP17* locus. The number of ewes being mated annually in these flocks was approximately 600, 100, and 300. Therefore, the same ratio, as far as possible, was applied to selecting samples for genotyping from the three flocks. Samples from 480 ewes were ultimately selected for genotyping. Blood samples from the ewes were obtained from the GADI-Biobank.

The three flocks were representative of animals across the Angora goat farming spectrum, and represented management systems from very extensive to fairly intensive. For details of management systems followed in the studs, see Snyman (2007; 2010a; 2010b), in which the current Flocks 1, 2, and 3 correspond to Stud 5, 7 and 12 in Snyman (2007; 2010a; 2010b). The average number of kids born per ewe mated in the three flocks was 99%, 72%, and 122% for Flocks 1, 2 and 3, respectively (Snyman, 2010a). The corresponding number of kids weaned per ewe mated was 78%, 58%, and 105%. Adult bodyweights of the ewes in the flocks were 37.0 kg, 33.4 kg, and 44.5 kg. Flock 2 was the only flock in which purposeful selection was carried out for decreased fibre diameter, while maintaining bodyweight and fleece weight, based on performance data (Snyman, 2002). Selection in the other two flocks was mostly done subjectively and was not based on performance data.

In addition to evaluating the reproductive performance of the ewes, testosterone production of Angora rams from the three genotypes was compared. For this part of the study, blood samples were collected from 100 sexually active Angora rams from the farms of three producers (Flock 1, Flock 4, and Flock 5). The rams had all been with the ewes until the week in which the blood samples were collected. Blood samples were also collected from 192 two-tooth Angora rams, which were to be sold at the annual Angora veld ram auctions in January 2013. These rams had been run under the same conditions on the veld since July 2012 and had not been exposed to ewes.

Genomic DNA was isolated from 200 µl blood from all the blood samples using the Quick-DNA™ Universal Kit (ZYMO Research). The extracted DNA samples were used to genotype the *CYP17* locus. Genotyping was carried out using an ARMS-qPCR assay. Primer and probe sequences were as follows:

ACS LP, 5'-ACAATGTGGGTGCTCTTGG-3'
 ACS- RP, 5'-CACGTCTGGGGAGGAACG-3'
 ACS+ RP, 5'-CACGTCTGGGGAGGAACA-3'
 ACS TaqMan Probe, FAM-AAGACCAAGCACTCTGCTGCCAAGTA-BHQ

qPCR reactions (20 µl) contained 500 nM of each primer (ACS LP and ACS- RP or ACS LP and ACS+ RP), 500 nM of the TaqMan probe, 1X KAPA PROBE FAST Universal qPCR Master Mix (KAPA biotechnologies) and 5 µl of purified genomic DNA. Amplifications were performed using the LightCycler 96 instrument (Roche Applied Science) with the following cycling conditions: initial denaturation at 95 °C for 3 min, followed by 1 cycle each of 95 °C for 2 sec, 65 °C for 3 sec with 1 °C decrease per cycle for 10 cycles and extension at 72 °C for 2 sec. The reaction was subsequently completed with 35 additional cycles with an annealing temperature of 55 °C. Fluorescence was measured at the end of each extension step (72 °C). A heterozygous (H_e) calibrator was included in each run. Data were analysed with LightCycler 96 software package (Roche Applied Science). Genotypes of 466 ewes were available for inclusion in the study.

Steroids were extracted from whole blood and quantified by ultra-performance liquid chromatography tandem mass spectrometry (UPLC-MS/MS), as described by Schloms *et al.* (2014).

The following production and reproduction data for the ewes were obtained from the Angora Biobank database of the GADI-Biobank:

- Reproductive performance of ewes
- Bodyweight of ewes before mating
- Fleece weight, fibre diameter, style and character of ewes recorded during the winter shearing
- Bodyweight and fleece data recorded at younger ages

Bodyweight, fleece data and reproduction data had been recorded for Flock 1 from 2000 to 2015, Flock 2 from 2000 to 2014, and Flock 3 from 2000 to 2010. Bodyweight data included birth weight, weaning weight,

8-, 12-, and 16-month bodyweight, as well as bodyweight recorded annually on the ewe flock before mating. Fleece data included fleece weight and fibre diameter recorded at the second and third shearings at 12 and 18 months old, respectively. Fleece weight, fibre diameter, style and character were also recorded annually for the ewe flocks during the winter shearing.

The PROC GLM procedure of SAS (2009) was used to analyse bodyweight and fleece data. The following model was used to analyse the effect of genotype on bodyweight from birth until 16 months old, as well as second and third shearing fleece data:

$$Y_{ijklmn} = \mu + h_i + g_j + b_k + r_l + a_m + b_1 \text{AGE} + e_{ijklmn}$$

Where: Y_{ijklmn} = trait of the n^{th} animal of the m^{th} age of dam of the l^{th} rearing group of the k^{th} birth/rearing status of the j^{th} genotype of the i^{th} flock-year of birth

μ = overall mean

h_i = fixed effect of the i^{th} flock-year of birth

g_j = fixed effect of the j^{th} genotype (H_e, H_o, H_u)

b_k = fixed effect of the k^{th} birth/rearing status (only bodyweights)

r_l = fixed effect of the l^{th} rearing group / shearing group

a_m = fixed effect of the m^{th} age of dam

b_1 = linear regression coefficient of the age of the animal at recording of the specific bodyweight (only bodyweight)

e_{ijklmn} = random error with zero mean and variance $1\sigma_e^2$

The following model, employing the PROC GLM procedure of SAS (2009), was used to analyse the effect of genotype on adult bodyweight and fleece data:

$$Y_{ijklm} = \mu + h_i + g_j + y_k + a_l + (hg)_{ij} + (ga)_{jl} + e_{ijklm}$$

Where: Y_{ijklm} = trait of the m^{th} animal of the l^{th} age of the k^{th} year of the j^{th} genotype of the i^{th} flock,

μ = overall mean

h_i = fixed effect of the i^{th} flock

g_j = fixed effect of the j^{th} genotype (H_e, H_o, H_u)

y_k = fixed effect of the k^{th} year of recording

a_l = fixed effect of the l^{th} age at recording

$(hg)_{ij}$ = effect of the interaction between the i^{th} flock and the j^{th} genotype

$(ga)_{jl}$ = effect of the interaction between the j^{th} genotype and the l^{th} age at recording

e_{ijklm} = random error with zero mean and variance $1\sigma_e^2$

Individual reproduction records included information about whether the ewe had kidded, whether she had aborted, number of kids born, stillborn kids, kids that died soon after birth, kids reared by a foster mother, kids reared as orphans, number of kids weaned and total weight of kids weaned. Total lifetime reproductive performance in the flock for the ewes genotyped was calculated for number of kids born, number of kids weaned and total weight of kids weaned. The same model that had been used for adult bodyweight and fleece data was used to analyse the effect of genotype on individual reproductive performance.

The following model, employing the PROC GLM procedure of SAS (2009), was used to analyse the effect of genotype on flock lifetime reproductive performance:

$$Y_{ijklm} = \mu + h_i + g_j + y_k + k_l + e_{ijklm}$$

Where: Y_{ijklm} = trait of the m^{th} animal of the l^{th} number of kidding opportunities of the k^{th} year of birth of the j^{th} genotype of the i^{th} flock

μ = overall mean

h_i = fixed effect of the i^{th} flock

g_j = fixed effect of the j^{th} genotype (H_e, H_o, H_u)

y_k = fixed effect of the k^{th} year of birth of ewe

k_l = fixed effect of the l^{th} number of kidding opportunities

e_{ijklm} = random error with zero mean and variance $1\sigma_e^2$

The CHISQ procedure of SAS (2009) was used to determine whether there were differences among the three genotypes in whether the ewe had kidded, whether the ewe had aborted, number of kids born,

stillborn kids, kids that died soon after birth, kids reared by a foster mother, kids reared as orphans and number of kids weaned.

The following model, employing the PROC GLM procedure of SAS (2009), was used to analyse the effect of genotype on testosterone level in the Angora rams:

$$Y_{ijkl} = \mu + o_i + a_j + g_k + (og)_{ik} + e_{ijkl}$$

Where: Y_{ijkl} = trait of the l^{th} animal of the k^{th} genotype of the j^{th} age of the i^{th} origin

μ = overall mean

o_i = fixed effect of the i^{th} origin (Flock 1, 4, 5)

a_j = fixed effect of the j^{th} age (4-, 6-, 8-tooth)

g_k = fixed effect of the k^{th} genotype (H_e , H_o , H_u)

$(og)_{ik}$ = effect of the interaction between the i^{th} origin and the k^{th} genotype

e_{ijkl} = random error with zero mean and variance $1\sigma_e^2$

For the veld rams, only genotype was included in the model, as all rams were the same age and had been treated as one contemporary group for a seven-month period preceding blood collection.

Results

The distribution of the ewes across the *CYP17* genotypes for the pooled data of the ewes and in the three flocks is summarised in Table 1. The highest percentage animals had the H_u genotype in all flocks, as well as when the flocks were pooled. H_o was the least represented, except in Flock 2, where H_o and H_e were evenly represented.

Table 1 Number of Angora ewes per *CYP17* genotype in the pooled dataset and in the three flocks included in the study

Genotype	All	Flock 1	Flock 2	Flock 3
H_e	171 (36.7%)	132 (41.5%)	6 (16.7%)	33 (29.5%)
H_u	240 (51.5%)	153 (48.1%)	24 (66.6%)	63 (56.2%)
H_o	55 (11.8%)	33 (10.4%)	6 (16.7%)	16 (14.3%)
Total	466	318	36	112

The fixed effects included in the analyses of the various traits until 16 months old are summarised in Table 2, while those included for the adult bodyweight and fleece traits are presented in Table 3. Genotype had a significant effect on 8-month bodyweight (Table 2), adult bodyweight, adult fleece weight, and style of the fleece (Table 3).

Fixed effects included in the models fitted for reproduction traits are given in Table 4. Genotype had no overall effect on number of kids born, number of kids weaned or total weight of kids weaned. A significant interaction between genotype and flock was observed for adult bodyweight, fleece weight, fibre diameter and the individual reproductive traits.

The effect of genotype on bodyweight from birth until adult age is presented in Table 5. Animals of the H_u genotype were heavier from weaning age onwards, although this difference in bodyweight was only significant at 8 months old and in the adult ewes. No differences were observed between the H_e and H_o animals.

The effect of genotype on the fleece traits from second shearing until adult age is presented in Table 6. No differences were evident at the second or third shearings. Adult ewes of the H_e genotype (1.35 kg) produced heavier ($P < 0.05$) fleeces than both the H_u (1.27 kg) and H_o (1.24 kg) genotypes. Fibre diameter of the fleeces of the H_o ewes (33.0 μm) was higher ($P < 0.05$) than that of the fleeces of the H_e ewes (32.2 μm). The fleeces of the H_o ewes had the best style.

Table 2 Fixed effects included for analyses of bodyweight and fleece traits recorded until 16 months of age on the Angora ewes included in the study

Trait	Genotype	Flock-Year of birth	Rearing group	Birth status	Rearing status	Shearing group	Age of dam	Age of animal
Birth weight (kg)	ns	**	-	**	-	-	**	-
Weaning weight (kg)	ns	**	**	-	**	-	**	**
8-month bodyweight (kg)	*	**	**	-	**	-	*	**
12-month bodyweight (kg)	ns	**	**	-	**	-	ns	**
16-month bodyweight (kg)	ns	**	**	-	*	-	ns	*
Fleece weight: 2 nd shearing (kg)	ns	**	-	-	-	ns	ns	-
Fibre diameter: 2 nd shearing (μm)	ns	**	-	-	-	ns	**	-
Fleece weight: 3 rd shearing (kg)	ns	**	-	-	-	*	**	-
Fibre diameter: 3 rd shearing (μm)	ns	**	-	-	-	ns	**	-

** $P < 0.001$; * $P < 0.05$; ns = not significant, - not included

Table 3 Fixed effects included for analyses of bodyweight and fleece traits recorded at adult age on the Angora ewes included in the study

Trait	Genotype	Flock-Year of birth	Age of animal	Genotype x Flock	Genotype x Age of animal
Adult bodyweight (kg)	**	**	**	**	ns
Adult fleece weight: winter shearing (kg)	**	**	**	**	ns
Adult fibre diameter: winter shearing (μm)	ns	**	**	*	ns
Style of fleece: winter shearing	*	**	**	-	ns
Character of fleece diameter: winter shearing	ns	*	**	-	ns

** $P < 0.001$; * $P < 0.05$; ns = not significant, - not included

As already stated, there was a significant interaction between flock and genotype in adult bodyweight ($P = 0.009$), fleece weight ($P = 0.0010$) and fibre diameter ($P = 0.0336$). These interactions are illustrated in Figures 1 to 3, respectively. There was no significant difference in bodyweight among the genotypes in Flock 1, while the H_u ewes in Flock 2 were heavier than the H_e ewes ($P < 0.05$) in Flock 2. The H_e and H_u ewes were heavier ($P < 0.05$) than the H_o ewes in Flock 3. H_e ewes produced the most hair in Flocks 1 and 2 ($P < 0.05$), while H_e and H_u ewes produced more hair than H_o ewes in Flock 3 ($P < 0.05$) (Figure 2). The biggest differences among genotypes in fibre diameter were recorded in Flock 2.

Table 4 Fixed effects included for analyses of the reproduction traits of the Angora ewes included in the study

Trait	Genotype	Flock	Ewe's birth year	Year of recording	Number of kidding opportunities	Age of animal	Genotype x Flock
Total weight of kids weaned / lifetime (kg)	ns	**	**	-	**	-	-
Number of kids born / lifetime	ns	**	*	-	**	-	-
Number of kids weaned / lifetime	ns	**	*	-	**	-	-
Individual records							
Total weight of kids weaned / year (kg)	ns	**	-	*	-	**	**
Number of kids born / year	ns	**	-	*	-	**	**
Number of kids weaned / year	ns	**	-	*	-	**	**

** $P < 0.001$; * $P < 0.05$; ns = not significant, - not included

Table 5 Effect of *CYP17* genotype on bodyweight of Angora ewes from birth until adult age

Trait	H_e	H_u	H_o
Birth weight (kg)	2.92 ± 0.11	2.90 ± 0.11	2.87 ± 0.11
Weaning weight (kg)	15.7 ± 0.6	16.0 ± 0.6	15.9 ± 0.7
8-month bodyweight (kg)	19.8 ± 0.7	20.4 ^b ± 0.7	19.3 ^a ± 0.8
12-month bodyweight (kg)	22.3 ± 0.9	22.5 ± 0.8	22.4 ± 0.9
16-month bodyweight (kg)	26.5 ± 0.9	27.2 ± 0.9	26.3 ± 1.0
Adult ewe bodyweight (kg)	40.1 ^a ± 0.4	40.9 ^b ± 0.3	39.8 ^a ± 0.4

^{a,b} Values with different superscripts differ significantly ($P < 0.05$)

Table 6 Effect of *CYP17* genotype on fleece traits of the Angora ewes from second shearing until adult age

Trait	H_e	H_u	H_o
Fleece weight: 2 nd shearing (kg)	1.29 ± 0.14	1.23 ± 0.13	1.22 ± 0.14
Fibre diameter: 2 nd shearing (µm)	26.3 ± 0.7	26.5 ± 0.7	26.3 ± 0.7
Fleece weight: 3 rd shearing (kg)	1.35 ± 0.06	1.33 ± 0.05	1.34 ± 0.06
Fibre diameter: 3 rd shearing (µm)	28.2 ± 0.5	28.4 ± 0.5	28.6 ± 0.6
Adult fleece weight: winter shearing (kg)	1.35 ^a ± 0.03	1.27 ^b ± 0.02	1.24 ^b ± 0.03
Adult fibre diameter: winter shearing (µm)	32.2 ^a ± 0.3	32.7 ± 0.2	33.0 ^b ± 0.3
Style of fleece: winter shearing	2.97 ± 0.04	2.92 ^b ± 0.04	3.04 ^a ± 0.07
Character of fleece: winter shearing	3.01 ± 0.04	2.98 ± 0.04	2.93 ± 0.06

^{a,b} Values with different superscripts differ significantly ($P < 0.05$)

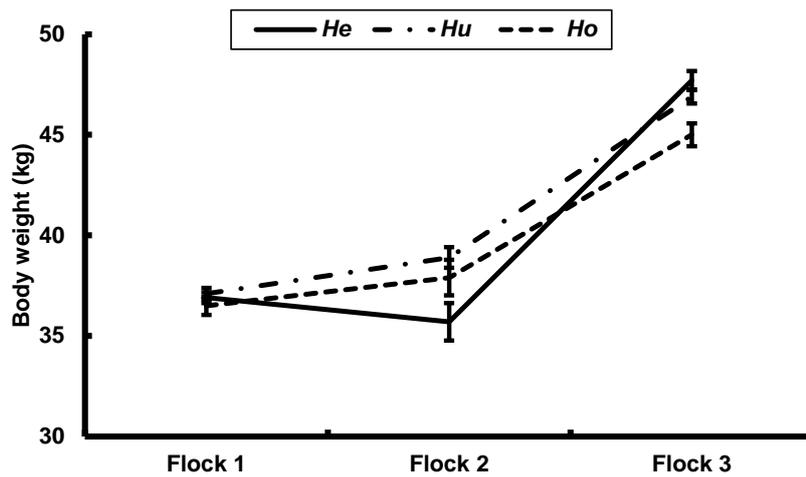


Figure 1 Interaction between flock and *CYP17* genotype for adult bodyweight

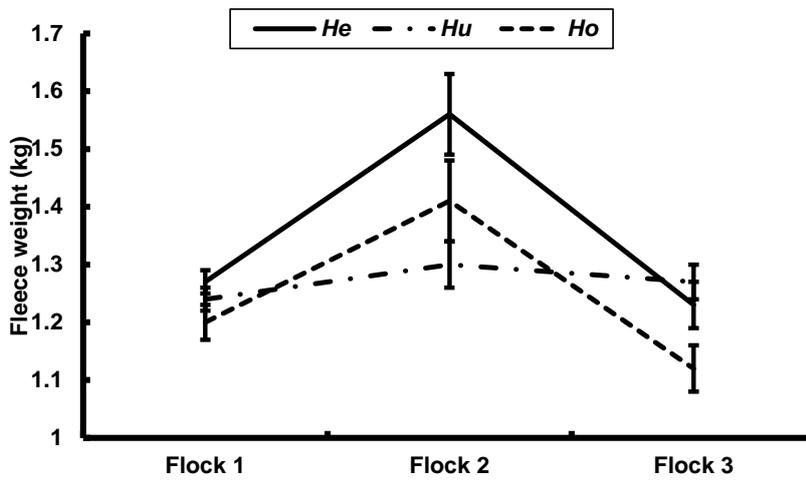


Figure 2 Interaction between flock and *CYP17* genotype for adult fleece weight

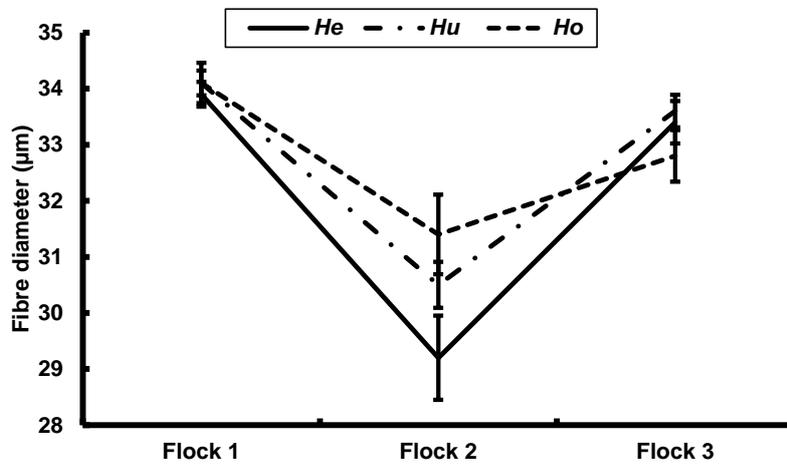


Figure 3 Interaction between flock and *CYP17* genotype for adult fibre diameter

The effect of genotype on the reproductive performance of ewes is presented in Table 7. The H_o and H_e genotypes had the lowest and highest number of kids born and weaned per year, respectively, while H_u ewes had the best lifetime flock reproductive performance. However, none of these recorded differences in reproductive performance among the genotypes were significant.

Table 7 Effect of *CYP17* genotype on reproduction of the Angora ewes

Trait	H_e	H_u	H_o
From individual reproduction records			
Total weight of kids weaned / year (kg)	18.3 ± 1.0	18.2 ± 0.8	18.1 ± 1.1
Number of kids born / year	1.07 ± 0.05	1.06 ± 0.04	1.03 ± 0.06
Number of kids weaned / year	0.93 ± 0.06	0.90 ± 0.04	0.89 ± 0.06
From lifetime flock reproduction			
Number of kidding opportunities	4.64	4.23	4.44
Total weight of kid weaned / lifetime (kg)	68.3 ± 4.4	72.1 ± 2.8	67.42 ± 4.9
Number of kids born / lifetime	4.71 ± 0.22	4.72 ± 0.14	4.39 ± 0.25
Number of kids weaned / lifetime	3.77 ± 0.24	3.83 ± 0.15	3.58 ± 0.26

The effect of genotype on the number of kids born in the various flocks in terms of percentage of ewes of each genotype which gave birth to either 0, 1, 2 or 3 kids is summarised in Table 8. For each flock, within each genotype, the percentage of ewes for all number of kids born categories adds up to 100%.

Table 8 Effect of *CYP17* genotype on number of kids born in Flocks 1, 2 and 3

Flock / Number of kids born	H_e	H_u	H_o
Percentage of ewes of a specific genotype that had x number of kids			
Flock 1 ($P = 0.131$)			
0	12.93	11.16	7.09
1	66.20	71.19	68.79
2	19.47	17.04	23.40
3	1.40	0.60	0.71
Flock 2 ($P = 0.142$)			
0	26.67	29.41	51.52
1	70.00	68.07	48.48
2	3.33	2.52	0.0
Flock 3 ($P = 0.060$)			
0	8.25	3.85	0.0
1	49.48	61.54	59.68
2	42.27	34.62	40.32
Pooled ($P = 0.142$)			
0	12.87	11.82	11.44
1	64.24	68.79	63.56
2	21.72	18.99	24.58
3	1.17	0.40	0.42

No significant trend was observed in Flock 1. In Flock 2 approximately 20 to 25% more H_o ewes did not give birth to any kids, compared to the H_u and H_e genotypes, while approximately 20% fewer H_o ewes gave birth to 1 kid. In Flock 3 there were no H_o ewes that did not produce a kid. Looking at the pooled data, there was no difference among the genotypes in terms of percentage of ewes of each genotype which gave birth to either 0, 1, 2 or 3 kids.

The effect of genotype on the number of kids weaned in the various flocks in terms of percentage of ewes of each genotype which weaned either 0, 1, 2 or 3 kids is summarised in Table 9. There was no significant trend observed in Flock 1, and ewes were spread evenly among genotypes in terms of number of kids weaned category. In Flock 2 more H_o ewes did not wean a kid compared to the H_e and H_u genotypes. Furthermore, fewer H_o ewes weaned 1 kid and none weaned 2 kids. In Flock 3 fewer H_o ewes weaned 0 kids, while no definite trend was observed among genotype for ewes weaning either 1 or 2 kids. As was the case with number of kids born, again there was no difference in the pooled data among the genotypes in terms of percentage of ewes of each genotype which weaned 0, 1, 2 or 3 kids.

Table 9 Effect of *CYP17* genotype on number of kids weaned in Flocks 1, 2 and 3

Flock / Number of kids weaned	H_e	H_u	H_o
	Percentage of ewes of a specific genotype that weaned x number of kids		
Flock 1 ($P = 0.655$)			
0	24.61	22.62	20.57
1	63.40	65.91	68.09
2	11.99	11.16	11.35
3	0.0	0.30	0.0
Flock 2 ($P = 0.377$)			
0	50.00	47.90	66.67
1	46.67	49.58	33.33
2	3.33	2.52	0.0
Flock 3 ($P = 0.131$)			
0	13.40	17.79	6.45
1	51.55	56.25	59.68
2	35.05	25.96	33.87
Pooled ($P = 0.772$)			
0	24.19	24.65	23.31
1	61.25	61.92	61.02
2	14.56	13.23	15.68
3	0.0	0.20	0.0

The effect of genotype on the occurrence of ewes that did not kid and ewes that aborted in the various flocks is summarised in Table 10. For these calculations, ewes that did not kid included ewes that aborted. No definite trend could be observed across the flocks. In Flock 1, no differences were recorded among genotypes, while in Flock 2, significantly more H_o ewes did not kid than ewes of the other genotypes. In Flock 3, there were significantly more H_e ewes that did not kid, while all the H_o ewes kidded. In the pooled data, no significant differences among genotypes were recorded. As far as abortions are concerned, no significant differences were observed among the genotypes, although the H_u ewes had the most abortions in Flocks 2 and 3 and in the pooled data.

Table 10 Effect of *CYP17* genotype on the occurrence of ewes that did not kid or aborted in Flocks 1, 2 and 3

Flock	H_e	H_u	H_o
	Percentage of ewes of a specific genotype that did not kid		
Flock 1 ($P = 0.133$)	12.93	11.16	7.09
Flock 2 ($P = 0.042$)	26.67	29.41	51.52
Flock 3 ($P = 0.039$)	8.25	3.85	0.0
Pooled ($P = 0.745$)	12.87	11.82	11.44
	Percentage of ewes of a specific genotype that aborted		
Flock 1 ($P = 0.838$)	2.18	1.96	1.42
Flock 2 ($P = 0.951$)	10.00	10.92	9.09
Flock 3 ($P = 0.491$)	1.03	1.92	0.0
Pooled ($P = 0.578$)	2.34	3.03	2.12

The effect of genotype on the occurrence of stillborn kids and kids that died soon after birth is presented in Table 11. No major differences were recorded among genotypes, except for Flock 2 where the only recorded stillborn kids were from ewes of the H_u genotype.

Table 11 Effect of *CYP17* genotype on the occurrence of stillborn kids and kids that died soon after birth in Flocks 1, 2 and 3

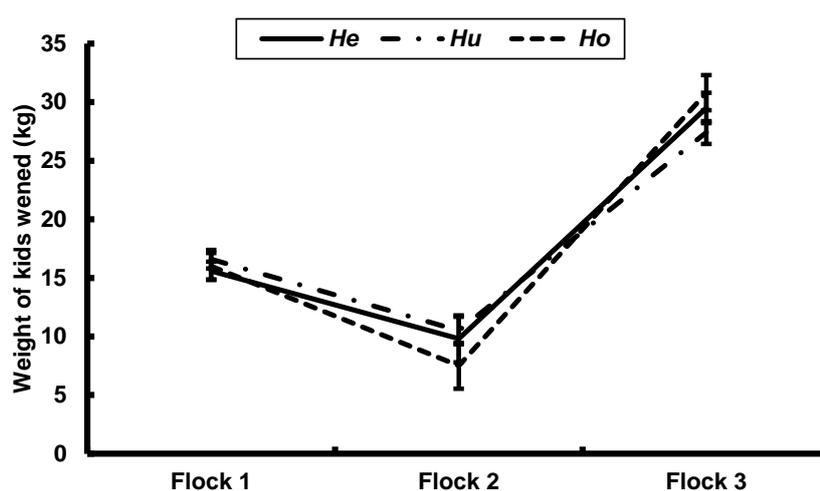
Flock	H_e	H_u	H_o
	Percentage of ewes of a specific genotype that had stillborn kids		
Flock 1 ($P = 0.794$)	2.18	2.71	2.84
Flock 2 ($P = 0.585$)	0.0	1.68	0.0
Flock 3 ($P = 0.839$)	3.09	2.40	1.61
Pooled ($P = 0.882$)	2.21	2.53	2.12
	Percentage of ewes of a specific genotype that had kids that died soon after birth		
Flock 1 ($P = 0.557$)	3.74	2.71	2.84
Flock 3 ($P = 0.629$)	1.03	1.44	0.0
Pooled ($P = 0.225$)	3.25	2.12	1.69

The effect of genotype on the occurrence of kids being fostered or reared as orphans in the various flocks is summarised in Table 12. The highest percentage of kids that had to be fostered was born to H_o ewes in Flock 1. Most kids that had to be reared as orphans were also born to H_o ewes in Flock 1. All orphans in Flock 3 were born to H_e ewes.

There was a significant interaction between flock and genotype in the reproductive traits. This interaction for total weight of kids weaned ($P < 0.0371$) is illustrated in Figure 4. There was no significant difference in weight of kids weaned among the genotypes in Flock 1, while H_o ewes weaned the lowest weight of kids in Flock 2 ($P > 0.05$) and the H_u ewes weaned the lowest weight of kids ($P < 0.05$) in Flock 3 (Figure 4). The same trends were observed for number of kids born and number of kids weaned.

Table 12 Effect of *CYP17* genotype on the occurrence of kids being fostered or reared as orphans Flocks 1 and 3

Flock	H_e	H_u	H_o
	Percentage of ewes of a specific genotype that had kids being fostered		
Flock 1 ($P = 0.042$)	2.34	0.75	2.84
	Percentage of ewes of a specific genotype that had kids being reared as orphans		
Flock 1 ($P = 0.661$)	3.43	2.87	4.26
Flock 3 ($P = 0.248$)	1.03	0.0	0.0
Pooled ($P = 0.343$)	2.99	1.92	2.54

**Figure 4** Interaction between flock and *CYP17* genotype for total weight of kids weaned

The distribution of the veld rams across the genotypes is summarised in Table 13. As was the case with the ewes, the highest percentage of the veld rams had the H_u genotype, while the H_o genotype was the least represented. The H_u genotype was also the most abundant among the Flock 5 sires, while the H_e genotype was the most abundant among the Flock 4 sires. All genotypes were equally represented among the Flock 1 sires.

Table 13 Number (%) of animals per *CYP17* genotype among the sires from Flocks 1, 4 and 5, as well as the Angora veld rams

Genotype	Flock 1 sires	Flock 4 sires	Flock 5 sires	Veld rams
H_e	6 (33.3)	11 (45.8)	2 (25.0)	73 (38.0)
H_u	6 (33.3)	4 (16.7)	4 (50.0)	89 (46.4)
H_o	6 (33.3)	9 (37.5)	2 (25.0)	30 (15.6)
Total	18	24	8	192

Testosterone levels of Angora rams from Flocks 1, 4 and 5 and the Angora veld rams are summarised in Table 14 for the three genotypes. No significant differences were observed in testosterone levels between rams of the three genotypes in any of the flocks. There was a significant difference when comparing the testosterone levels of rams from Flock 4 ($P < 0.01$) to those from Flock 1 and Flock 5 (Figure 5).

Testosterone levels of the rams from Flock 4 were approximately 4 times higher than those from Flocks 1 and 5.

Table 14 Testosterone levels of Angora rams from Flocks 1, 4 and 5, as well as the Angora veld rams

Genotype	Flock 1 sires	Flock 4 sires	Flock 5 sires	Pooled (1,4,5)	Veld rams
H_e	14.42 ± 10.17	35.63 ± 7.51	8.32 ± 17.61	19.46 ± 7.23	8.21 ± 2.79
H_u	13.26 ± 10.17	44.80 ± 12.45	8.79 ± 12.45	22.28 ± 6.78	11.44 ± 2.79
H_o	9.15 ± 10.17	41.66 ± 8.30	17.16 ± 17.61	22.66 ± 7.32	8.74 ± 2.79

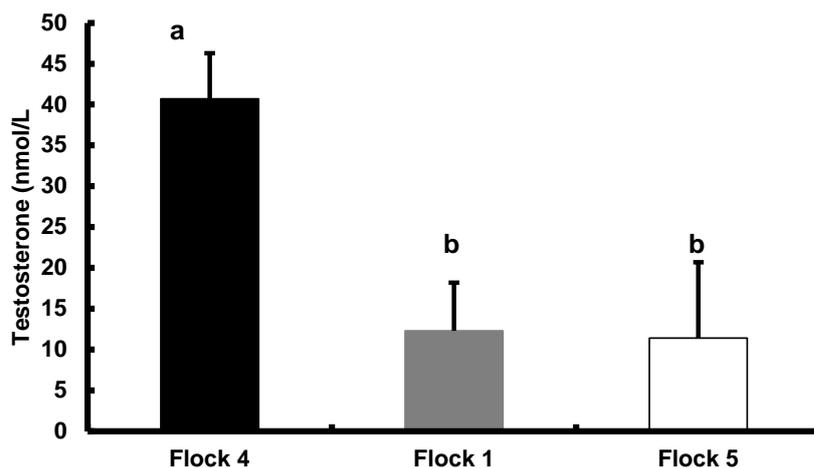


Figure 5 Comparison of testosterone levels of Angora rams from Flocks 1, 4 and 5 (a, b levels differed significantly between flocks ($P < 0.05$))

Discussion

The distribution of the ewes across the three *CYP17* genotypes of 36.7% for H_e , 51.5% for H_u , and 11.8% for H_o is in accordance with that of the Angora veld rams in which 38.0% rams had a H_e , 46.4% a H_u , and 15.6% a H_o genotype. The sample size from the other localities was much smaller and could thus not be regarded as representative of the population. However, the high proportion H_o sires used in Flock 1 and Flock 4 indicates that a higher proportion of H_o sires were selected, as the H_o genotype only comprised 10% of the ewes in Flock 1. The current distribution differs somewhat from earlier genotyping using a different genotyping method (HybProbe method), where 42.9% H_e , 40.6% H_u , and 16.5% H_o animals were observed (Storbeck *et al.*, 2011). However, this previous method could not always accurately distinguish between H_e and H_u genotypes. An 80% correlation between the two genotyping methods was observed (Swart, 2011).

In a random mating population with the same number of H_e , H_u and H_o animals, in which all possible matings among the genotypes have an equal opportunity of taking place, four of each possible six matings would yield H_u genotypes as one of the progeny genotypes. Over the years, this could have contributed to the occurrence that the H_u animals are the most abundant in most of the flocks.

In this study, animals of the H_u genotype were heavier from weaning age onwards, although this difference in bodyweight was significant only at eight months old and in the adult ewes. No differences were observed between the H_e and H_o animals. These results are in accordance with preliminary results found for the fine hair goats kept at the Jansenville Experimental Station that were born between 2000 and 2008, which included 117 H_e , 119 H_u , and 62 H_o animals. No significant differences in bodyweight were observed among the genotypes for these ewes genotyped with the earlier method (Storbeck *et al.*, 2011). This preliminary study is the only one that is available in which the production performance of Angora *CYP17* genotypes was evaluated. No other literature studies could be found that related *CYP17* isoforms to production traits in goats or sheep.

In the current study, adult ewes of the H_e genotype produced the heaviest fleeces with the lowest fibre

diameter. In the earlier study on fine hair ewes, no significant differences in any of the fleece traits were observed among the genotypes (Storbeck *et al.*, 2011).

In the current study, no significant differences were recorded in reproductive performance among the genotypes, although the H_o ewes had the lowest (1.03 and 0.89) and the H_e ewes the highest (1.07 and 0.93) number of kids born and weaned per year, respectively. In a preliminary study, 98 ewes of Flock 1 were genotyped with the method used in the current study. In this earlier study, 62.5% of the H_o ewes were poor reproducers, while the H_u and H_e groups had 35% and 42% poor producers, respectively. Ewes were classified as poor reproducers when they weaned fewer kids than they had kidding opportunities. However, only eight ewes with H_o genotypes were identified in the sample group and there was no significant difference between the H_o and other genotypes (Swart, 2012). Hough (2012) also reported that reproduction of Merino sheep seemed to be unaffected by the *CYP17* genotype.

Results of the rams indicated that the *CYP17* genotype had no effect on testosterone production by Angora rams. The observation that the testosterone levels of the rams from Flock 4 were approximately four times higher than those from Flocks 1 and 5 could be because Flock 4 rams were kept under kraal conditions on a high protein and high energy diet, while the rams from Flocks 1 and 5 were kept under veld conditions.

Angora stud breeders use different selection indices, in which emphasis is placed on fibre diameter, fleece weight and bodyweight in varying ratios (Snyman *et al.*, 1996; Snyman & Olivier, 1996). Snyman (2002) concluded that selection for decreased fibre diameter, while maintaining or increasing bodyweight and fleece weight, led to genetic improvement of these traits in South African Angora goats. This has led to a decrease in the fibre diameter of the South African clip. The clip composition changed from 51% strong adult mohair, 17% fine adult mohair, 15% young goat mohair and 17% kid mohair in 2001 (Mohair South Africa, 2005) to 33% strong adult mohair, 26% fine adult mohair, 23% young goat mohair and 19% kid mohair in 2015 (SAMGA, 2016). Recently, many breeders have moved away from putting too much emphasis on fibre diameter, arguing that it has reached sufficiently fine levels, to selecting strategies in which more emphasis is placed on fleece weight.

The aim of the current study was to determine if preference were given to a specific genotype, H_e for example, would there be a detrimental effect on production or reproduction? The results have indicated that there were no significant effects of genotype on production or reproduction, which is a positive finding in this case. Thus it does not matter which *CYP17* genotype Angora producers select for. Production and reproduction would not be adversely affected. Selection for production and reproduction traits could continue independently of the selection for a specific *CYP17* genotype if producers want to incorporate selection for hardiness into their breeding programme.

The *CYP17* genotype exerts its effect on the stress coping ability of the animal via cortisol production in the adrenal cortex. The H_e *CYP17* genotype was previously identified as the hardest genotype pertaining to stress coping ability in the Angora goat. For breeders interested in incorporating the *CYP17* genotype into their selection strategy, it is recommended that all H_o genotype rams should be culled as a first step. Preferably only H_e sires should be used. Because the H_u genotype is in abundance in most of the flocks, it would not be feasible to cull possible H_u sires with desirable production characteristics. These sires, however, should be mated only to H_e genotype ewes, as these matings would yield only H_e and H_u genotype offspring. Mating of H_u sires to H_o ewes would yield H_o and H_u progeny, while a mating between a H_u sire and H_u ewes would yield H_o , H_u and H_e progeny. It is not possible to get rid of the ACS- gene, as all the animals possess it. An effort, however, could be made to decrease the number of animals that do not have the ACS+ gene (the H_o genotype), thereby increasing the frequency of the ACS+ gene in the population.

Conclusions

From the results of this study, no evidence could be found that selection for any of the three genotypes would adversely affect any growth, mohair production or reproduction function of Angora ewes. The *CYP17* genotype had no observable effect on the reproductive fitness of rams, as measured by testosterone production. A breeding strategy could be followed that incorporated selection for productive traits and the *CYP17* genotype, aimed at increasing the frequency of the ACS+ gene and thus the H_e genotype in the population, without negatively impacting on genetic progress in the productive traits.

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Authors' contributions

MAS: drafting of project proposal, identification and selection of samples, data preparation and data analyses, writing of manuscript. K-HS: genotyping of samples, assisting with drafting of project proposal and writing of manuscript,

final reviewing of manuscript. PS: assisting with drafting of project proposal, reviewing of manuscript.
All authors read and approved the final manuscript.

Conflict of Interest Declaration

None of the authors have any conflicts of interest to declare.

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