# Quantitative trait loci associated with pre-weaning growth in South African Angora goats

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**Abstract**

This study aimed to identify chromosomal regions associated with genetic variation in pre-weaning growth traits in Angora goats. A genome-wide scan was performed by genotyping 1042 offspring from 12 half-sib families using 88 microsatellite caprine markers covering 1368cM. Phenotypes were recorded at birth (BW) and weaning (WW) and analysed using GridQTL software. A total of six putative QTL were detected on six different chromosomes, all at chromosome-wide significance level. Four QTL were identified for BW on CHI 4, 8, 17 and 27 and two QTL for WW on CHI 16 and 19. QTL effects ranged from -0.32 to 0.25 in units of residual standard deviation in different families. Some of these QTL correspond to chromosomes where QTL associated with growth have been identified in other species. These chromosomal segments hold potential to influence weight gain in young goats.

**Keywords:** MAS, microsatellite markers, pre-weaning growth, QTL

## Introduction

Genetic improvement based on the selection of quantitative traits still presents challenges with regard to low heritable traits, sex-limited traits and those difficult and expensive to measure (Pollak, 2005; Dodds *et al.,* 2007). In the selection of Angora goats, breeders are faced with the unfavourable positive genetic correlation between body weight and fibre diameter (Snyman *et al.,* 1996; Snyman, 2002; Swan *et al.,* 2008). Over many decades, South African Angora goats have been

intensely selected for increased fine mohair production, resulting in a decrease in fibre diameter and an increase in yield. Body weight was however compromised leading to smaller, unthrifty animals with an inability to survive sub-optimum conditions. To mitigate this, breeding objectives and selection criteria used by breeders were reviewed in the 1990s (Snyman *et al*., 1996; Snyman & Olivier, 1996). A selection index (SI) aimed at increasing body weight, decreasing fibre diameter and maintaining fleece weight was developed for application by the stud breeders (Snyman *et al*., 1996; Snyman & Olivier, 1996). In 2002 this 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, was a feasible option for the genetic improvement of fleece traits in South African Angora goats.

Despite the use of the above-mentioned SI, the South African Angora industry is still hampered by the severe loss of young, especially newly shorn goats (Storbeck *et al.,* 2009). Survival rate of kids are one of the most important factors influencing economic viability of an Angora goat production unit. The survivability of young animals 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 South African 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). This problem could be moderated by management practices, but selection for genetic improvement of the trait should result in a long-term solution.

Body weight is also directly related to the reproductive ability of young does. The body weight and growth rate of Angora kids under different management systems were evaluated by Snyman (2007), who found that post-weaning growth rate of kids without supplementary feeding was unacceptably low. Most farmers do not supply ewe kids with supplementary feeding after weaning, due to the direct financial implication. This results in many young does not reaching the target weight of 25kg at 18 months and a low conception rate when they are mated for the first time. Snyman (2012) reported genetic correlation between weights at different ages for Angora goats, ranging from 0.36 between birth and weaning weight to 0.57 between birth and 16-month weight. These estimates

were somewhat lower than what has previously been found in wool sheep, but increased for weaning weight with later age stages (0.73 to 0.93). Genetic correlations of respectively 0.69 and 0.81 between weight at 3 months, weight at 6 months and weight at 12 months were found in Menz sheep by Gizaw *et al*. (2007). Estimates of 0.80 were also reported by Mandal *et al.* (2009) between weight at 6 months and yearling weight in Muzaffarnagari sheep, and 0.73 between weights at weaning and yearling age in Merino sheep (Swan *et al.,* 2008). These correlations indicate that selection for increased birth and weaning weight should result in higher mature weight and improved reproduction rates of young does.

While body weight at either 8 or 16 months is currently incorporated in the Angora goat selection index, it is unlikely that another (earlier) body weight will be included, as this will detract selection intensity from fleece characteristics. Although inter-age genetic correlations for body weight are strongly positive, this correlation decreases as time between measurements increases, indicating separate QTL that govern different growth stages (Hadjipavlou & Bishop, 2008). Snyman (2012) reported that no increase in direct or maternal birth weight was found over the past ten years in South African Angora goat stud herds making use of the current SI. This emphasises the need to identify chromosomal segments of interest for birth and weaning weight in order to improve survivability and reproduction efficiency.

The development of DNA technology and sequencing of farm animal genomes, including the goat genome have created new opportunities for studying traits of economic importance (Dekkers, 2004). To date molecular studies in goats have been limited to mainly genetic diversity studies using microsatellite markers (Iamartino *et al.,* 2005; Kumar *et al.,* 2005; Gour *et al.,* 2006; Qi *et al.,* 2009; Visser & Van Marle-Koster, 2009), parentage verification (Luikart *et al.,* 1999; Ganai & Yadav, 2005; Glowatzki-Mullis *et al.,* 2007; Bolormaa *et al.,* 2008; De Araujo *et al.,* 2010; Visser *et al.,* 2011b) and identification of QTL for fibre traits (Cano *et al.* 2007 & 2009; Mohammed Abadi *et al.* 2009; Debenedetti *et al.* 2010; Visser *et al*. 2011a) in different breeds. DNA marker information will assist conventional selection by increasing selection accuracy and improving the rate of genetic improvement, as well as leading to a better understanding of the physiological background of quantitative traits (Pollak, 2005; Jeon *et al.,* 2006; Dodds *et al.,* 2007). The selection for

chromosomal areas that directly contribute to the genetic variation of traits of economic importance will lead to increased genetic progress and offers the opportunity to better understand and exploit phenotypic variation (Dekkers, 2004).

Very limited information has however been published with regards to chromosomal fragments associated with growth traits in goats. QTL for birth and weaning weight were reported by Mohammed Abadi *et al.* (2009) in Rayini goats, while Marrube *et al.* (2007) failed to detect any QTL associated with weaning weight in Angora goats. QTL affecting growth traits have been reported in various sheep breeds (McRae *et al.,* 2005; Hadjipavlou & Bishop, 2008; Esmailizadeh, 2010), but still need to be validated in goat breeds. The aim of this study was to identify QTL associated with pre-weaning growth in South African Angora goats.

## Materials and Methods

### *Animals and phenotypic data:*

The data resource consisted of a total of 1042 offspring from twelve Angora bucks originating from four different farms. Family sizes were on average 87 and ranged between 43 and 132 offspring per sire. Families were generated over a three-year period (2004 – 2006) during which blood samples were routinely collected and stored in a DNA bank for small stock research (Grootfontein Agricultural Development Institute, National Department of Agriculture). Phenotypes were recorded at birth (BW) and weaning (4 months - WW).

### *DNA and genotyping:*

DNA extraction and the selection of a microsatellite panel for genome coverage were the same as that described by Visser *et al.* (2011a). A total of 88 microsatellite markers were finally selected for genotyping. PCR reactions were performed in a 384 well i-cycler (Bio-rad) or Ti Thermocycler (Biometra) in a 6µl final volume using 100ng DNA, 2.94 µl of the ABgene® PCR Master Mix (ABGene, UK) and 0.03 µl reverse and forward primer each of 40pmol/µl. The PCR amplification was conducted at the following conditions: 95°C for 5 minutes, followed by 35 cycles of 96°C for 30s, 45s at annealing temperature and 90s at 72°C with a final extension step of 10min at

72°C. PCR products were analysed using an automated ABI 373/377 sequencer (Perkin-Elmer) and allele calling was performed with GeneMapper (Applied Biosystems).

***Statistical analysis:***

Phenotypic records were pre-adjusted for herd (levels 1-4), year of birth (2004, 2005 or 2006), birth status (single or twin) and sex. QTL analysis was performed using half-sib regression (Knott *et al.,* 1996) as implemented in the GridQTL software (Seaton *et al.,* 2006). The following least-squares regression model used was:

$$y_{ij} = Sire_i + \beta_i x_{ij} + e_{ij}$$

where $y_{ij}$ is the phenotype (corrected for fixed effects) of individual $ij$, offspring of sire $i$,

$Sire_i$ is the mean of sire family $i$,

$\beta_i$ is the allele substitution effect of the QTL within family $i$,

$x_{ij}$ is the probability that the animal $ij$ inherited the first allele of sire $i$ and

$e_{ij}$ is the residual.

The 10 000 permutations were used to generate a test-statistic under the null hypothesis and to determine thresholds for both chromosome-wide and experiment-wide Type 1 error rates. The confidence intervals of the QTL locations were estimated using 2 000 bootstraps. The QTL variance was calculated according to Knott *et al.* (1996).

**Results:**

The descriptive statistics for birth weight (BW) and weaning weight (WW) of the 12 families belonging to four different breeders are shown in Table 1. Family 5 had the highest average body weight at birth (3.48 kg) while family 12 had the lowest BW (2.68 kg on average). The heaviest weaning weights were recorded for kids in Family 6 (Average WW = 24.16) No birth weights were however recorded for this family.

**Table 1** Descriptive statistics for growth traits of 12 Angora goat half-sib families

| Breeder | Family | n* | BW (kg) | n | WW (kg) |
|---|---|---|---|---|---|
| A | 1 | 84 | 3.20±0.56 | 84 | 15.67±4.43 |
| | 2 | 106 | 3.16±0.57 | 103 | 15.06±3.79 |
| | 3 | 99 | 3.14±0.51 | 98 | 15.63±3.67 |
| | 4 | 105 | 3.15±0.46 | 104 | 16.77±4.04 |
| B | 5 | 106 | 3.48±0.54 | 132 | 21.71±3.50 |
| | 6 | - | - | 80 | 24.16±4.09 |
| C | 7 | 52 | 3.34±0.56 | 51 | 17.53±3.82 |
| | 8 | 92 | 3.44±0.53 | 85 | 18.06±3.54 |
| | 9 | 103 | 3.32±0.60 | 103 | 17.09±3.80 |
| | 10 | 81 | 3.36±0.60 | 76 | 18.87±3.66 |
| D | 11 | 40 | 2.73±0.33 | 43 | 17.65±5.27 |
| | 12 | 62 | 2.68±0.29 | 65 | 16.13±3.57 |
| | Average | | 3.18±0.50 | | 17.86±3.93 |

*Number of records measured per trait

Families 5 and 6, both from breeder B, had the highest means for WW, while Family 5 also had the highest mean for BW. Families 1, 2 and 3 were poor performers in WW. Although Families 11 and 12 showed the lowest BW, they improved with later measurement and were heavier than Families 1-3 at weaning.

Based on the most recently published goat linkage map (Visser *et al*., 2010), a total of 1368cM of the goat genome was covered with 88 microsatellite markers. An average of four markers per chromosome was used. Only one chromosome had only two markers (CHI14), while CHI 5 was the most densely populated with seven markers (Table 2). The proportion of heterozygous sires averaged over all markers per chromosome ranged between 0.53 (CHI8) and 0.81 (CHI25).

**Table 2** Goat genome coverage by chromosome

| CHI | N markers | CHI length | Proportion of heterozygous sires | IC[a] | Markers (position in cM)* |
|---|---|---|---|---|---|
| 1 | 6 | 127 | 0.57 | 0.35 | BM1312 (0), BM3205 (39), CSSM19 (45), CSSM32 (92), MAF64 (113), INRA11 (137) |
| 2 | 4 | 61 | 0.54 | 0.40 | BMS2782 (0), OARFCB11 (1), INRA40 (11), SRCRSP24 (62) |
| 3 | 4 | 74 | 0.71 | 0.47 | CSSM54 (0), MCM58 (30), INRA3 (58), INRA6 (74) |
| 4 | 6 | 129 | 0.75 | 0.50 | OARHH64 (0), OARCP26 (41), MAF50 (50), |

| | | | | | |
|---|---|---|---|---|---|
| | | | | | *OARHH35 (82),* BMS1788 (97), MAF70 (129) |
| 5 | 7 | 121 | 0.57 | 0.42 | OARFCB5 (0), *LSCV25 (12),* BMS1248 (15), BM2830 (65), BMC1009 (90), ILSTS34 (100), BM321 (121) |
| 6 | 6 | 81 | 0.71 | 0.58 | BM143 (0), BM415 (18), BM1329 (39), BM4621 (67), ILSTS087 (74), SRCRSP08 (81) |
| 7 | 3 | 27 | 0.75 | 0.46 | INRABERN192 (0), *OARAE129 (18),* MCM527 (27) |
| 8 | 3 | 26 | 0.53 | 0.57 | *CSSM47 (0),* MCM64 (8), SRCRSP10 (26) |
| 11 | 3 | 41 | 0.58 | 0.36 | INRA177 (0), OARCP34 (4), ILSTS45 (41) |
| 12 | 5 | 77 | 0.67 | 0.50 | BMS712 (0), INRA5 (24), BMS2252 (43), SRCRSP9 (59), ILSTS33 (77) |
| 13 | 3 | 31 | 0.61 | 0.44 | IL2RA (0), BMC1222 (25), ILSTS59 (31) |
| 14 | 2 | 111 | 0.54 | 0.56 | BM4630 (0), ILSTS11 (11) |
| 16 | 3 | 68 | 0.75 | 0.39 | BM719 (0), BM121 (18), *HUJ614 (68)* |
| 17 | 4 | 57 | 0.75 | 0.52 | OARVH98 (0), OARFCB48 (17), ILSTS58 (51), BM8125 (57) |
| 18 | 3 | 26 | 0.72 | 0.64 | INRA210 (0), *INRA63 (11),* MCM104 (26) |
| 19 | 4 | 55 | 0.65 | 0.40 | MCM210 (0), BMS745 (33), LSCV36 (44), *OARFCB193 (46)* |
| 20 | 4 | 77 | 0.75 | 0.44 | MAF214 (0), TGLA304 (11), BM1225 (32), BM3517 (60) |
| 23 | 5 | 40 | 0.73 | 0.63 | OARCP73 (0), OLA-DRB (8), BM1818 (19), DRBP1 (26), BM1258 (40) |
| 24 | 3 | 41 | 0.69 | 0.48 | MCM136 (0), BMS1332 (38), BMS2526 (41) |
| 25 | 3 | 26 | 0.81 | 0.51 | BP28 (0), INRA206 (12), TGLA40 (26) |
| 26 | 4 | 42 | 0.77 | 0.69 | HEL11 (0), INRABERN172 (14), LSCV52 (22), LSCV46 (42) |
| 27 | 3 | 30 | 0.78 | 0.55 | BM6526 (0*), CSSM43 (8),* TGLA179 (30) |

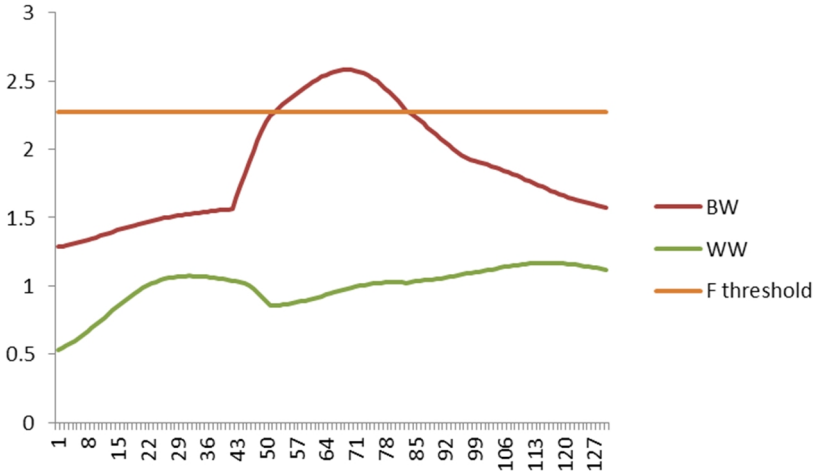
* Closest marker(s) to putative QTL in italics

The putative QTL identified in this study are shown in Table 3. Four chromosomal regions of interest with an influence on BW were identified on CHI 4, 8, 18 and 27. Analyses indicated two candidate regions for WW on CHI 16 and 19 respectively. All the putative QTL were identified at chromosome-wide significance levels ($P<0.05$) using across-family analyses.

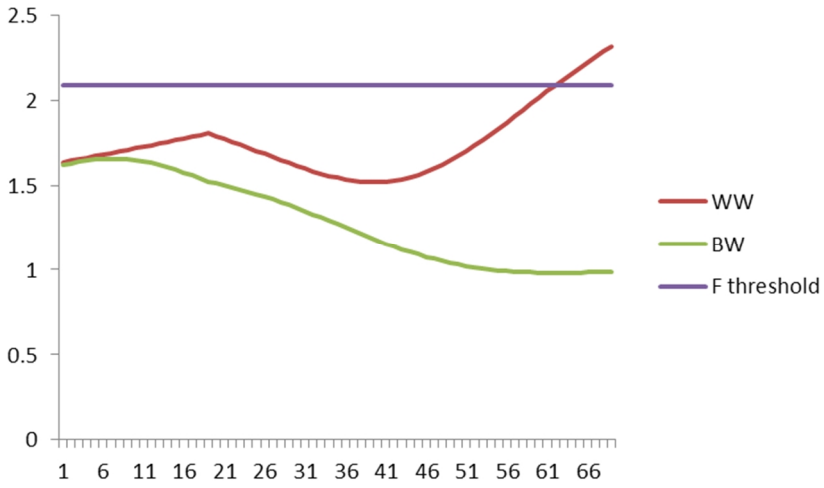
**Table 3** Putative QTL identified for pre-weaning growth traits

| Trait | CHI | Position (cM) | *F* Statistic | *F* Threshold | Segregating family | n | Effect / SD | Variance (%) |
|---|---|---|---|---|---|---|---|---|
| BW | 4 | 68 | 2.58 | 2.27 | 5 | 106 | -0.32 | 7.62 |
| BW | 8 | 0 | 2.03 | 2.04 | 2 | 106 | -0.01 | 5.22 |
| BW | 18 | 17 | 2 | 1.98 | 9 | 103 | -0.21 | 4.85 |
| BW | 27 | 6 | 2.27 | 1.99 | 5 | 106 | 0.25 | 6.17 |
| WW | 16 | 68 | 2.32 | 2.09 | 1 | 84 | -0.17 | 7.04 |
| WW | 19 | 46 | 2.3 | 2.09 | 12 | 65 | 0.04 | 6.54 |

The estimates of QTL contributions to the phenotypic variance ranged from 4.85% to 7.62% for BW on CHI18 and 4, respectively. All QTL variance estimates were lower than 8%. The QTL effects (scaled by the standard deviation of the trait) varied from -0.32 to 0.25 standard deviation units for different traits and families. The plot of the F-statistics for CHI 4 is shown in Figure 1.




CHI 4 in cM




CHI 16 in cM

**Figure 1** F-statistics depicting the locations of putative QTL for BW and WW.

**Discussion:**

The phenotypic averages of the kids for pre weaning growth traits were in the same range as previously reported in South African Angora goats. Birth weight of Angora goat kids under different

management systems have been noted to vary from 2.55kg to 3.21kg and that of weaning weight between 14.7kg and 20.5kg (Snyman, 2010).

Four chromosomal regions associated with BW were identified on CHI 4, 8, 18 and 27 in this study. Mohammed Abadi *et al.* (2009) reported a putative QTL for BW on CHI 5 in Rayini goats, while QTL associated with birth weight in sheep has been detected on OAR 14 (corresponding to CHI18) in Scottish Blackface sheep (Hadjipavlou & Bishop, 2008) and on OAR 3 in Merino sheep in a scan including OAR 1, 3, 4 and 11(Roldan *et al.* (2010). In a partial genome scan on Kermani sheep, Esmailizadeh (2010) however identified QTL for birth weight on three chromosomes namely, OAR 1, 3, and 6 (corresponding to CHI 1 and 3, CHI 5 and 1 and CHI 6 respectively). In cattle putative QTL associated with dystocia and still birth were detected on BTA 8 and 18 (corresponding to CHI 8 and 18, respectively) by Kühn *et al.* (2003) in a German Holstein population. The only gene that has been mapped to any of these regions that could possibly affect BW is the DYF gene which is associated with Dairy Form (Ashwell *et al.,* 2005) and that is located very close to marker CSSM 43. No other relevant genes have been identified in the QTL regions in cattle, sheep or humans. These fitness traits have high genetic correlations with BW and indicate that genes of interest to reproductive efficiency are possible located on these chromosomes, but are still unidentified. A number of putative QTL for BW in cattle have been identified on BTA 5 (Casas *et al.,* 2003; Gutiérrez-Gil *et al.,* 2009; Rogberg-Muñoz *et al.,* 2011) and at least two relevant genes, namely Myogenic factor 5 (*Myf5*) and Insulin-like Growth Factor 1 (*IGF1*) playing a role in growth physiology has been mapped to this chromosome (Rogberg-Muñoz *et al.,* 2011). No such association was however found on corresponding chromosome CHI 5 in the current study. It is clear that putative QTL identified for BW and other fitness traits still require verification in larger reference populations and with increased marker densities.

Putative QTL for WW were detected on CHI 16 and 19. The growth hormone gene (GH1) has been mapped to BTA 19 (corresponding to CHI 19), 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 ADG in cattle (Kneeland et al., 2004) and weight at first shearing in sheep (Roldan *et al.,*

2010). Only two studies have yet aimed to identify QTL for growth traits in goats. Mohammed Abadi *et al.* (2009) found putative QTL affecting WW on CHI 1, 2 and 5 while Marrube *et al.* (2007) failed to detect any QTL influencing WW in Argentinean Angora goats.

Usually more associations between genotypes and phenotypic traits are detected for traits with higher heritability estimates than for lower heritable traits. Identifying the polymorphisms linked to the genes controlling lowly heritable traits are more difficult and require substantially more data (Snelling *et al.,* 2010). BW and WW have a higher proportion of variance due to maternal influences compared to later-measured growth traits and thus the relative low variance estimates due to putative QTL were expected.

Currently small, unthrifty Angora kids and low reproductive efficiency in young does constitute a large problem to the Angora goat industry in South Africa. These fitness traits show a slow selection response to conventional selection and incorporation of marker assisted selection (MAS) could result in faster genetic gains. 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 (Snyman, 2012). Additional research would however first be required to decrease the confidence interval ranges significantly in order to determine the precise locations of the QTL.

The effect of QTL identified in this study explained limited variation for the trait. This has been found to be one of the main limitations of MAS in various QTL studies across livestock species (Nicholas, 2006; Hayes & Goddard, 2010). A large number of QTL with small effects contribute to the variation in complex traits, and therefore MAS is not the most effective way of facilitating genetic improvement in these traits. 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 chip has become available at a commercial level during 2012 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 increasing rate of genetic gain via MAS is currently a more feasible option.

## Conclusion

Most of the putative QTL identified in this study were localized on fairly large chromosomal segments and were only confirmed at chromosome-wide significance levels. These QTL regions need to be further investigated and narrowed down before they can contribute to the improvement of growth traits in the Angora goat industry. As this industry in South Africa is quite small, genomic selection will probably not be applied in the foreseeable future. With this in mind, genetic progress might still be accelerated by making use of alternative molecular tools like MAS.

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