The inheritance of fibre traits in a crossbred population of cashmere goats

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SUMMARY

Genetic parameters were calculated for fibre traits measured on patch samples taken at 5 months of age on a crossbred population of cashmere goats, comprising goats of Scottish feral, Icelandic, Tasmanian, New Zealand and Siberian origin. Within-strain heritabilities, fitting genetic origin as a covariable, were: live weight, 0.71 (s.e. 0.08), fibre diameter, 0.63 (0.07), diameter standard deviation 0.43 (0.08), log(patch cashmere weight), 0.60 (0.06), log(estimated annual cashmere production), 0.51 (0.07), and fibre length, 0.49 (0.15). Including between strain information increased these values to 0.74, 0.68, 0.45, 0.73, 0.67 and 0.57, respectively. Maternal effects for all fibre traits were negligible. Expressions were derived to relate cashmere weight to fibre diameter and length, using functional relationships between these traits. Logarithmic regressions showed cashmere weight to be proportional to diameter[2.7], indicating that selection to reduce fibre diameter will have a disproportionate effect on cashmere weight. Analyses of subsets of the data confirmed this and showed that correlated responses to selection can be accurately predicted by considering the functionally related fibre traits on the log scale.

INTRODUCTION

Cashmere production is a potentially viable alternative enterprise for hill and upland farmers in the UK and other European countries. The benefits of cashmere goats are twofold. Cashmere, the down from the secondary hair follicles of some breeds of goats, is a valuable commodity used, but not currently produced to any significant extent, in Europe. Secondly, the goats' grazing preferences can benefit pasture management and have a positive ecological impact (Gordon and Fraser, 1993; del Pozo and Wright, 1995).

Because no economically viable breeds of cashmere-bearing goats are indigenous to the UK, goats, semen and embryos were imported from Iceland, Siberia, Tasmania and New Zealand and an extensive crossbreeding programme involving these genotypes and native feral goats was undertaken to produce genotypes suitable to Scottish conditions (Bishop and Russel, 1994). Bishop and Russel (1994) found, that although considerable variation existed between each of the strains, none had sufficient merit for all traits of interest to justify concentrating solely on that particular strain. Moreover, heterosis effects were generally small for the fibre production traits and did not merit a structured crossbreeding programme to exploit the heterosis.

The best means of improving the crossbred population of cashmere bearing goats in Britain would therefore appear to be through selection for genetic merit, regardless of genetic origin. To achieve this effectively, and to predict correlated responses to selection, genetic parameters are required for the traits of interest to enable the development of a selection index or multiple-trait BLUP based selection. Whilst previously published genetic parameters for cashmere goats are promising, insofar as heritabilities for important traits are high (Pattie and Restall, 1989; Bigham, Morris, Southey and Baker,1993), appropriate values for the crossbred population under consideration are not available. Moreover, functional relationships exist between important fibre production traits, e.g. cashmere weight is a function of fibre diameter, suggesting that these traits may be non-linearly related. Such non-linear relationships are generally ignored by conventional theory when predicting responses to selection.

The aim of this paper is two-fold: firstly to present genetic parameters appropriate to the crossbred population of cashmere-bearing goats which currently exists in the UK, and secondly, to investigate how the non-linear relationships which may exist between some of the fibre traits can be accounted for when predicting responses to selection.

MATERIALS AND METHODS

Source of data

A detailed description of the origin of the goats comprising the population considered here has been given by Bishop and Russel (1994). The goats described in this paper were derived from Scottish feral (F) goats and

importations of animals, embryos and semen of goats from Iceland (I), Tasmania (T), New Zealand (N) and the Gorno Altai region of Siberia (S), made between 1986 and 1988. A crossbreeding programme amongst these strains of goats produced a variety of purebred, two- and three-way crosses, distributed across a total of 18 commercial farms, including the MLURI Sourhope Research Station, which served as a nucleus. The numbers of kids evaluated each year and included in the dataset described below, are shown in Table 1 tabulated by sex, as well as sires contributing to this dataset. From 1992 onwards, only kids born on the nucleus farm were evaluated and this herd was subdivided into lines selected for (i) increased value of fibre, (ii) decreased fibre diameter and (iii) an unselected control line. A schematic diagram of the mating history of the goats is shown in Figure 1.

TABLE 1

Structure of dataset analysed

| Year of | Number of Observations | | | No. of |
Birth	Male	Female	Castrate	Sires
1987	71	0	0	4
1988	68	0	0	7
1989	31	0	0	7
1990	55	84	37	19
1991	138	66	3	38
1992	181	177	0	14
1993	184	203	0	16

Kids were evaluated on the basis of 10 cm^2 mid-side patch fleece samples taken at approximately 5 months of age (155 days onm average). The "mid-side" sampling site was over the last rib, halfway up the side of the animal, and it is the site which is most representative of the fleece as a whole (Pattie, Restall and Smith, 1984). Each year kids were sampled and recorded from all available lines and crosses.

Characteristics directly related to overall productivity were measured and recorded for each kid. These included live weight (LW), cashmere weight in the 10 cm^2 patch sample (P_CASH), mean fibre diameter (DIAM) and the
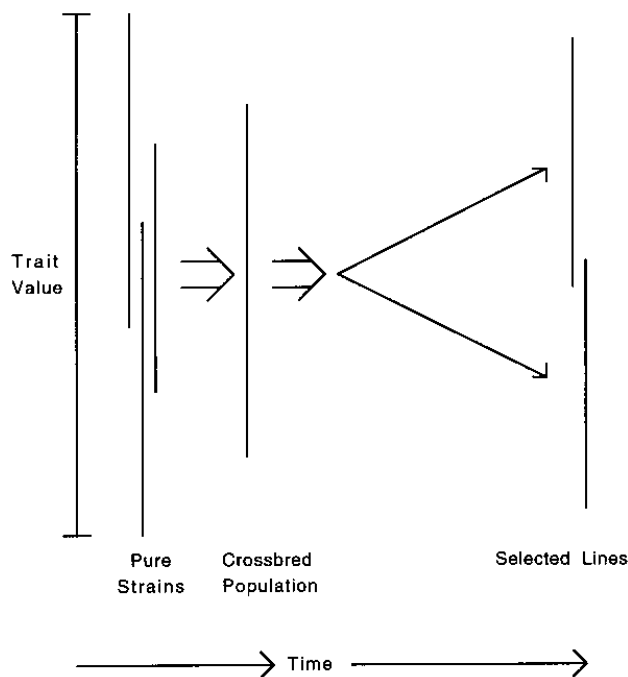
Figure 1. Mating history of crossbred cashmere goat herd

standard deviation of fibre diameters in each sample (DIAM_sd). Fibre diameter was measured, following manual separation and weighing of guard hair and cashmere fibres, by projection microscopy using standard procedures (IWTO, 1989). In the first two years of the trial, fibre length was measured directly on the animal at the time of sampling, however this measurement was subsequently discontinued. From 1992 onwards, staple length was measured on the laboratory samples, and for purposes of analyses this is treated as the same trait as fibre length.

From the sample cashmere weight, estimated annual cashmere production (EAP) was calculated using the equation of Couchman and McGregor (1983) to relate skin area of the animal to live weight, i.e. area $(cm^2) = 536.1 x LW^{0.703}$, and by assuming that 0.40 of total annual cashmere production is present in 5 month old kids (A.J.F. Russel, unpublished). This latter assumption was arbitrary and although it is critical in determining the absolute estimated cashmere production, it does not affect the ranking of animals, provided that there is no interaction between genotype and patterns of fibre growth. Therefore: $EAP = 53.6 x LW^{0.703} x P\_CASH/0.4$.

Estimation of genetic parameters

Genetic parameters were estimated for all traits described above using Residual Maximum Likelihood (REML) techniques, solving the equations using a derivative-free algorithm (DFREML, Meyer, 1989) and fitting an animal model with a pedigree including all known ancestors. Observations on 237 kids born as a result of embryo transfer between 1987 and 1991 were deleted from the dataset as their inclusion inflated the observed error variances even after fitting embryo transfer as a fixed effect, possibly because of suspected preferential treatment. These animals were, however, retained in the pedigree. Prior to the REML analyses the distributions of each trait were investigated. EAP and P_CASH were both significantly positively skewed and a log transformation was found to be adequate to remove this skewness for each trait. These traits were therefore analysed on both the observed and log transformed scales.

Heritabilities were calculated from univariate REML analyses, both including and ignoring maternal genetic effects, fitting the fixed effects of farm, year and sex, with age at sampling as a covariate. The genetic origin of the goat has a large effect on all fibre traits (Bishop and Russel, 1994) and was accounted for by regressing the measurement for each kid on the proportion of each of the five original strains which comprise its own genotype. This assumes no heterosis effects, which is a reasonable assumption for the fibre traits (Bishop and Russel, 1994), but less satisfactory for live weight. The resulting heritabilities may be thought of as "within-strain" heritabilities.

Genetic correlations between all traits were calculated using a bivariate DFREML algorithm (Thompson, Crump, Juga and Visscher, 1995). This algorithm enables different fixed effects and different numbers of observations for the pair of traits in each analysis, and hence makes full use of the data in the situation where there may be many missing observations for one of the traits, e.g. fibre length. For some of the pairs of traits, convergence was not achieved using this algorithm and the correlations were estimated using the technique described by Thompson and Hill (1990). This algorithm required restricting the dataset to animals with both traits measured in the bivariate analyses. These cases are indicated in the results section.

Composite genetic parameters, combining both within- and between-strain information were calculated by augmenting the genetic and phenotypic variances for each trait by the value $Sp_i^2b_i^2$, where p_i is the mean contribution

of each genotype to the population and b_i is the regression of the trait on the genotype proportion, defined such that $Sp_i b_i = 0$. The value $Sp_i^2 b_i^2$ may be thought of as the between strain genetic variance, and differs as the genetic makeup of the population changes. Hence, appropriate between strain variances may be calculated for the population at any point in time by substituting appropriate p_i values. Composite genetic and phenotypic correlations were likewise calculated from the augmented standard deviations and from covariance terms augmented by $Sp_i p_j b_i b_j$.

Standard errors for each heritability and genetic correlation estimate were calculated from the second derivative of the log likelihood, evaluated at the parameter estimate. To enable this derivative to be evaluated, a log likelihood profile was obtained by fixing the points at, and on either side of, the parameter estimate and estimating the likelihood for each point. For the genetic correlations, the likelihood was remaximised across all other parameters. Standard errors are not available for the correlations calculated using the Thompson and Hill (1990) method.

Relationships between traits

The traits analysed in this paper differ from many commonly considered traits of commercial importance in farm livestock insofar as there are functional relationships between them which may result in non-linear relationships. Consider P_CASH, which is simply the sum of the weights of the constituent fibres in the patch sample. A derivation of the relationship between P_CASH and fibre diameter is shown in appendix 1. Even in the absence of knowledge relating to follicle density, cashmere weight is complex function of the mean, variance and skewness of fibre diameter, as well as the relationship between fibre length and diameter within a sample.

What emerges from these functional relationships is that some traits may be multiplicative or power functions of other traits, making traditional methods of predicting responses to selection inappropriate. Considering some of the traits on the log scale will linearise these relationships, however, and may facilitate more accurate predictions of selection responses. Possible non-linear relationships between traits will be investigated in this dataset using regressions of log transformed variables, and subsets of the data will be used to investigate the prediction of correlated responses to selection for decreased fibre diameter.

RESULTS AND DISCUSSION

Means and genetic parameters

Mean values and the number of measurements analysed for each trait are presented in Table 2 with phenotypic standard deviations calculated using univariate REML analyses. Both the within-strain and the total phenotypic standard deviations, calculated by augmenting the within-strain phenotypic variances by $Sp_i^2 b_i^2$ (the between-strain variance) for each trait are shown. EAP and P_CASH were both significantly positively skewed, however a log transformation rendered both traits approximately normally distributed. Results are also shown for the logarithm of DIAM in this table and throughout the paper, since consideration of the relationships between traits (see above) showed that it may be useful to investigate these traits on the log scale.

TABLE 2.

Mean values, within strain phenotypic standard deviations and total phenotypic standard deviations†.

	LW (kg)	DIAM (mm)	DIAM_sd (mm)	P_CASH (g)	EAP ('g')	Length (cm)	Logarithm of: DIAM	Logarithm of: P_CASH	Logarithm of: EAP
Mean	16.1	15.6	3.35	0.220	212	3.39	2.74	-1.65	5.28
No. obs¶	1245	1298	1298	1321	1244	521	1298	1321	1244
$s_p(w)$	2.72	1.12	0.458	0.098	95	0.882	0.0724	0.363	0.358
$s_p(T)$	2.88	1.21	0.467	0.126	118	0.967	0.0784	0.446	0.435

† $s_p(w)$ and $s_p(T)$ are the within strain and total phenotypic standard deviations
¶ Number of observations

Univariate heritabilities, with their standard errors, calculated after fitting strain or genetic group as a covariate are shown in Table 3. These may be considered to be "within strain" heritabilities. Heritability values for all traits on the observed measurement scale are moderate to high, in general agreement with previously published values (Pattie and Restall, 1989; Bigham, Morris, Southey and Baker, 1993; Couchman and Wilkinson, 1987; Gifford, Ponzoni, Ellis, Levinge and Milne, 1990.). Unusual values are observed for live weight, with 0.71 being greatly in excess of values normally

quoted for live weight in any domestic species, and also for EAP, where a value of 0.30 is somewhat lower than normally reported for cashmere weight. EAP and P_CASH were both positively skewed, however, and after a log transformation the heritabilities of these traits increased so that they were similar to previously reported values. The heritability for DIAM was little affected by the log transformation.

The results from univariate analyses where both additive and maternal genetic components of variation were estimated are presented in table 4. For all fibre traits, the maternal genetic (m^2) effects were negligible, and with the exception of DIAM_sd and Length, the heritability values were unaffected by fitting a maternal genetic effect. For live weight, however, the fitting of a maternal genetic effect has had a large effect on the heritability estimate, reducing it from 0.71 to 0.35; associated with this change in heritability is a large maternal effect, of a magnitude similar to that often observed in sheep (e.g. Burfening and Kress 1993; Maria, Boldman and Van Vleck, 1993; and Tosh and Kemp, 1994). Increasing the complexity of the model further, by including a covariance between the additive and maternal genetic values resulted in h^2 and m^2 values of 0.71 and 0.31, with a genetic correlation between these effects of -0.45, however a likelihood ratio test revealed that including the correlation did not improve the fit of the model ($p > 0.5$). Previous analyses of strain differences in this population of goats (Bishop and Russel, 1994) showed live weight to be the only trait which consistently showed heterosis, although in these previous analyses it was not possible to disentangle heterosis from maternal genetic effects. In these analyses it has, conversely, been necessary to assume heterosis effects to be not important. Therefore, it is unclear as to whether the high h^2 value for live weight is due to confounding the additive genetic values with maternal effects, with heterosis effects or a combination of these two factors.

The heritabilities shown in Tables 3 and 4 are strictly "within strain" values. Composite heritabilities, i.e. values where the within and between strain genetic variances are combined, are presented in table 5. Also shown are the actual genetic within and between strain components of variance. Again, heritability values which should be used for P_CASH and EAP are those for the logarithm of these traits. All composite heritability values are, of course, larger than the within strain heritabilities, with the increase being a function of the relative magnitude of the within and between strain components of variance. These composite heritabilities describe the population as a whole. If heritability values relevant to any point in time are required, then they can

TABLE 3.

Heritabilities (and s.e.s) for all traits fitting genetic group as a covariable

	LW	DIAM	DIAM_sd	P_CASH	EAP	Length	Logarithm of:		
							DIAM	P_CASH	EAP
h^2	0.71	0.63	0.43	0.39	0.30	0.49	0.61	0.60	0.51
s.e.	0.08	0.07	0.08	0.05	0.05	0.15	0.07	0.06	0.07

TABLE 4.

Heritabilities and maternal (m^2) effects for all traits fitting genetic group as a covariable

	LW	DIAM	DIAM_sd	P_CASH	EAP	Length	Logarithm of:		
							DIAM	P_CASH	EAP
h^2	0.35	0.61	0.35	0.38	0.28	0.43	0.58	0.60	0.51
m^2	0.21	0.01	0.02	0.02	0.01	0.03	0.01	0.00	0.00

TABLE 5.

Within and between strain genetic variances and "composite" heritabilities for all traits†

	LW	DIAM	DIAM_sd	P_CASH	EAP	Length	Logarithm of:		
							DIAM	P_CASH	EAP
s_{AW}^2	5.24	0.784	0.0897	0.00371	2684	0.379	0.00319	0.0784	0.0654
s_{AB}^2	0.92	0.223	0.0083	0.00631	5030	0.157	0.00090	0.0674	0.0610
h^2	0.74	0.68	0.45	0.63	0.55	0.57	0.67	0.73	0.67

† s_{AW}^2 and s_{AB}^2 are the within and between strain genetic variances

be calculated utilising the distribution of genotype frequencies at that particular time, together with the appropriate regression coefficients.

It is of interest to quantify the difference between the composite heritabilities, and values that would be obtained if the fact that the animals originate from a diverse range of genotypes were to be ignored. Ignoring the origins of the goats, the heritabilities for live weight, DIAM, DIAM_sd, Length and the logarithm of P_CASH and EAP were 0.77, 0.74, 0.47, 0.94, 0.75 and 0.70. With the exception of Length, where the dataset is poorly structured for estimating genetic parameters, the values are slight overestimates of the composite values. It should be noted, however, that there is no means of breaking these values down into the within and between strain components, and hence no means of adjusting the heritability to suit the current structure of the population.

Within-strain genetic and phenotypic correlations between traits are shown in Table 6.

TABLE 6.

Genetic correlations (with s.e.s)(above diagonal) and phenotypic (below diagonal) correlations between all traits, fitting genetic group as a covariable †

	LW	DIAM	DIAM_sd	P_CASH	EAP	Length	log(P_CASH)	log(EAP)
LW		0.03	-0.13	-0.25	0.13	0.02	-0.29	0.03
		0.12	0.14	0.10	0.12	0.12	0.12	0.12
DIAM	0.18		0.68	0.65	0.83	0.60	0.81	0.79
			0.09	0.08	0.07	0.14	0.07	0.08
DIAM_sd	-0.01	0.50		0.37	0.31	-0.08	0.37	0.29
				0.12	0.14	0.30	0.12	0.13
P_CASH	-0.08	0.41	0.17		0.90	0.57	0.95	0.89
EAP	0.26	0.43	0.15	0.94		0.76	0.93	0.96
						0.13		
Length	0.08	0.32	-0.06	0.44	0.47		0.89	0.84
							0.06	0.10
log(P_CASH)	-0.08	0.43	0.17	0.90	0.86	0.52		0.75
log(EAP)	0.23	0.46	0.14	0.85	0.91	0.54	0.47	

† Genetic correlations without standard errors were calculated using Thompson and Hill (1990) methodology

These results confirm previously published findings (Pattie and Restall, 1989; Bigham *et al,* 1993; Couchman and Wilkinson, 1987; Gifford *et al,* 1990) that fibre diameter and fibre weight are positively (unfavourably) correlated, as would be expected from the functional relationships between these traits. Of particular importance is the observation that the genetic correlation between these traits is larger than the phenotypic correlation, implying that an index which aims to improve both traits simultaneously will have a lower heritability than that observed for the two component traits. This is illustrated by the observation that the within-strain and composite heritabilities of log(cashmere production index) (the cashmere production index is a phenotypic indication of the value of cashmere produced, calculated as EAP(1-0.2(DIAM-DIAM)), see Bishop and Russel, 1994) were only 0.25 and 0.35, respectively. The other important observation to be made in Table 6 is that live weight is essentially uncorrelated with the fibre traits.

Composite genetic and phenotypic correlations are shown in Appendix 2. These correlations are generally similar to those in table 6, although some systematic differences are apparent, e.g. all correlations with live weight are more negative. Although these are the most relevant correlations when dealing with this population of animals, the within-strain correlations in table 6 are probably more relevant when extrapolating to other populations.

Functional Relationships between traits

Results of the logarithmic regressions investigating the relationships between P_CASH, length and fibre diameter are shown in Table 7. These regression coefficients may be interpreted as : P_CASH a $Length^{0.99}$, P_CASH a $DIAM^{2.70}$, P_CASH a $(DIAM^2+DIAM\_sd^2)^{1.32}$, and P_CASH a $Length^{0.74}DIAM^{1.79}$, respectively. In the last equation the exponents are a little less than may be expected from the individual traits due to the positive correlation between Length and DIAM. The important point to note from these results is that although P_CASH is linearly related to fibre length, it is not linearly related to fibre diameter, being proportional to a power significantly greater than 2.0. This is explicable from the observation that fibre diameter and length are positively correlated. Therefore, samples with coarser fibres will also tend to have longer fibres, hence P_CASH a $DIAM^k$, where k is greater than 2.0. Although the actual exponent is possibly of limited predictive value, it does imply that selection to decrease fibre diameter may cause a disproportionately large reduction in cashmere weight. This is investigated below.

TABLE 7.

Regressions of log(P_CASH) of functionally related traits

	log(Length)	log(DIAM)	log(DIAM*)	†log(length)	+ log(DIAM)
b	0.99	2.70	2.65	0.74	1.79
s.e.	0.06	0.10	0.10	0.06	0.18

† DIAM* = _(DIAM^2+DIAM_sd^2)

A mentioned above, the number of fibres present in the sample, N, was not counted in this population. Only when this information comes available can possible non-linear relationships between traits be fully investigated. Another relationship of potential interest is that between total cashmere production and live weight. Unfortunately, EAP does not allow this relationship to be determined as EAP, itself, is calculated as a non-linear function of live weight and P_CASH.

Predicting responses to selection

The effects of the non-linear relationships between fibre traits on responses to selection can be investigated in this dataset, for the specific example of fibre diameter and cashmere weight. Amongst the bucks used to produce the kids born in 1992 and 1993 were males selected on the basis of fibre diameter as well as unselected "control" males. These bucks were mated at random to unselected females. Thus the population may be considered to be partitioned at this stage into separate lines, including *diameter* and *control* lines, with 1992 and 1993 born kids representing replicated rounds of selection. Line means for traits of interest for both sets of kids are shown in Table 8. Comparing actual responses with those expected from achieved selection differentials and estimated genetic parameters (using composite heritabilities relevant to each year) the responses in the diameter line, expressed as a deviation from the *control* line, were -0.62 mm vs an expected value of -0.57 mm and -0.31 mm vs -0.56 mm, in 1992 and 1993, respectively.

Of particular interest in these result are the correlated responses to selection. In both years, the response in the *diameter* line was accompanied by a large decrease in both EAP and P_CASH. Assuming no non-linear relationships between traits, the correlated response in P_CASH can be easily predicted

TABLE 8.

Line means (and s.e.s) for selected and control line kids 1992 born kids

Line	No. Kids	No. Sires	Live Weight (kg)	Fibre Diameter (mm)	EAP (g)	P_CASH (g)	logarithm of P_CASH	DIAM
diameter	112	5	15.2 (0.3)	15.5 (0.2)	189 (21)	0.214 (0.011)	-1.63 (0.04)	2.73 (0.008)
control	125	5	14.8 (0.3)	16.1 (0.2)	240 (20)	0.271 (0.011)	-1.38 (0.04)	2.78 (0.008)

1993 born kids

Line	No. Kids	No. Sires	Live Weight (kg)	Fibre Diameter (mm)	EAP (g)	P_CASH (g)	logarithm of P_CASH	DIAM
diameter	81	5	16.7 (0.4)	14.5 (0.1)	208 (20)	0.218 (0.011)	-1.61 (0.04)	2.67 (0.007)
control	62	4	17.3 (0.4)	14.8 (0.2)	264 (21)	0.269 (0.014)	-1.39 (0.05)	2.69 (0.009)

from selection theory. Using composite heritabilities, genetic correlations and phenotypic standard deviations relevant to 1990 and 1991, predicted mean values for P_CASH in the *diameter* line in 1992 and 1993 were 0.233 and 0.232, respectively. These values underestimate the actual correlated responses, as the observed mean values were 0.214 and 0.218, respectively. The functional relationships investigated between the fibre traits suggests that on the log scale these traits may be linear functions of each other. Calculating correlated responses to selection for P_CASH, considering all traits and selection differentials on the log scale and then backtransforming to the observed scale, again using composite heritabilities and standard deviations appropriate to each year, yielded predicted mean values for P_CASH in 1992 and 1993 of 0.213 and 0.212, respectively. These values are very close to the observed values and indicate that selection to reduce fibre diameter will result in a decrease in fibre weight that is, proportionately, even larger than the direct response to selection. Mean EAP values in the *diameter* line were also more accurately predicted when using log-transformed values to make the predictions.

It can be concluded that traits which are non linearly related to each other, e.g. cashmere weight and fibre diameter, may show unexpected correlated responses to selection if linear relationship are assumed. A simple solution to this problem may simply be to transform the traits to the log scale and make all selection decisions and predictions on this scale. For the case of single trait selection, this will not affect the candidates selected, but it may have a large effect on the predicted responses to selection.

CONCLUSIONS

Several conclusions may be drawn from the results presented in this paper. Firstly, it has been demonstrated that fibre traits in cashmere goats are very strongly inherited, in agreement with previously published results. Accompanying this strong additive genetic control is the observation that the maternal genetic effects on these fibre traits are negligible, indicating that they can safely be ignored in genetic improvement programmes.

Secondly, the diverse genetic origin of the goats contributing to this crossbred population has been shown to contribute considerable genetic variation to most of the traits measured. This extra information can be incorporated into the heritability estimates to reflect the structure at any point in time, and hence be used in the construction of appropriate selection indices.

Thirdly, consideration of the functional relationships which exist between the fibre traits explains the unfavourable correlations observed between fibre diameter and cashmere weight, and reveals non-linear relationships between these two traits. Consideration of these traits on the log scale helps with the interpretation of these traits, and on a subset of the data it enabled the correlated decrease in cashmere weight to be accurately predicted when selection was made to decrease fibre diameter.

The information now exists to construct selection indices to meet any desired objective in the improvement of cashmere production. The challenge still remains to devise strategies which will successfully jointly improve both cashmere weight and fibre diameter.

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APPENDIX 1

The relationship between cashmere weight and fibre diameter may be considered as follows.

Defining L_i and D_i and N to be the length, diameter and number of fibres in the patch sample, then:

$$
\begin{aligned}
\text{P\_CASH} &= k\, S\, L_i\, D_i^2 \\
&= kN\{(L - bD)E(D_i^2) + bE(D_i^3)\} \qquad \text{... (i)} \\
&= kN\{L(s_D^2 + D^2) + b(2Ds_D^2 + gs_D^3)\} \quad \text{... (ii)}
\end{aligned}
$$

where b is the within-sample regression of fibre length on diameter, g is the coefficient of skewness for fibre diameter and k is a scaling factor.

Equation (i) requires the assumption: $E(e_i, D_i^2) = 0$, where e_i is the residual from the linear regression of L on D. Regression analyses showed this assumption to be robust for between animal relationships, but the validity for within-sample relationships is unknown. Equation (ii) shows that the weight of cashmere is, theoretically, a complex function of the mean, variance and skewness of fibre diameter, as well as the relationships between fibre length,

fibre diameter and follicle density within a sample.

Assuming that the within sample correlation between fibre length and diameter is substantially less than unity and that the coefficient of variation for fibre length is not large then:

$$P\_CASH = kN\{L(s_D^2 + D^2) \quad \text{(approx.)}$$

i.e. $\quad P\_CASH = kN\{Length \times (DIAM^2 + DIAM\_sd^2) \text{ (approx.)}$

This equation will in turn be dominated by $kN \times Length \times DIAM^2$, as expected.

APPENDIX 2

Composite genetic (above diagonal) and phenotypic (below diagonal) correlations between all traits

	LW	DIAM	DIAM_sd	P_CASH	EAP	Length	log(P_CASH)	log(EAP)
LW		-0.11	-0.18	-0.35	-0.12	-0.16	-0.39	-0.15
DIAM	0.02		0.71	0.70	0.79	0.69	0.83	0.81
DIAM_sd	-0.05	0.53		0.44	0.41	0.08	0.46	0.40
P_CASH	-0.20	0.53	0.25		0.97	0.66	0.96	0.95
EAP	0.08	0.54	0.23	0.97		0.74	0.95	0.98
Length	-0.05	0.42	0.02	0.44	0.55		0.87	0.82
log(P_CASH)	-0.20	0.54	0.25	0.94	0.91	0.60		0.87
log(EAP)	0.06	0.56	0.22	0.91	0.95	0.60	0.65	