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McGregor, B.A., Butler, K.L. and Ferguson, M.B. 2013, Variation in mohair staple length over the lifetime of Angora goats, *Animal production science*, vol. 53, no. 6, pp. 479-486.

DOI: [10.1071/AN12288](https://doi.org/10.1071/AN12288)

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**Available from Deakin Research Online:**

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1 Variation in mohair staple length over the lifetime of Angora goats

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15 Short title: Variation in mohair staple length

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19

1 **Abstract**

2 Previous work has shown that, within an Angora goat flock, clean fleece weight is  
3 proportional to fleece-free liveweight (FFLwt)<sup>2/3</sup> and for goats of the same age and cohort, the mean  
4 mohair fibre diameter is proportional to FFLwt<sup>1/3</sup>. This indicates that fibre length might not be related  
5 to the size of animals. This study examines how mohair staple length (SL) is related to FFLwt of  
6 Angora goats of different genetic origins over their lifetime and how the relationship varies with other  
7 lifetime factors. Measurements were made over 11 shearing periods on a population of Angora goats  
8 representing the current range and diversity of genetic origins in Australia, including South African,  
9 Texan and interbred admixtures of these and Australian sources. Records of breed, sire, dam, date of  
10 birth, dam age, birth weight, birth parity, weaning weight, liveweight, fleece growth and fleece quality  
11 were taken for castrated males (wethers) (*n*=94 animals). FFLwt were determined for each goat at  
12 shearing time by subtracting the greasy fleece weight from the liveweight recorded immediately prior  
13 to shearing. The average of the FFLwt at the start of the period and the FFLwt at the end of the period  
14 was calculated. Liveweight change (LwtCh) was the change in FFLwt over the period between  
15 shearings. A restricted maximum likelihood (REML) model was developed for SL, which allowed the  
16 observations of the same animal at different ages to be correlated in an unstructured manner. Average  
17 SL differed from about 12 cm to about 14½ cm, depending on age. There were no consistent effects of  
18 season. At any age, an increase of 10 kg LwtCh between animals results in about a 0.34 (s.e. = 0.087)  
19 cm increase in SL. There was no evidence of an effect of FFLwt on SL. The results confirm our  
20 hypothesis that within a single age cohort of Angora goats, there is very little, if any, relationship  
21 between the liveweight and staple length of individual animals. This implies that the biological  
22 determinants of size of fibres related to cross-sectional area are substantially different to the size  
23 determinants of fibre length.

24

25 **Additional keywords:** age effects, fibre morphology, liveweight, mohair production, nutrition  
26 management.

# 1 **Introduction**

2

3 The size of mohair fibres depends on the length of those fibres and the cross-sectional area along the  
4 length of the fibre. In Merino wool, fibre length is related to the length of cortical cells (Hynd 1994a)  
5 or to a change in the number of cells entering the fibre proper due to alterations in the rate of cell  
6 division or the distribution of cells to either the fibre or to the inner root sheath (Hynd 1994b). We  
7 have shown that mohair mean fibre diameter (MFD) is related to the size (liveweight) of animals  
8 within a flock, and thus the cross-sectional area will be related to the size of animal. In fact, for goats  
9 of the same age and cohort, the MFD is proportional to the cube root of animal size indicating that the  
10 mean cross-sectional area will be related to the liveweight<sup>2/3</sup> (McGregor *et al.* 2012). If fibres grow in a  
11 manner so that they maintain similar shape then fibre length would also be expected to be  
12 proportional to the cube root of liveweight, leading to an expectation of fleece weight being  
13 proportional to liveweight. On the other hand, if fibres respond to increased liveweight through  
14 increased cross sectional area but no change in fibre length, it would be expected that fleece weight  
15 would be proportional to liveweight<sup>2/3</sup>.

16 Previous work has shown that, within an Angora flock, clean fleece weight (CFwt) is  
17 allometrically related to size of the animal, measured as fleece-free liveweight (FFLwt) (McGregor *et*  
18 *al.* 2013). In particular, with goats of the same age, CFwt is proportional to FFLwt<sup>2/3</sup> when the animal  
19 is not losing or gaining FFLwt. This indicates that fibre length might not be related to size of animals  
20 of the same age and cohort. This is different to the hypothesis discussed in McGregor *et al.* (2012)  
21 which was based on fibre length being proportional to the cube root of FFLwt.

22 Whan (1972) concluded that staple length (SL) may be a useful predictor of the average fibre  
23 length in wool tops. It has been shown that straight SL bears an approximately constant ratio to mean  
24 fibre length and to the crimped fibre length of the staple (Lang and Chaudhri 1948). The  
25 measurement of SL is an accepted measurement used by the wool textile processing industry to  
26 indicate the length of wool fibres (IWTO-30 2007). Thus, it would be reasonable to expect that the  
27 relationship between SL and FFLwt would be a reasonable proxy for the relationship between fibre  
28 length and FFLwt.

1           The relationship between mohair SL and FFLwt is also of importance because mohair SL  
2 determines the processing route for mohair in textiles. Long mohair is required for worsted processing  
3 as longer staples produce tops with longer Hauteur allowing greater spinning speeds and producing  
4 higher quality yarns and fabrics (Hunter 1993). Consequently mohair SL comes second after MFD in  
5 importance as a fibre attribute and this is reflected in mohair auction prices over time (McGregor and  
6 Butler 2004). There are large premiums for mohair with longer SL compared with shorter SL,  
7 although the discounts for shorter length are less at lower MFD (McGregor and Butler 2004).

8           This study examines how mohair SL is related to liveweight of Angora goats of different  
9 genetic origins over their lifetime and how the relationship varies with other lifetime factors.

## 11 **Materials and methods**

### 12 *General*

13 Management details have been provided by McGregor and Butler (2008) and McGregor *et al.* (2012,  
14 2013). In brief, Angora goats born in September 2002 in a progeny testing evaluation at Horsham,  
15 Victoria, (36°42'50"S, 142°18'30"E, altitude 180 m) with pedigree breeding records from known sires,  
16 were grazed on pasture from birth until 6 years of age. The goats were progeny of various genetic  
17 sources including sires of 100% South African origin ( $n = 2$ ), 100% Texan origin ( $n = 4$ ), and other  
18 interbred admixtures that included sires of South African, Texan and Australian origin ( $n = 4$ ). These  
19 sires were representative of the genotypes available in Australia (Ferguson and McGregor 2004,  
20 2005). Records of dam, birth weight, birth parity, liveweight, fleece growth and fleece quality were  
21 taken for castrated males (wethers). All animals were shorn every 6 months from 6 months of age,  
22 except as described below. One month after shearing in February 2004 the castrated male goats  
23 ( $n=94$ ) were transported to Attwood, Victoria (37°40'S, 144°53'E, altitude 135 m) and grazed as a  
24 flock until November 2008.

### 26 *Management*

27 Goats were grazed as one flock, at near the recommended stocking rate on improved annual pasture  
28 (McGregor 2010*a,b*). Goats were moved between paddocks to match feed requirements. Shelter was

1 available in the form of covered and enclosed shedding that was always accessible and could  
2 accommodate all goats. Fresh water was provided in all paddocks. During most years in autumn and  
3 winter, pastoral conditions were affected by drought and supplementary feeding was undertaken  
4 following Australian practice (McGregor 2005) from mid May to early September to maintain  
5 liveweight (McGregor and Butler 2008). A mineralised stock block was always available (Ridley  
6 AgriProducts Pty. Ltd., Melbourne) with the following content: Minimum content Ca 4.9%; P 1%; S  
7 2%; Cu 600 mg/kg; Co 60 mg/kg; I 60 mg/kg; Zn 1000 mg/kg; Fe<sup>+2</sup> 1100 mg/kg; Se 5 mg/kg; based  
8 on NaCl 75 to 85%.

9         The goats were given a full crutching and wiggling three months prior to any shearing. Goats  
10 were vaccinated against 5 in 1 *Clostridia spp.* and “drenched” with an effective anthelmintic to  
11 control gastro-intestinal parasites no more frequently than once per year. All goats were weighed to  
12 the nearest 0.2 kg one day prior to any shearing except for the third shearing when the nearest  
13 liveweight prior to shearing was taken three months earlier at 15 months of age and following  
14 shearing one month later. All goats were fasted overnight prior to shearing or crutching. Goats were  
15 returned to pasture together following shearing.

16

### 17 *Design*

18 The goats studied were the castrated male progeny of a sire evaluation project (Ferguson and  
19 McGregor 2004, 2005). Between February 2004 and February 2006 the goats were part of a replicated  
20 experiment studying the influence of shearing treatments. There were four or eight individual goat  
21 replicates of 21 treatments arranged as a 7 Shearing treatments by 3 Genetic strains factorial  
22 (McGregor and Butler 2008). The shearing treatments were:

- 23 • Three different six month shearing intervals, each with different months of shearing: February-  
24 August, April-October, June-December;
- 25 • Two 12 months shearing intervals with different months of shearing: August-August, September-  
26 September;
- 27 • One 3 month shearing interval (Often treatment); and

1 • One seven-month winter shearing interval, February-September.

2 Genetic strain was based on sire line as follows:

3 • South African: Sires 100% South African bloodline;

4 • Texan: Sires 100% Texan bloodline; and

5 • Mixed: Sires of approximately 50% South African and 50% Texan bloodlines.

6 Some strains of wethers, whose breeding did not fit within these criteria, were culled.

7

### 8 *Mohair measurement and testing*

9 The practices were exactly as previously described (McGregor and Butler 2008). At crutching and  
10 shearing, fleeces, pieces, bellies and locks and samples were weighed to the nearest 1 g. Mid-side  
11 samples were taken at shearing, identified and stored in a plastic bag. Three staples from the mid side  
12 sample were measured for SL to the nearest 0.5 cm following the removal of adhesions and twists,  
13 and then stretched along a ruler to straighten the crimps. The assessed SL was not the longest fibres in  
14 the staple tip but was subjectively determined with the aim of measuring to the point where most of  
15 the fibres were present before any significant narrowing of the staple near the tip, as per industry  
16 selling broker practice.

17

### 18 *Statistical methods*

19 Fleece-free liveweights (FFLwt) were determined for each goat at shearing time by subtracting the  
20 greasy fleece weight from the liveweight recorded immediately prior to shearing. Average FFLwt  
21 between shearings (AvFFLwt) was determined as the average of the FFLwt at the start of the period  
22 and the FFLwt at the end of the period. Liveweight change (LwtCh) was the change in FFLwt over  
23 the period between shearings.

24 A restricted maximum likelihood (REML) model was developed for SL which allowed the  
25 observations of the same animal at different ages to be correlated in an unstructured manner. Thus, for  
26 individual animals, the variance was allowed to differ between ages and the covariance was allowed  
27 to differ between each pair of ages. Within this framework, a parsimonious model for fixed effects

1 was developed using Wald *F*-tests (Payne 2011). Once a parsimonious fixed effects model had been  
2 established, random sire effects and random dam effects were examined for inclusion in the model but  
3 the sire effect was rejected based on a Chi-squared change in deviance test, and the dam effect was  
4 rejected based on the lack of numerical convergence when fitting a model with an extra term for a  
5 dam effect. Small random effects commonly lead to over-parameterization and this often leads to  
6 numerical convergence difficulties. Confidence intervals are constructed using asymptotic normal  
7 approximations.

8

## 9 **Results**

10 During the study SL varied between 7.2 and 18.0 cm (Fig. 1). Average SL for a six month shearing  
11 interval differed with age, ranging from 11.8 cm at 4 years to 14.7 cm at 6 years. For the animals in  
12 the study, average FFLwt was equal to 36.9 kg, standard deviation was equal to 14.0 kg, the minimum  
13 was equal to 8.3 and the maximum was equal to 72.0 kg . Average LwtCh was equal to 4.1 kg,  
14 standard deviation was equal to 5.9 kg varying from a lowest value of -13.8 to a largest value of +22.8  
15 kg.

16 The fixed effects in the model for SL can be represented as (Table 1, 2):

$$17 \quad \text{SL} = \text{Shearyears} * \text{Shearregime} + \text{Age} + \text{LwtCh}.$$

18 Although the date of birth was statistically significant ( $P < 0.05$ ), date of birth was no longer  
19 statistically significant ( $P < 0.05$ ) when one statistically influential kid that was born 5 days earlier  
20 than all the other kids used in the statistical analysis was excluded from analysis. Thus date of birth  
21 was not included in the chosen model (Table 2). There was no evidence ( $P > 0.1$ , Table 2) for a sire  
22 effect. The dam effect could not be tested because a model that included an extra term for dam did not  
23 numerically converge. This, in itself, is an indication of over-parameterization that can occur when  
24 there is little dam effect.

25 Average SL differed from about 12 cm to about 14½ cm, depending on age (Fig. 2). There  
26 were no consistent effects of season.



1 Angora goats which gained liveweight had longer SL than goats which lost liveweight but  
2 this effect was small compared with the age effect (Figs. 2 and 3). At any age, an increase of 10 kg  
3 LwtCh between animals results in about a 0.34 (s.e. = 0.087) cm increase in SL.

4 There was no evidence of an effect of FFLwt on SL (Table 2, Fig. 4). The narrow confidence  
5 intervals in Fig. 4 show, that not only is there no evidence of any effect, but also that any non-detected  
6 effect is small.

7 The residual standard deviation of SL was greater for 1.0 and 1.5 year olds than for older ages  
8 (Table 3). The residual standard deviation was relatively stable between ages 2.0 and 6.0 years old.

9 Generally, correlations declined between shearing ages further apart (Table 4). This trend is  
10 particularly evident when making shearing age comparisons with shearing ages 1, 1.5 and 2 years.  
11 The correlations for shearing ages 1 and 1.5 with shearing ages  $\geq 3$  years were  $\leq 0.40$ , average 0.15,  
12 but at shearing ages  $\geq 3$  years the correlations at any older age averaged 0.40 (range 0.16–0.67).

## 14 Discussion

15 The results confirm our hypothesis that within a single age cohort of Angora goats, there is very little,  
16 if any, relationship between the liveweight and staple length of individual animals. The lack of  
17 relationship we have found between SL and FFLwt, strongly contrasts with the relationship we  
18 previously found between MFD and FFLwt. This partially agrees with phenotypic correlations  
19 obtained from previous genetic studies with Angora goats (Shelton and Bassett, 1970; Yalçin *et al.*  
20 1979; Gifford *et al.* 1991). In these 3 studies phenotypic correlations were small for SL and  
21 liveweight (0.04, 0.05 and 0.21), but larger for MFD and liveweight (0.13, 0.26 and 0.23). In two  
22 other genetic studies (Nicoll *et al.* 1989; Snyman and Oliver, 1996) the phenotypic correlations  
23 between MFD and liveweight were larger again (0.37 and 0.55). One possible reason that a small  
24 positive phenotypic correlation between SL and liveweight was found in previous genetic studies is  
25 that in those studies it is likely that liveweight was not fleece free. Thus, the liveweight would include  
26 fleece weight which is likely to have a relationship with SL. Another possible reason is that in our  
27 modeling we have taken into account the effect of LwtCh, which has some positive relationship with

1 FFLwt (McGregor *et al.* 2013, Fig. 2). Thus, unadjusted, there will be some relationship between SL  
2 and liveweight caused indirectly by the direct relationship between LwtCh and SL.

3         If we assume that the relationships of SL with FFLwt and MFD with FFLwt are driven purely  
4 by morphological processes, then we can suggest mechanisms for the form of relationships. If as an  
5 animal gets larger it remains morphologically and compositionally similar, then the MFD will be  
6 proportional to  $\text{FFLwt}^{1/3}$  (McGregor *et al.* 2012). If, despite an animal getting larger, the fibre follicle  
7 depth, or at least the depth of follicle involved in producing fibre cells, does not change then fibre  
8 length (and hence staple length) might be expected to be unrelated to FFLwt. These are the  
9 relationships observed in our studies.

10         A previous study (McGregor 1992) showed that skin weight of Angora goats was  
11 allometrically related to FFLwt, with an allometric constant not different from 1. That is, skin weight  
12 could be considered to be proportional to FFLwt. For this to occur by morphological process, then  
13 total skin depth would need to be proportional to  $\text{FFLwt}^{1/3}$  in addition to MFD being proportional to  
14  $\text{FFLwt}^{1/3}$ . This would occur if, at the macro level, the skin is morphologically similar for different size  
15 animals. Our suggested morphological mechanism for the relationship between SL and FFLwt is still  
16 possible, but it would imply that the depth of follicle involved in producing fibre cells is not related to  
17 the skin thickness. A consequence is that, in larger animals, a smaller proportion of the skin will be  
18 associated with producing fibre cells.

19         There were differences of more than 2.5 cm between ages in SL (Fig. 2). While the  
20 differences between ages shown in Fig. 2 are to a small extent confounded with the effects of LwtCh,  
21 the differences between ages are much too large to be explained by this confounding (Figs. 2 and 3). The  
22 effect of age on SL are likely to be environmental because the effect does not change in a simple  
23 systematic way as the goats age or between the summer and winter half year. This indicates that there  
24 are major environmental effects that affect SL, which are not reflected in the average liveweight or  
25 changes in liveweight of the animal.

26

27

1 *Influence of LwtCh*

2 Both AvFFLwt and LwtCh should reflect differences in nutrition over the longer and shorter term  
3 respectively. That these indices of nutritional status had little effect suggests that other factors were in  
4 play. Hynd (1994a) has shown that changes in nutrition affect the size of cortical cells in wool fibres  
5 and hence the length of wool fibres. It is likely that changes in nutrition in Angora goats have similar  
6 effects on the length of mohair fibres. It is also possible that negative LwtCh may reduce average SL  
7 by affecting the number of growing fibres. This effect may operate as a relative increase in the  
8 number of non-growing fibres when liveweight declines, leading to marginally reduced SL (Fig. 3).

9

10 *Influence of other factors*

11 There may be differences in season which affect nutritional intake, perhaps related to pasture  
12 structure, such as proportion of green and dead herbage, which may have affected the ease of dietary  
13 selection and so grazing time, or digestion of forage as described for sheep (Birrell 1989). However  
14 in the present work, season of fibre growth had no consistent effect on SL (Fig. 2).

15 At the time of the shearing experiment (fleeces harvested from 2 year old to 3.5 years old)  
16 there were major nuisance effects of shearing regime (Table 2). This relates to the previous results  
17 that shearing interval has a major effect on fleece weight, SL and other fleece attributes (McGregor  
18 and Butler 2008).

19 Neither birth weight, dam age, nor single births versus multiple births had an effect once other  
20 terms in the model had been accounted for (Table 2). On farms, the main effect of these factors is to  
21 alter weaning weight. Weaning weight also had no effect, most probably because we directly  
22 measured liveweight during the course of this study.

23 Surprisingly, there was no evidence of any genetic effects of breed, sire identity or dam  
24 identity in the model (Table 2). This suggests that the genetic effects on SL are quite small. While a  
25 positive phenotypic relationship between liveweight and mohair SL has been reported in previous  
26 studies of Angora goats from Texas, Turkey and Australia, the correlations are small and in two cases  
27 not significantly different from zero: 0.04 (Shelton and Bassett 1970); 0.05 (Yalçın *et al.* 1979); 0.21  
28 (Gifford *et al.* 1991). Taken together with the present work, it appears that SL is not associated with

1 the size of the Angora goat. Wool SL is also phenotypically positively related to liveweight of Merino  
2 sheep (Huisman and Brown 2008). In their study, the highest correlations occurred between staple  
3 length and liveweight taken at the same time with lower correlations when these measures were  
4 compared at different times.

5 It is unlikely that differences in fibre crimp would bias our measure of SL as the staples were  
6 straightened prior to measurement.

7

### 8 *Random variation*

9 The higher residual standard deviation of SL between animals at ages 1 and 1.5 years may reflect the  
10 effects of drought conditions which existed between weaning and 1.5 years of age. During the last  
11 year of this study, the wear of 30% of the first permanent incisors was associated with a 7.5% decline  
12 in SL (McGregor and Butler 2011) but this effect has not increased the residual standard deviation  
13 above that seen between 2 to 5 years of age (Table 3). Variation in mohair SL differs over the body of  
14 Angora goats, and there are differences between farms, and between age of goats (McGregor and  
15 Butler 2009).

16 The within animal correlation generally declined to levels well below 0.3 when comparing  
17 shearings at <2 years old with shearings at older ages (Table 4). This indicates that ranking of animals  
18 for SL can change substantially as the goats become older.

19

### 20 **Conclusion**

21 Despite the cross-sectional area of mohair fibres being related to the size of animals within a flock,  
22 the SL and thus presumably fibre length is not related to the size of the animals. This implies that the  
23 biological determinants of size of fibres related to cross-sectional area are substantially different to the  
24 size determinants of fibre length. As an animal grows, the skin surface area increases, skin follicle  
25 density declines and skin follicle bulb size increases. This results in increased fibre cross-sectional  
26 area but the larger skin surface area does not give any advantage in relation to mohair fibre length  
27 growth.

28

1 **Acknowledgements**

2 The Rural Industries Research and Development Corporation and the Victorian Department of  
3 Primary Industries funded this project. Robert and June Liddy and Rowena and Glen Doyle provided  
4 their property, animals and labour for the initial two years of the project. The participating mohair  
5 breeders who supplied their genetic material and other DPI colleagues are gratefully thanked (see  
6 Ferguson and McGregor 2005). Terry Couzens, Attwood, is thanked for assisting with animal  
7 management.

8

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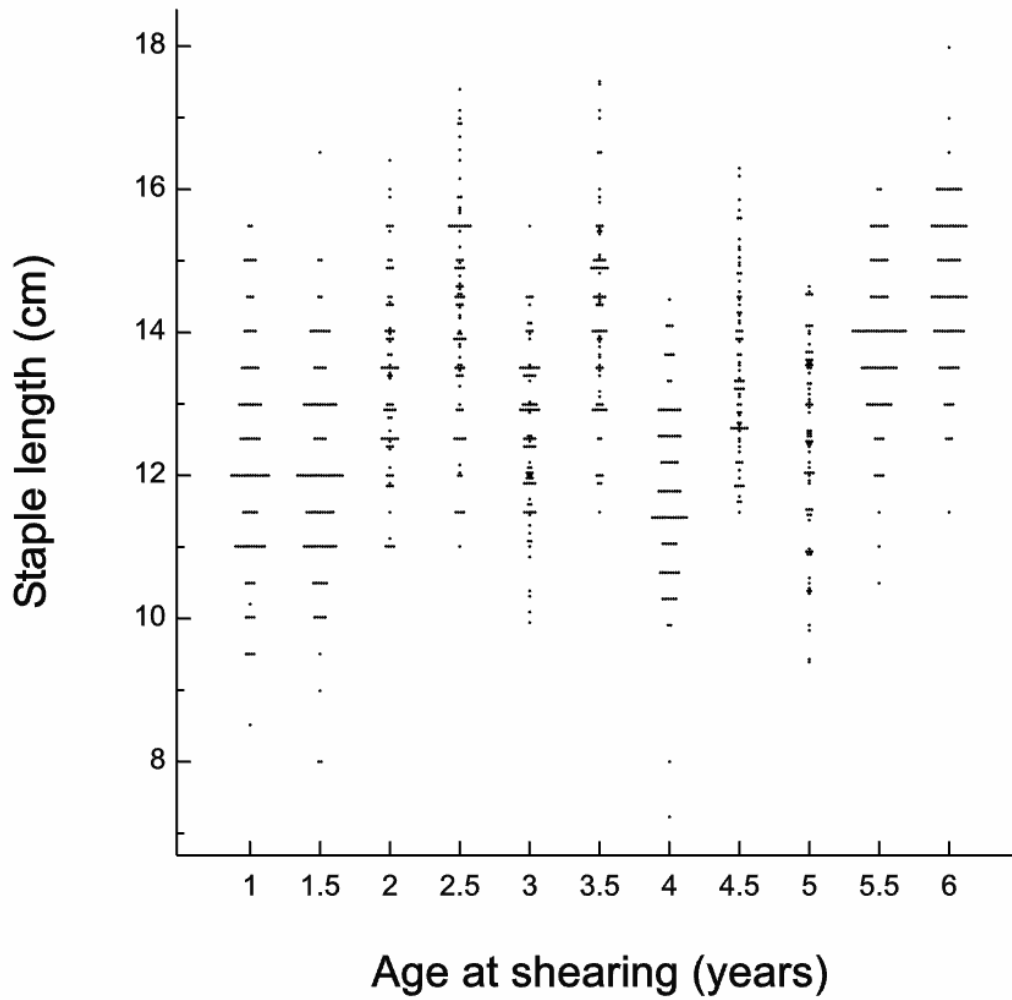
17 Whan RB (1972) Fibre-length variation in greasy wool. *Journal of the Textile Institute* **63**, 84-90.

18 Yalçın BC, Ariturk E, Imeryuz F, Sincer N, Muftuoglu, S. (1979). Genetic and environmental aspects  
19 of Angora goat production. 2. Phenotypic and genetic parameters for the important production traits.  
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1 **Figure captions**

2 **Fig. 1.** The range in mohair staple length at each age of shearing during the study, adjusted to a 6-  
3 month growing period.

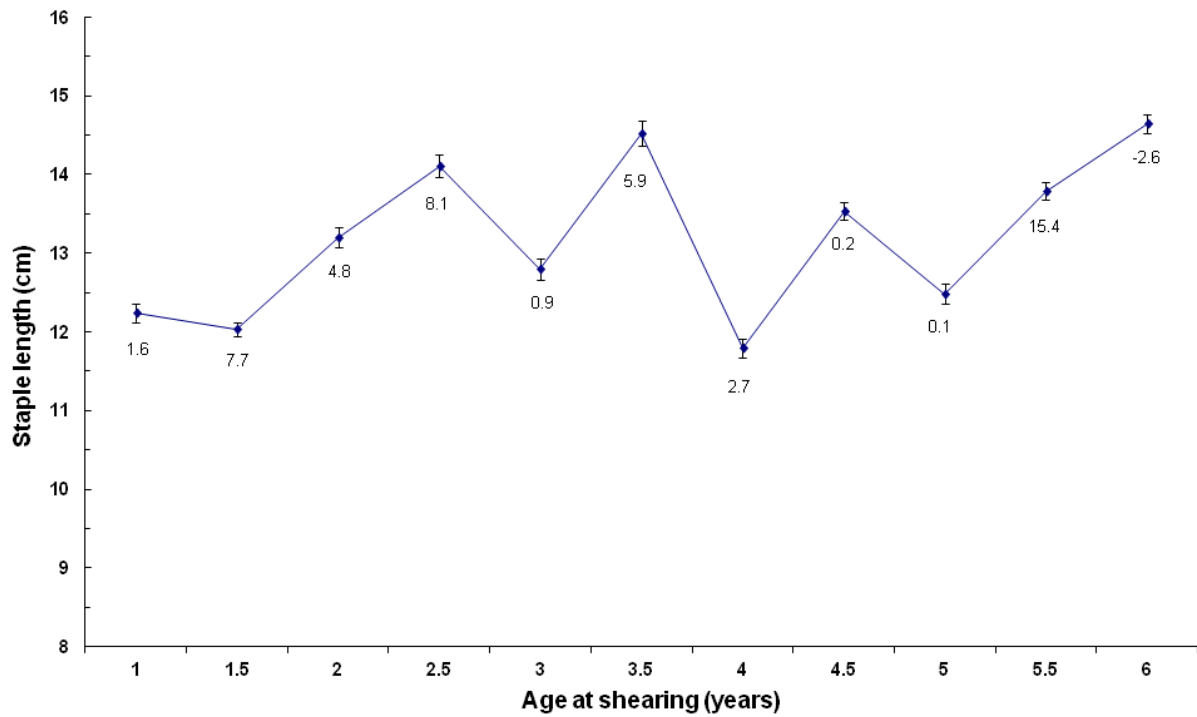


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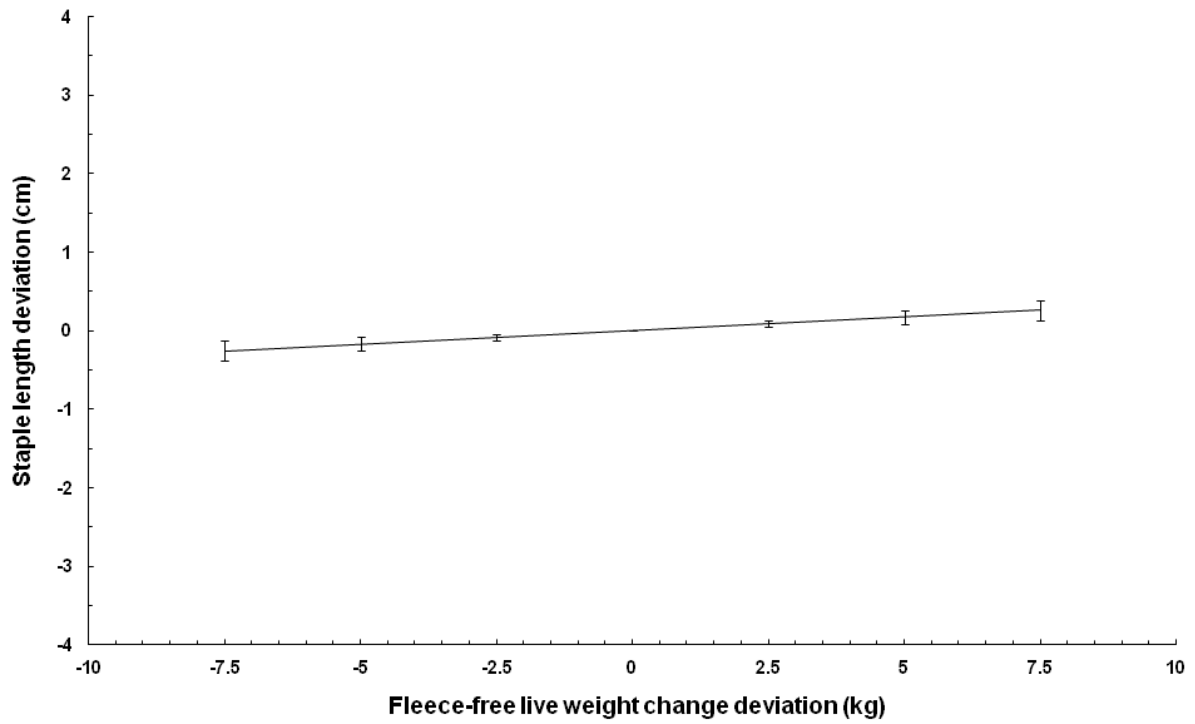
1 **Fig. 2.** Effect of age at shearing on average staple length. Values are given for the average liveweight  
2 change (kg) of goats during the growing period. These liveweight change values are presented as  
3 numbers on the graph. During the shearing experiment years, predicted means are equally weighted  
4 for shearing regimes occurring at each particular age. The error bars represent the 95% confidence  
5 intervals.



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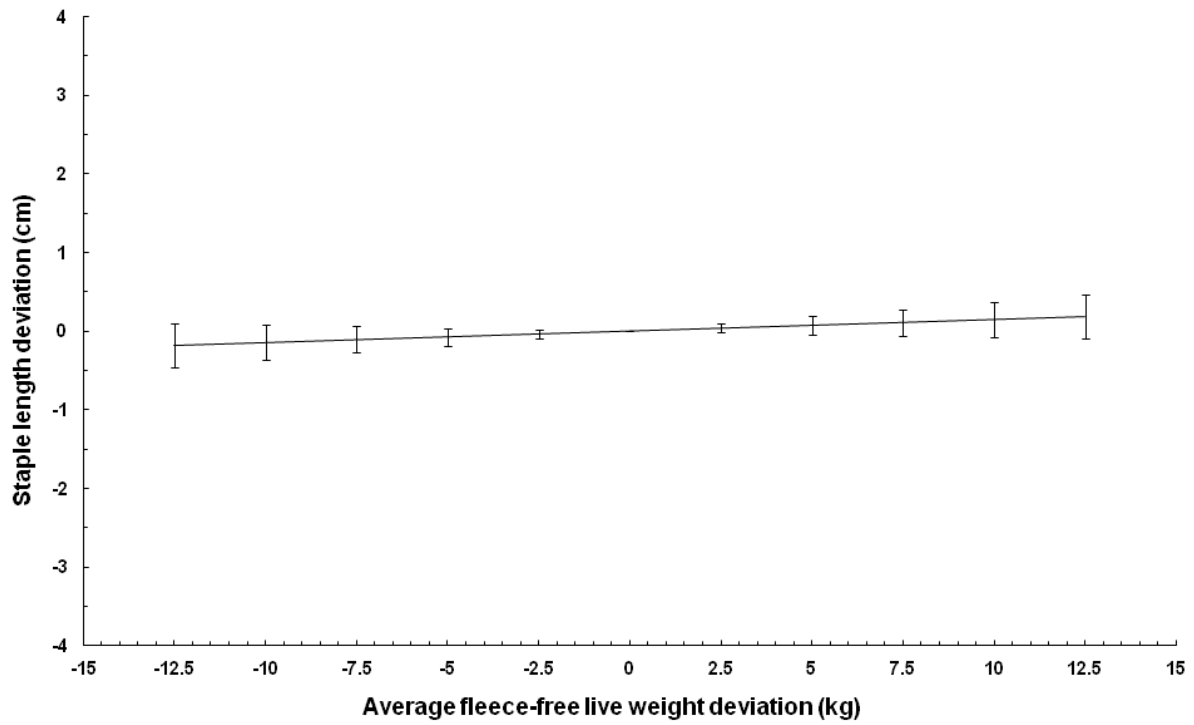
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1 **Fig. 3.** Effect of deviation of fleece-free liveweight change from average fleece-free liveweight  
2 change on staple length deviation, at a given age. Error bars show the 95% confidence intervals. The  
3 y-axis covers the same range in staple length as Fig. 1. Effect is adjusted for other terms in the model.



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1 **Fig. 4.** Effect of deviation of average fleece-free liveweight from average fleece-free liveweight on  
2 staple length deviation, at a given age. Error bars show the 95% confidence intervals. The y-axis  
3 covers the same range in staple length as Fig. 1. Response is adjusted for all terms in the model (i.e.  
4 using parsimonious model with extra term for fleece-free liveweight).



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**Table 1. Fixed terms in parsimonious model for mohair staple length**

Acronym	Factor/variante	Number of levels	Description
Shearyears	Factor	5	4 if CFWt measured at 2 - year - old shearing 5 if CFWt measured at 2½ - year - old shearing 6 if CFWt measured at 3 - year - old shearing 7 if CFWt measured at 3½ - year - old shearing NA otherwise
Shearregime	Factor	8	FebAug if animal was in February and August shearing regime and measured in Shearyears 4 to 7 FebSept if animal was in February and September shearing regime and measured in Shearyears 4 to 7 AprOct if animal was in April and October shearing regime and measured in Shearyears 4 to 7 JunDec if animal was in June and December shearing regime and measured in Shearyears 4 to 7 AugAug if animal was in August and August shearing regime and measured in Shearyears 4 to 7 SeptSept if animal was in September and September shearing regime and measured in Shearyears 4 to 7 Often if animal was in every 3 months shearing regime and measured in Shearyears 4 to 7 NA if measurement taken in other Shearyears
LwtCh	Variate	Not applicable	The change in fleece-free liveweight over the period between shearings
Age	Factor	11	Age (years) at shearing (1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 5.5, 6)

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**Table 2. Tests for including and excluding effects in the model**

*P*-values in bold are significant at the 5% level

Adjustment to model	Type of test	$\chi^2/F$ -value	Degrees of freedom	<i>P</i> -value
<i>Terms included</i>				
Shearyears by Shearregime interaction	Wald F	13.27	12, 108.1	<b>2.2 × 10<sup>-16</sup></b>
Age effect outside Shearing experiment years	Wald F	98.88	6, 98.8	<b>1.7 × 10<sup>-39</sup></b>
LwtCh	Wald F	15.47	1, 254.6	<b>0.00011</b>
<i>Terms excluded</i>				
Square of LwtCh	Wald F	0.03	1, 227.0	0.87
LwtCh differs with age	Wald F	0.97	10, 252.4	0.47
LwtCh differs with Shearregime	Wald F	1.67	7, 131.3	0.12
Liveweight	Wald F	1.60	1, 233.1	0.21
Single v. Twins	Wald F	0.84	1, 88.8	0.36
Dam age	Wald F	0.18	1, 90.9	0.67
Weaning weight	Wald F	0.56	1, 89.4	0.46
Birth weight	Wald F	0.24	1, 86.8	0.63
Breed	Wald F	0.37	2, 85.3	0.69
Date of birth	Wald F	2.05	16, 69.2	<b>0.021</b>
Date of birth when animal born 5 days earlier than all others omitted	Wald F	1.68	15, 70.2	0.075
Sire effect	Deviance	2.58	1	0.11
Dam effect	Deviance		Did not converge	

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1 **Table 3. Residual standard deviation (r.s.d.) of staple length (cm) at each age**

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Age	Residual standard deviation	s.e.(r.s.d.)
1	1.572	0.0304
1.5	1.504	0.0279
2	1.173	0.0247
2.5	1.009	0.0221
3	0.941	0.0203
3.5	1.327	0.0268
4	1.250	0.0249
4.5	1.178	0.0232
5	1.278	0.0255
5.5	1.096	0.0220
6	1.127	0.0228

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5 **Table 4. Within animal correlation between ages, after adjusting for fixed terms in the model**

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Age (years)	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5
1	–	–	–	–	–	–	–	–	–	–
1.5	0.42	–	–	–	–	–	–	–	–	–
2	0.46	0.24	–	–	–	–	–	–	–	–
2.5	0.30	0.43	0.38	–	–	–	–	–	–	–
3	0.16	0.28	0.40	0.37	–	–	–	–	–	–
3.5	0.04	0.17	0.38	0.26	0.50	–	–	–	–	–
4	0.16	0.09	0.26	0.26	0.35	0.51	–	–	–	–
4.5	0.15	0.21	0.30	0.41	0.41	0.53	0.67	–	–	–
5	0.10	0.08	0.31	0.25	0.34	0.28	0.24	0.50	–	–
5.5	0.11	0.25	0.24	0.16	0.32	0.32	0.16	0.50	0.49	–
6	0.15	0.16	0.20	0.21	0.45	0.31	0.23	0.39	0.41	0.56

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