Genetic relationship between skin and wool traits in Merino sheep

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Contents

1 Acknowledgement

The data analysed here were collected while I worked at CSIRO Division of Animal Genetics and Division of Animal Production. I would like to acknowledge the contributions of Dr Ted Nay and Mr Ian Maddocks, and the encouragement given by Dr Helen Newton Turner, Dr J M Rendel, Dr A A Dunlop, and Dr T W Scott. I would also like to acknowledge the encouragement of Dr J M Watts in resurrecting this material for re-analysis with more advanced statistical technology, and in suggesting that the emphasis should be on fibre characteristics related to processing performance and procduct quality as well as production characteristics such as clean wool weight.

2 Abstract

3 Introduction

Some years ago an attempt was made to study the relationship between components of clean wool weight and skin characteristics obtained from histological examination of skin biopsy samples (Jackson, Nay, and Turner(1975) [3]. What came out of that study was that skin characteristics could explain a large proportion of the genetic variatrion in clean wool weight, and that the genetic covariance between skin characteristics and wool weight components could be partitioned into three independent functional relationships which were interpreted as three independent sets of genes.

The three independent factors were identified as

- large number of secondary follicles
- straight deep follicles
- primary follicle density

This analysis led to a selection experiment (AB32 in CSIRO jargon) which attempted to select for

- large follicles
- large total number of follicles
- both large follicles and large number of follicles simultaneously

in three selected lines. There was also an unselected control line.

During the course of that experiment some image analysis technology was developed for skin section images. This allowed measurement of the diameter of primary and secondary follicles, in addition to counting their density. These new measurements are available only on the last three years of the experiment but are an important extension which may change the scope and focus of the above multivriate analyses.

There has also been some important progress in our understanding of follicle development in sheep. The work of Moore(....) has shown that follicles develop from a population of pre-papilla cells and that if primary follicle development is suppressed (fewer or smaller primaries) then there are more pre-papilla cells left over to divide, and to develop into secondary follicles. The dynamics of the pre-papilla cell population can be modelled mathematically, so that the relationship between primary development and secondary development can be quantified. The consequences of this for a genetic analysis of primary and secondary follicle development are significant - there is nonlinearity and an element of functional relationships between traits neither of which are taken into account in traditional quantitative genetic analyses.

The objectives of this study are diverse and probably overambitious. Briefly we would like to

- summarize the response to selection which was obtained in the above experiment

- estimate additive genetic parameters for a comprehensive range of skin and wool characteristics
- redo the multivariate analyses mentioned above with an emphasis on fibre quality as well as wool production
- work out how to include knowledge of the developmental relationships between characteristics in a quantitative genetic analysis and apply this to the Moore model mentioned above
- do a systematic check for nonlinearities and shifts in genetic parameters, and find a way of including these in a quantitative genetic analysis

One of the benefits of setting out such a broad objective is that the areas where we fail become indicators of future research directions.

4 Materials and methods

The sheep and the measurements thereon included in this study represent a substantial investment of CSIRO resources over 11 years of a breeding trial and several more years of laboratory measurement work. Unfortunately the experiment was terminated abruptly by a political decision and was never properly analysed or published. What we have, for the present study, is a set of measurements exhibiting various degrees of incompleteness. The present analysis is therefore somewhat complicated and the results may be affected by the severe imbalance with respect to some traits.

4.1 Sheep population studied

The selection experiment is known as AB32 in CSIRO jargon. It commenced in 1974. For two years (1974 and 1975) matings were made of a set of introduced Fine Merino rams across a set of CSIRO bred Medium Merino ewes to generate the base generation animals for a selection trial. Measurements were made on these base generation progeny.

Then, starting with the 1976 mating, the base generation animals were allocate at random to three selection lines and then selected as follows

Line 1 selected for large follicle depth

Line 2 selected for large number of follicles per head (estimated by multiplying follicle density by body surface area)

Line 3 selected for both large follicle depth and large number of follicles per head

Selection continued until 1985, the animals born in 1985 being the last progeny of the selected lines with measurements available.

There was also an unselected control line (AB20 in CSIRO jargon) which was a group of Medium Merino sheep which served as an unselected control for all sheep selection experimants at 'Longford' Research Station. The control line structure is described in Watson, Jackson, and Whiteley(1977) [14].

Pedigree information was available on all sheep, in the case of AB32 extending back to 1974, and in the case of AB20 extendoing back to 1968.

4.2 Traits measured

There were several categories of traits considered for analysis.

4.2.1 Traits for which direct measurements were available

A brief description of the traits for which measurements were available is given in Table 1.

Table 1: Definition of traits measured

Trait name	Abbreviation	Units	Age measured	Description
Staple length	Stal	mm	14 months	Length of wool staple 10 months growth
Crimp frequency	Crimp	no per 2.5cm	14 months	Staple crimp frequency
Fibre diameter	Diam	microns	14 months	Mean fibre diameter by airflow technique
Greasy Fleece Weight	Gfw	Kg	14 months	Weight of fleece in shearing shed
Yield	Yld	percentage	14 months	Percent of clean wool in fleece at 16% regain
Clean wool weight	Cww	Kg	14 months	Weight of clean fibre at 16% regain
Bodyweight	Bwt	Kg	14 months	Live weight of animal
Neck wrinkle	WrN	score 0-6 (0=plain,6=wrinkled)	14 months	Score for skin wrinkle on neck region
Body wrinkle	WrB	score 0-5 (0=plain,5=wrinkled)	14 months	Score for skin wrinkle on body region
Total wrinkle	WrT	sum of WrN and WrB	14 months	Sum of neck and body wrinkle scores
Face cover	Face	score 1-7 (1=open, 7=muffled)	14 months	Score for wool cover on the face
Adjusted staple length	Staladj	mm per 365 days	14 months	Staple length adjusted to a growth period of 365 days
Adjusted clean wool weight	Cwwadj	Kg per 365 days	14 months	Clean wool weight adjusted to a growth period of 365 days
Adjusted greasy fleece weight	Gfwadj	Kg per 365 days	14 months	Greasy fleece weight adjusted to a growth period of 365 days
Follicle number per unit area	Fnua	no per mm_2	14 months	No of primary and secondary follicles per mm_2 from skin biopsy
Follicle S/P ratio	Fr	no units	14 months	Ratio of no of primary to no of secondary follicles from skin biopsy

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Table 1 – *Continued from previous page*

Trait name	Abbreviation	Units	Age measured	Description
Total follicle number	Fnt	no per head x 10^6	14 months	No of follicles on the animal (estimated from Fnua and skin surface area)
Surface area	Sarea	m^2	14 months	Smooth skin surface area (estimated from Bwt with no allowance for wrinkle)
Follicle depth	Fd	mm	14 months	Average follicle depth from skin biopsy and vertical section
Follicle curvature	Fc	score 1-7 (1=straight, 7=curved)	14 months	Follicle curvature score from skin biopsy and vertical section
Follicle unevenness	Fu	score 1-5 (1=even, 5=uneven)	14 months	Score for unevenness of follicle depth from skin biopsy and vertical section
Birth weight	Birwt	Kg	day of birth	Weight of lamb on day of birth
Birthcoat score side	Bcts	score 1-6 (1=no halo hairs on side, 6=fully covered)	day of birth	Score for pattern of halo hairs on side of lamb at day of birth
Birthcoat score back	Bctb	score 1-6 (1=no halo hairs on mid backline, 6=dense halo hairs)	day of birth	Score for density of halo hairs on mid backline on day of birth
Weaning weight	Weanwt	Kg	approx 4 months	Weight of lamb on day of weaning
Weaner greasy fleece weight	WeanGfw	Kg	approx 4 months	Weaner greasy fleece weight at post-weaning shearing
No of lambs born	NLB	no	day of birth	Number of lambs in litter at birth
No of lambs weaned	NLW	no	approx 4 months	Number of lambs in litter at weaning
Greasy wool colour	Colour	score 1-7 (1=white, 7=yellow)	14 months	Score for greasy yolk colour ignoring any stain present

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Table 1 – *Continued from previous page*

Trait name	Abbreviation	Units	Age measured	Description
Flystrike	Fly	score 0-9 (0=absent, 1-9=present to various degrees)	14 months	Score for presence or absene of flystrike at any site
Fleece rot	Flcrot	score 0-9 (0=absent, 1-9=present to various degrees)	14 months	Score for presence or absence of fleece rot
Bacterial stain	Bactst	score 0-9 (0=absent, 1-9=present to various degrees)	14 months	Score for presence or absence of bacterial stain
Mycotic dermatitis	MycD	score 0-9 (0=absent, 1-9=present to various degrees)	14 months	Score for presence or absence of mycotic dermatitis
Mean diameter of primaries	Dp	microns	14 months	Mean diameter of primary fibres from biopsy and horizontal section
Mean diameter of secondaries	Ds	microns	14 months	Mean diameter of secondary fibres from biopsy and horizontal section
Mean diameter of primaries and secondaries	Dps	microns	14 months	Mean diameter of primary and secondary fibres from biopsy and horizontal section
Primary to secondary diameter ratio	DpovDs	no units	14 months	Ratio of mean diameter of primary fibres to mean diameter of secondary fibres
CV of primary diameter	CVDp	no units	14 months	Coefficient of variation of primary fibre diameter
CV of secondary diameter	CVDs	no units	14 months	Coefficient of variation of secondary fibre diameter
Maximum diameter of primaries	MaxDp	microns	14 months	Diameter of the largest primary fibre

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Table 1 – *Continued from previous page*

Trait name	Abbreviation	Units	Age measured	Description
Minimum diameter of primaries	MinDp	microns	14 months	Diameter of the smallest primary fibre
Maximum diameter of secondaries	MaxDs	microns	14 months	Diameter of the largest secondary fibre
Minimum diameter of secondaries	MinDs	microns	14 months	Diameter of the smallest secondary fibre
SD of primaries	SDDp	microns	14 months	Standard deviation of primary fibre diameter
SD of secondaries	SDDs	microns	14 months	Standard deviation of secondary fibre diameter
SD of all fibres	SDD	microns	14 months	Standard deviation of primary and secondary fibre diameter
CV of all fibres	CVD	no units	14 months	Coefficient of variation of primary and secondary fibre diameter
Primaries greater than 30 microns	Gt30Dp	frequency	14 months	Proportion of primary fibres exceeding 30 microns in diameter
Secondaries greater than 30 microns	Gt30Ds	frequency	14 months	Proportion of secondary fibres exceeding 30 microns in diameter
Fibres greater than 30 microns	Gt30D	frequency	14 months	Proportion of fibres exceeding 30 microns in diameter

All of these measured traits were not available on all of the sheep. In particular the traits obtained by image analysis measurement on skin sections were only obtained for the 1982 to 1985 drops of selected lines and only the 1983 and 1985 drops of the control line. Also Crimp Frequency was only measured for 1974 to 1977 and 1982 to 1985. Various other subsets of traits had various patterns of missing observations.

The actual numbers of sheep measured for each trait and each pair of traits is given in Tables 2 to 6. It can be seen that each pair of traits has a different number of observations, with the exception that there are some subsets of traits (such as the 17 image analysis traits from Dp to Gt30D) for which the replication almost identical. Two traits, Birwt and WeanGfw, had very few observations when paired with the image analysis traits (Dp, etc) and had to be omitted from most of the analyses.

This heterogeneity of numbers of observations across traits and pairs of traits required a special approach in statistical analysis which is discussed in section 4.3.

4.2.2 Traits calculated from measured traits using a known functional relationship

These traits are really just another way of looking at the same measurements. If the functional relationship(s) are nonlinear, then we are not introducing redundant information by adding these calculated traits to the multivariate set. Sometimes it helps with biological interpretation to view the trait space from another perspective.

The traits calculated in this way are defined in Table 7.

Some of the traits classed as measurements and included in the previous section should, if one wishes to be pedantic, be included here. Examples are Sarea, Fnt, and Cww. Also Staladj, Cwwadj, and Gfwadj are functions of Stal, Cww, and Gfw but the function coefficients varied from year to year depending on the interval between shearings. We are going to keep things simple and only use the present section for some of the more unusual calculated traits.

4.2.3 Traits predicted from measured traits using an empirical relationship obtained from a statistical fit of a model to external data

There are two predictions of interest here

- Standard deviation of follicle depth (SDFd) predicted from follicle unevenness score
- Intrinsic radius of fibre curvature (IRad) predicted from follicle curvature score

Table 2: Numbers of sheep measured for each pair of traits: Part 1/5.

	Stal	Crimp	Diam	Gfw	Yld	Cww	Bwt	WrN	WrB	WrT
Stal	3651	2227	3632	3638	3632	3632	3622	3619	3616	3616
Crimp	2227	2227	2213	2218	2213	2213	2205	2202	2199	2199
Diam	3632	2213	3638	3637	3637	3637	3620	3617	3614	3614
Gfw	3638	2218	3637	3643	3637	3637	3624	3621	3618	3618
Yld	3632	2213	3637	3637	3637	3637	3619	3616	3613	3613
Cww	3632	2213	3637	3637	3637	3637	3619	3616	3613	3613
Bwt	3622	2205	3620	3624	3619	3619	3629	3625	3622	3622
WrN	3619	2202	3617	3621	3616	3616	3625	3626	3623	3623
WrB	3616	2199	3614	3618	3613	3613	3622	3623	3623	3623
WrT	3616	2199	3614	3618	3613	3613	3622	3623	3623	3623
Face	3644	2220	3630	3635	3629	3629	3620	3617	3614	3614
Staladj	3572	2157	3553	3559	3553	3553	3543	3540	3538	3538
Cwwadj	3553	2143	3558	3558	3558	3558	3540	3537	3535	3535
Gfwadj	3559	2148	3558	3564	3558	3558	3545	3542	3540	3540
Fnua	3092	1768	3084	3087	3083	3083	3078	3076	3073	3073
Fr	3093	1768	3085	3088	3084	3084	3079	3077	3074	3074
Fnt	3074	1751	3075	3077	3074	3074	3079	3076	3073	3073
Sarea	3074	1752	3074	3077	3073	3073	3078	3075	3072	3072
Fd	2587	1281	2580	2582	2579	2579	2575	2573	2570	2570
Fc	2587	1281	2580	2582	2579	2579	2575	2573	2570	2570
Fu	2587	1281	2580	2582	2579	2579	2575	2573	2570	2570
Birwt	925	645	924	925	923	923	919	918	918	918
Bcts	3641	2219	3628	3633	3627	3627	3619	3616	3613	3613
Bctb	3161	1739	3148	3151	3147	3147	3139	3137	3134	3134
Weanwt	3646	2223	3633	3638	3632	3632	3624	3621	3618	3618
WeanGfw	1679	1015	1679	1681	1679	1679	1674	1671	1668	1668
NLB	3645	2221	3632	3637	3631	3631	3623	3620	3618	3618
NLW	3645	2221	3632	3637	3631	3631	3623	3620	3618	3618
Dp	825	468	823	824	823	823	821	821	821	821
Ds	825	468	823	824	823	823	821	821	821	821
Dps	825	468	823	824	823	823	821	821	821	821
DpovDs	825	468	823	824	823	823	821	821	821	821
CVDp	825	468	823	824	823	823	821	821	821	821
CVDs	825	468	823	824	823	823	821	821	821	821
MaxDp	825	468	823	824	823	823	821	821	821	821
MinDp	825	468	823	824	823	823	821	821	821	821
MaxDs	825	468	823	824	823	823	821	821	821	821
MinDs	825	468	823	824	823	823	821	821	821	821
SDDp	825	468	823	824	823	823	821	821	821	821
SDDs	825	468	823	824	823	823	821	821	821	821
SDD	825	468	823	824	823	823	821	821	821	821
CVD	825	468	823	824	823	823	821	821	821	821
Gt30Dp	825	468	823	824	823	823	821	821	821	821
Gt30Ds	825	468	823	824	823	823	821	821	821	821
Gt30D	825	468	823	824	823	823	821	821	821	821
Colour	3393	1971	3388	3391	3387	3387	3377	3375	3375	3375
Fly	3396	1972	3391	3394	3390	3390	3380	3378	3378	3378
Flcrot	3396	1972	3391	3394	3390	3390	3380	3378	3378	3378
Bactst	2279	855	2270	2273	2269	2269	2271	2270	2270	2270
MycD	2279	855	2270	2273	2269	2269	2271	2270	2270	2270

Table 3: Numbers of sheep measured for each pair of traits: Part 2/5.

	Face	Staladj	Cwwadj	Gfwadj	Fnua	Fr	Fnt	Sarea	Fd	Fc
Stal	3644	3572	3553	3559	3092	3093	3074	3074	2587	2587
Crimp	2220	2157	2143	2148	1768	1768	1751	1752	1281	1281
Diam	3630	3553	3558	3558	3084	3085	3075	3074	2580	2580
Gfw	3635	3559	3558	3564	3087	3088	3077	3077	2582	2582
Yld	3629	3553	3558	3558	3083	3084	3074	3073	2579	2579
Cww	3629	3553	3558	3558	3083	3084	3074	3073	2579	2579
Bwt	3620	3543	3540	3545	3078	3079	3079	3078	2575	2575
WrN	3617	3540	3537	3542	3076	3077	3076	3075	2573	2573
WrB	3614	3538	3535	3540	3073	3074	3073	3072	2570	2570
WrT	3614	3538	3535	3540	3073	3074	3073	3072	2570	2570
Face	3649	3565	3550	3556	3092	3093	3074	3074	2587	2587
Staladj	3565	3572	3553	3559	3043	3044	3025	3025	2567	2567
Cwwadj	3550	3553	3558	3558	3034	3035	3025	3024	2559	2559
Gfwadj	3556	3559	3558	3564	3038	3039	3028	3028	2562	2562
Fnua	3092	3043	3034	3038	3097	3097	3078	3079	2590	2590
Fr	3093	3044	3035	3039	3097	3098	3079	3079	2591	2591
Fnt	3074	3025	3025	3028	3078	3079	3079	3078	2574	2574
Sarea	3074	3025	3024	3028	3079	3079	3078	3079	2573	2573
Fd	2587	2567	2559	2562	2590	2591	2574	2573	2592	2592
Fc	2587	2567	2559	2562	2590	2591	2574	2573	2592	2592
Fu	2587	2567	2559	2562	2590	2591	2574	2573	2592	2592
Birwt	925	899	897	899	580	580	579	579	484	484
Bcts	3639	3562	3548	3554	3090	3091	3072	3072	2585	2585
Bctb	3163	3088	3074	3078	2670	2671	2655	2655	2164	2164
Weanwt	3644	3567	3553	3559	3095	3096	3077	3077	2590	2590
WeanGfw	1676	1656	1656	1658	1476	1476	1473	1473	1428	1428
NLB	3643	3572	3558	3564	3091	3092	3073	3073	2588	2588
NLW	3643	3572	3558	3564	3091	3092	3073	3073	2588	2588
Dp	825	798	796	797	824	825	821	821	338	338
Ds	825	798	796	797	824	825	821	821	338	338
Dps	825	798	796	797	824	825	821	821	338	338
DpovDs	825	798	796	797	824	825	821	821	338	338
CVDp	825	798	796	797	824	825	821	821	338	338
CVDs	825	798	796	797	824	825	821	821	338	338
MaxDp	825	798	796	797	824	825	821	821	338	338
MinDp	825	798	796	797	824	825	821	821	338	338
MaxDs	825	798	796	797	824	825	821	821	338	338
MinDs	825	798	796	797	824	825	821	821	338	338
SDDp	825	798	796	797	824	825	821	821	338	338
SDDs	825	798	796	797	824	825	821	821	338	338
SDD	825	798	796	797	824	825	821	821	338	338
CVD	825	798	796	797	824	825	821	821	338	338
Gt30Dp	825	798	796	797	824	825	821	821	338	338
Gt30Ds	825	798	796	797	824	825	821	821	338	338
Gt30D	825	798	796	797	824	825	821	821	338	338
Colour	3390	3320	3314	3318	2844	2845	2833	2833	2339	2339
Fly	3393	3320	3314	3318	2845	2846	2834	2834	2340	2340
Flcrot	3393	3320	3314	3318	2845	2846	2834	2834	2340	2340
Bactst	2280	2214	2204	2208	1812	1813	1809	1809	1307	1307
MycD	2280	2214	2204	2208	1812	1813	1809	1809	1307	1307

Table 4: Numbers of sheep measured for each pair of traits: Part 3/5.

	Fu	Birwt	Bcts	Bctb	Weanwt	WeanGfw	NLB	NLW	Dp	Ds
Stal	2587	925	3641	3161	3646	1679	3645	3645	825	825
Crimp	1281	645	2219	1739	2223	1015	2221	2221	468	468
Diam	2580	924	3628	3148	3633	1679	3632	3632	823	823
Gfw	2582	925	3633	3151	3638	1681	3637	3637	824	824
Yld	2579	923	3627	3147	3632	1679	3631	3631	823	823
Cww	2579	923	3627	3147	3632	1679	3631	3631	823	823
Bwt	2575	919	3619	3139	3624	1674	3623	3623	821	821
WrN	2573	918	3616	3137	3621	1671	3620	3620	821	821
WrB	2570	918	3613	3134	3618	1668	3618	3618	821	821
WrT	2570	918	3613	3134	3618	1668	3618	3618	821	821
Face	2587	925	3639	3163	3644	1676	3643	3643	825	825
Staladj	2567	899	3562	3088	3567	1656	3572	3572	798	798
Cwwadj	2559	897	3548	3074	3553	1656	3558	3558	796	796
Gfwadj	2562	899	3554	3078	3559	1658	3564	3564	797	797
Fnua	2590	580	3090	2670	3095	1476	3091	3091	824	824
Fr	2591	580	3091	2671	3096	1476	3092	3092	825	825
Fnt	2574	579	3072	2655	3077	1473	3073	3073	821	821
Sarea	2573	579	3072	2655	3077	1473	3073	3073	821	821
Fd	2592	484	2585	2164	2590	1428	2588	2588	338	338
Fc	2592	484	2585	2164	2590	1428	2588	2588	338	338
Fu	2592	484	2585	2164	2590	1428	2588	2588	338	338
Birwt	484	927	923	862	926	549	927	927	95	95
Bcts	2585	923	3648	3164	3643	1678	3642	3642	825	825
Bctb	2164	862	3164	3164	3159	1196	3160	3160	825	825
Weanwt	2590	926	3643	3159	3653	1684	3647	3647	825	825
WeanGfw	1428	549	1678	1196	1684	1685	1681	1681	48	48
NLB	2588	927	3642	3160	3647	1681	3652	3652	823	823
NLW	2588	927	3642	3160	3647	1681	3652	3652	823	823
Dp	338	95	825	825	825	48	823	823	825	825
Ds	338	95	825	825	825	48	823	823	825	825
Dps	338	95	825	825	825	48	823	823	825	825
DpovDs	338	95	825	825	825	48	823	823	825	825
CVDp	338	95	825	825	825	48	823	823	825	825
CVDs	338	95	825	825	825	48	823	823	825	825
MaxDp	338	95	825	825	825	48	823	823	825	825
MinDp	338	95	825	825	825	48	823	823	825	825
MaxDs	338	95	825	825	825	48	823	823	825	825
MinDs	338	95	825	825	825	48	823	823	825	825
SDDp	338	95	825	825	825	48	823	823	825	825
SDDs	338	95	825	825	825	48	823	823	825	825
SDD	338	95	825	825	825	48	823	823	825	825
CVD	338	95	825	825	825	48	823	823	825	825
Gt30Dp	338	95	825	825	825	48	823	823	825	825
Gt30Ds	338	95	825	825	825	48	823	823	825	825
Gt30D	338	95	825	825	825	48	823	823	825	825
Colour	2339	926	3390	2911	3394	1434	3394	3394	825	825
Fly	2340	927	3393	2914	3397	1435	3397	3397	825	825
Flcrot	2340	927	3393	2914	3397	1435	3397	3397	825	825
Bactst	1307	630	2277	2277	2278	835	2278	2278	825	825
MycD	1307	630	2277	2277	2278	835	2278	2278	825	825

Table 5: Numbers of sheep measured for each pair of traits: Part 4/5 .

	Dps	DpovDs	CVDp	CVDs	MaxDp	MinDp	MaxDs	MinDs	SDDp	SDDs
Stal	825	825	825	825	825	825	825	825	825	825
Crimp	468	468	468	468	468	468	468	468	468	468
Diam	823	823	823	823	823	823	823	823	823	823
Gfw	824	824	824	824	824	824	824	824	824	824
Yld	823	823	823	823	823	823	823	823	823	823
Cww	823	823	823	823	823	823	823	823	823	823
Bwt	821	821	821	821	821	821	821	821	821	821
WrN	821	821	821	821	821	821	821	821	821	821
WrB	821	821	821	821	821	821	821	821	821	821
WrT	821	821	821	821	821	821	821	821	821	821
Face	825	825	825	825	825	825	825	825	825	825
Staladj	798	798	798	798	798	798	798	798	798	798
Cwwadj	796	796	796	796	796	796	796	796	796	796
Gfwadj	797	797	797	797	797	797	797	797	797	797
Fnua	824	824	824	824	824	824	824	824	824	824
Fr	825	825	825	825	825	825	825	825	825	825
Fnt	821	821	821	821	821	821	821	821	821	821
Sarea	821	821	821	821	821	821	821	821	821	821
Fd	338	338	338	338	338	338	338	338	338	338
Fc	338	338	338	338	338	338	338	338	338	338
Fu	338	338	338	338	338	338	338	338	338	338
Birwt	95	95	95	95	95	95	95	95	95	95
Bcts	825	825	825	825	825	825	825	825	825	825
Bctb	825	825	825	825	825	825	825	825	825	825
Weanwt	825	825	825	825	825	825	825	825	825	825
WeanGfw	48	48	48	48	48	48	48	48	48	48
NLB	823	823	823	823	823	823	823	823	823	823
NLW	823	823	823	823	823	823	823	823	823	823
Dp	825	825	825	825	825	825	825	825	825	825
Ds	825	825	825	825	825	825	825	825	825	825
Dps	825	825	825	825	825	825	825	825	825	825
DpovDs	825	825	825	825	825	825	825	825	825	825
CVDp	825	825	825	825	825	825	825	825	825	825
CVDs	825	825	825	825	825	825	825	825	825	825
MaxDp	825	825	825	825	825	825	825	825	825	825
MinDp	825	825	825	825	825	825	825	825	825	825
MaxDs	825	825	825	825	825	825	825	825	825	825
MinDs	825	825	825	825	825	825	825	825	825	825
SDDp	825	825	825	825	825	825	825	825	825	825
SDDs	825	825	825	825	825	825	825	825	825	825
SDD	825	825	825	825	825	825	825	825	825	825
CVD	825	825	825	825	825	825	825	825	825	825
Gt30Dp	825	825	825	825	825	825	825	825	825	825
Gt30Ds	825	825	825	825	825	825	825	825	825	825
Gt30D	825	825	825	825	825	825	825	825	825	825
Colour	825	825	825	825	825	825	825	825	825	825
Fly	825	825	825	825	825	825	825	825	825	825
Flcrot	825	825	825	825	825	825	825	825	825	825
Bactst	825	825	825	825	825	825	825	825	825	825
MycD	825	825	825	825	825	825	825	825	825	825

Table 6: Numbers of sheep measured for each pair of traits: Part 5/5.

	SDD	CVD	Gt30Dp	Gt30Ds	Gt30D	Colour	Fly	Flcrot	Bactst	MycD
Stal	825	825	825	825	825	3393	3396	3396	2279	2279
Crimp	468	468	468	468	468	1971	1972	1972	855	855
Diam	823	823	823	823	823	3388	3391	3391	2270	2270
Gfw	824	824	824	824	824	3391	3394	3394	2273	2273
Yld	823	823	823	823	823	3387	3390	3390	2269	2269
Cww	823	823	823	823	823	3387	3390	3390	2269	2269
Bwt	821	821	821	821	821	3377	3380	3380	2271	2271
WrN	821	821	821	821	821	3375	3378	3378	2270	2270
WrB	821	821	821	821	821	3375	3378	3378	2270	2270
WrT	821	821	821	821	821	3375	3378	3378	2270	2270
Face	825	825	825	825	825	3390	3393	3393	2280	2280
Staladj	798	798	798	798	798	3320	3320	3320	2214	2214
Cwwadj	796	796	796	796	796	3314	3314	3314	2204	2204
Gfwadj	797	797	797	797	797	3318	3318	3318	2208	2208
Fnua	824	824	824	824	824	2844	2845	2845	1812	1812
Fr	825	825	825	825	825	2845	2846	2846	1813	1813
Fnt	821	821	821	821	821	2833	2834	2834	1809	1809
Sarea	821	821	821	821	821	2833	2834	2834	1809	1809
Fd	338	338	338	338	338	2339	2340	2340	1307	1307
Fc	338	338	338	338	338	2339	2340	2340	1307	1307
Fu	338	338	338	338	338	2339	2340	2340	1307	1307
Birwt	95	95	95	95	95	926	927	927	630	630
Bcts	825	825	825	825	825	3390	3393	3393	2277	2277
Bctb	825	825	825	825	825	2911	2914	2914	2277	2277
Weanwt	825	825	825	825	825	3394	3397	3397	2278	2278
WeanGfw	48	48	48	48	48	1434	1435	1435	835	835
NLB	823	823	823	823	823	3394	3397	3397	2278	2278
NLW	823	823	823	823	823	3394	3397	3397	2278	2278
Dp	825	825	825	825	825	825	825	825	825	825
Ds	825	825	825	825	825	825	825	825	825	825
Dps	825	825	825	825	825	825	825	825	825	825
DpovDs	825	825	825	825	825	825	825	825	825	825
CVDp	825	825	825	825	825	825	825	825	825	825
CVDs	825	825	825	825	825	825	825	825	825	825
MaxDp	825	825	825	825	825	825	825	825	825	825
MinDp	825	825	825	825	825	825	825	825	825	825
MaxDs	825	825	825	825	825	825	825	825	825	825
MinDs	825	825	825	825	825	825	825	825	825	825
SDDp	825	825	825	825	825	825	825	825	825	825
SDDs	825	825	825	825	825	825	825	825	825	825
SDD	825	825	825	825	825	825	825	825	825	825
CVD	825	825	825	825	825	825	825	825	825	825
Gt30Dp	825	825	825	825	825	825	825	825	825	825
Gt30Ds	825	825	825	825	825	825	825	825	825	825
Gt30D	825	825	825	825	825	825	825	825	825	825
Colour	825	825	825	825	825	3398	3398	3398	2277	2277
Fly	825	825	825	825	825	3398	3401	3401	2280	2280
Flcrot	825	825	825	825	825	3398	3401	3401	2280	2280
Bactst	825	825	825	825	825	2277	2280	2280	2280	2280
MycD	825	825	825	825	825	2277	2280	2280	2280	2280

Table 7: Definition of traits calculated from measured traits using a known functional relationship

Trait name	Abbreviation	Units	Functional relationship
Primary follicle density	Fnpua	no per mm^2	$Fnpua = \frac{Fnua}{(Fr+1)}$
Secondary follicle density	Fnsua	no per mm^2	$Fnsua = \frac{(Fr)(Fnua)}{(Fr+1)}$
Total primary follicle number	Fnpt	No per head x 10^6	$Fnpt = (Fnpua)(Sarea)$
Total secondary follicle number	Fnst	No per head x 10^6	$Fnst = (Fnsua)(Sarea)$
Crimp wavelength	Crwvl	mm	$Crwvl = \frac{25.4}{Crimp}$
Crimps per staple	Crst	number	$Crst = Crimp * Stal/25.4$
Crimps per 365 days (crimp frequency in time)	Crstadj	number per 365 days	$Crstadj = Crimp * Staladj/25.4$
Crimp wavelength in time	Crwvt	days	$Crwvt = \frac{365}{Crstadj}$

The empicical prediction equations for SDFd and IRad are

$$SDFd = -0.4874 + 1.8282(Fu) \quad (1)$$

$$ICurv = 0.22447 + 0.25223(Fc) \quad (2)$$

$$IRad = \frac{1}{(ICurv)} \quad (3)$$

Notice that predicting IRad is a 2 step procedure, we first predict ICurv, then calculate a reciprocal transformation to get IRad.

In the case of SDFd ...

In the case of $IRad$ there are a number of traits which we can calculate from IRad and crimp wavelength (Crwvl) based on the model for crimp formation in staples developed by Jackson and Watts(2015) [4]. The relevant equations, assuming a stretched helix model for staple crimp formation, are

$$Crampl = \sqrt{(Irad)^2 - \left(\frac{Crwvl}{2\pi}\right)^2} \quad (4)$$

$$\frac{L_f}{L_s} = \frac{2\pi Irad}{Crampl} \quad (5)$$

$$L_f = L_s\left(\frac{L_f}{L_s}\right) \quad (6)$$

These equations and the development of the method of predicting Irad from Fc are described in Jackson and Watts(2016) [5].

A complete list of predicted traits and traits derived from predicted traits is given in Table 8.

4.2.4 Traits predicted from a model describing skin development

4.2.5 Traits introduced to accomodate nonlinearity

4.3 Statistical techniques

The initial step in analysing these data was to fit a mixed model which adjusted for appropriate fixed effects and estimated additive genetic, environmental, and phenotypic variance/covariance components. This was followed by multivariate analysis of the additive genetic variance/covariance matrix with the goal of underatanding what dimensions of genetic variation were operating in the wool and skin trait spaces.

An attempt was made to incorporate knowledge from a model of skin development in to these quantitative genetic analyses.

A search was made for nonlinear behaviour in the relationships between traits. An attempt was made to estimate genetic parametes separately for various subgroups of the data to see if parameters were heterogeneous.

Table 8: Definition of traits predicted from measured traits using an empirical relationship and of traits calculated from predicted traits

Trait name	Abbreviation	Units	Obtained by
Standard deviation of follicle depth	SDFd	mm	$SDFd = -0.4874 + 1.8282(Fu)$
Intrinsic fibre curvature	Icurv	radians/mm	$ICurv = 0.22447 + 0.25223(Fc)$
Intrinsic fibre radius of curvature	Irad	mm	$IRad = \frac{1}{(ICurv)}$
Crimp amplitude	Crampl	mm	$Crampl = \sqrt{(Irad)^2 - \left(\frac{Crwvl}{2\pi}\right)^2}$
Fibre length to staple length ratio	LfovLs	no units	$\frac{L_f}{L_s} = \frac{2\pi Irad}{Crampl}$
Fibre length	Lf	mm	$L_f = L_s\left(\frac{L_f}{L_s}\right)$

4.3.1 Mixed model fitting

The software used for mixed model fitting and estimation of variance components and genetic parameters is known as *dmm*. *dmm* is free software available under the GPL licence from the CRAN repository. *dmm* runs as a package under the R statistical language [11]. *dmm* has a comprehensive user's guide (Jackson(2015) [6]) which covers the statistical theory used for estimation and a set of worked examples.

Variance component estimation is one of the most difficult areas of statistics. It is comprehensively documented by Searle et al (1992) [12]. The procedure which current wisdom seems to consider most appropriate is called REML. The procedures used by *dmm* are MINQUE and bias-corrected-ML. In most cases where data are not extremely unbalanced, there is very little difference between procedures. For the current task, *dmm* is most suited, because it handles multiple traits with unequal replication, because it estimates both variance/covariance components and genetic parameters arising therefrom, because it allows estimation of maternal as well as individual genetic and environmental vriance components and the covariances between them, and because it makes extensive use of procedures developed by Wolak(2014) [15] for computing additive and non-additive relationship matrices for both autosomal and sexlinked genetic variation, thus allowing estimation of dominance and epistatic variance components where the data allows.

The procedure followed by *dmm* is heirarchical. We first fit a model for fixed effects modelling observations on individual sheep as follows

$$Y_{ijk} = \mu + Sex_i + YearbixLine_j + r_{ijk} \tag{7}$$

where

Y_{ijk} is an observation on the kth individual of the ith Sex and the jth Year of birth x Line combination

μ is an overall mean of the observations

Sex_i is an effect due to the ith Sex

$YearbixLine_j$ is an effect due to the jth combination of Year of birth and Line

r_{ijk} is a residual deviation for the kth individual of the ith Sex and the jth Year of birth x Line combination

Equation 7 is stated as a univariate model for simplicity. It can, of course be fitted to each of a set of traits. The residual deviations from model 7 represent the observations *adjusted for* the fixed effect.

The next step is to fit a dyadic model to the residuals from model 7. A dyad is a pair of individuals. A dyadic model is a model for the covariances between the residuals for pairs of individuals. The dyadic model attempts to fit various genetic and environmental variance/covariance components to the covariances between the residuals for each dyad. In the present case we first attempt an elementary partitioning of the dyadic covariances into additive genetic and environmental variance/covariance components. The dyadic model for this simple case can be written

$$Cov(r_k, r_{k'}) = A_{kk'} VarG(Ia) + E_{kk'} VarE(I) + \Delta_{kk'} \tag{8}$$

where

$Cov(r_k, r_{k'})$ is the covariance of the kth and k'th residuals from the fitting of model 7

$A_{kk'}$ is the kk'th element of the additive genetic relationship matrix, that is the relationship coefficient between the kth and k'th individuals

$VarG(Ia)$ is the individualadditive genetic variance

$E_{kk'}$ is the kk'th element of the environmental relationship matrix which is usually assumed to be an identity matrix

$VarE(I)$ is the individual environmental variance

$\Delta_{kk'}$ is the k'th residual for the dyadic model 8

Again, equation 8 is stated as a univariate model for simplicity, and only the most elementary partitioning into $VarG(Ia)$ and $VarE(I)$ is presented. There is a full exposition in Jackson(2015) [6].

The dyadic model 8 represents a set of equations which can be solved by ordinary least squares regression techniques to yield estimates of $VarG(Ia)$ and $VarE(I)$. This yields MINQUE estimates for the two variance components. Given these estimates we can then go back to the monadic model 7 and obtain GLS estimates of the fixed effects and residuals. If we then use the GLS residuals in the dyadic model 8 we obtain bias-corrected-ML estimates for the two variance components. There is a full presentation of variance component estimation in Jackson(2015) [6].

Given variance component estimates we can readily transform each component to a heritability (if it is univariate) or to a genetic(or environmental) correlation (if it is a between trait covariance component). These transforms, and the accompanying standard error estimates, are fully covered in Jackson(2015) [6]

Because of the complication of different numbers of replicates for each trait and each pair of traits it was necessary to perform the model fitting part of the analysis separately for each pair of traits, except that some economy was obtained by blocking together sets of traits for which the replication was almost identical. The blockings used for the measured traits of Tables 2 to 6 were as follows

Block1 "Stal" "Diam" "Bwt"

Block2 "WrN" "WrB" "WrT" "Face"

Block3 "Gfw" "Yld" "Cww"

Block4 "Staladj" "Gfwadj" "Cwwadj"

Block5 "Crimp"

Block6 "Dp" "Ds" "Dps" "DpovDs" "CVDp" "CVDs" "MaxDp" "MinDp""MaxDs" "MinDs" "SDDp" "SDDs" "SDD" "CVD" "Gt30Dp" "Gt30Ds" "Gt30D"

Block7 "Fnua" "Fr" "Fnt" "Sarea"

Block8 "Fd" "Fc" "Fu"

Block9 "Colour" "Fly" "Flcrot"

Block10 "Bactst" "MycD"

Block11 "Bcts" "Bctb" "Weanwt"

Block12 "NLB" "NLW"

Note that two traits, Birwt and WeanGfw, have been omitted because of small subclass numbers in pairings with the Block6 traits. The blocking is based on similarity of subclass numbers and in some cases where the replication was high

it was necessary to reduce the number of traits per block to conserve computer memory. The blocking is merely a computational device. The fixed effect model had to contain the same effects for every pair of blocks, but the number of levels of each effect could vary between block pairs.

After obtaining the variance component estimates and genetic parameters for each pair of blocks, it was necesary to condense these 144 sets of estimates back into a single genetic covariance matrix estimate (and a single genetic correlation matrix estimate). There is no guarantee that the 48 x 48 matrices thus obtained are positive definite, even though the 12 x 12 blocks which make then up are individually positive definite. This was therefore checked and if required an iterative amendment made using the R routine *nearPD()* which is available in the *Matrix* package.

When the 'calculated' and 'predicted' traits were added the number of blocks was extended as required. For the 'calculated' traits, those related to crimp (Crwvl, Crst, Crstadj, Crwvt) were added to Block 5, and the primary and secondary density traits (Fnpua, Fnsua, Fnpt, Fnst) were made Block 13.

4.3.2 Genetic models

The simple partitioning of phenotypic (co)variances into additive genetic and environmental (co)variances given in equation 8 is almost always the starting point for quantitative genetic analysis. It should be noted that just beacuse a considerable proportion of the phenotypic (co)variancees come out as additive genetic does not mean that most of the gene effects have to be additive. Dominance and epistatic gene effects also generate some additive genetic variance.

Dominance and epistatic (co)variances can be estimated where the data are adequate. In the present case the data probably do not have sufficient closely related animals in the pedigree to permit estimation of nonadditive genetic (co)variances. We shall check, but I am not optimistic.

It is possible to consider a model where the individual's phenotype is made up of individual additive genetic and individual environmental components from its own genes plus maternal additive genetic and maternal environmental components from its mother's genes and its mother's environment. This leads to four components of variance, and to maternal additive genetic correlations as well as individual additive genetic correlations. Such maternal effects tend to occur where the trait is obviously influenced by the mother (eg Birth weight of a lamb is influenced by its own genes and by its mother's genes). This could easily be the case for skin development so maternal inheritance has to be investigated. The *dmm* software can analyse maternal inheritance and its Users Guide (Jackson(2015) [6] contains a full presentation of the genetic theory and some worked examples. Again, the data must have adequate pedigree relationships to permit maternal genetic analysis.

It is possible that some of the genes affecting skin and wool traits are on the X chromasome. The *dmm* software can partition genetic (co)variances into autosomal and sex-linked. There is evidence in one of the example analyses in Jackson(2015) [6] that some wool traits have sex-linked inheritance. This

has consequences for selection procedures since selected rams to not pass their sexlinked genes to male offspring, so the male-to-male pathway of improvement does not operate. Again there are pedigree requirements for the data to be adequate for estimation of sexlinked components.

Genetic parameters are not necessarily the same in all populations. There is some evidence that parameters for wool traits are sex-specific (Jackson et al(1986) [7], and they are almost certainly age-specific. They may also differ between single-born and twin-born animals and this is behind the decision to include *NLB* and *NLW* as traits rather than as fixed effects. Fitting a fixed effect which is partly genetic may remove or distort genetic variation for other traits. The present data may not be adequate to examine any of these heterogeneities.

4.3.3 Multivariate analysis

The initial approach was to simply look at the dimensionality of the genetic trait space using principal component analysis. The size and shape of the additive genetic trait space is given by the additive genetic covariance matrix. A large covariance matrix is not an easy object to comprehend. To help with this one can reduce the marix to *cononical form* which simply means finding the directions in which genetic variation is greatest, and the directions in which genetic variation is small. The technique for doing this on a single covariance matrix is known as principal components analysis.

One of the difficulties of principal components analysis is that its results are seriously biased if all traits are not measured in the same units. The traditional way of dealing with this is to do everything in standard deviation units, that is to use a correlation matrix instead of a covariance matrix. In our case this would amount to scaling to genetic standard deviation units. However we are not going to do that, we are going to scale to phenotypic standard deviation units which is the traditional approach of quantitative genetics to scaling. To do this we need to do a principal component analysis on the matrix shown below for the two trait case

$$\boldsymbol{H_{G(Ia)}} = \begin{bmatrix} h_1^2 & h_1 h_2 r_{G(Ia)} \\ h_1 h_2 r_{G(Ia)} & h_2^2 \end{bmatrix}$$

where

h_1^2 is heritability of trait 1

h_2^2 is heritability of trait 2

$r_{G(Ia)}$ is the genetic correlation between traits 1 and 2

One reason for this approach is to avoid giving excess weight to traits for which the proportion of variance ie heritability) is small. By putting heritabilities (or proportion of variance) on the diagonal we are weighting each trait by its heritability. That is what is required if we wish to compare genetic variation of various traits.

The $\boldsymbol{H}$ matrices are not the same as the matrix $\boldsymbol{GP^{-1}}$ from the multivariate breeders equation **??**. That matrix is in trait units and is not symmetric and is for prediction of genetic change. Here we are attempting to study genetic variation itself, not prediction.

Following this, traits were grouped into fleece observations, skin observations, and fibre traits of textile significance, and the genetic covariances between these groupings analysed using canonical regression techniques.

The traits included in each group were as follows

Fleece observations Cww, Yls, Gfw, Stalen, Diam, Crimp, Crwvl

Skin observations Fnua, Fr, Fnt, Fd, Fc, Fu, Dp, Ds

Fibre traits Lf, Diam, SDLf, SDD

4.3.4 Nonlinearities

4.3.5 Genetic parameter shifts

4.4 Quantitative genetic theory

5 Results

5.1 Fixed effects

Model 7 was fitted to all 56 measured traits. The resulting estimates of fixed effects are reported as fitted constants in Tables 9 to 15. The constants are fitted as contrasts defined to sum to zero over all the levels of each effect. Hence the notation *C(Sex, sum)1* refers to the level coded as 1 for a contrast named *Sex*, ie rams. The level coded as 2 (ie ewes) is not reported as its effect is equal to minus the ram effect (because they sum to zero).

The mean is reported as *(Intercept)*. If one wants the mean for rams one simply adds the *C(Sex, sum)1* effect to the *(Intercept)*, ie to the mean.

The effect reported as *C(YbxLi, sum)yyl* refers to combinations of *Year born in* (yy) and *Line* (l). Year born in (yy) ranges from 74 to 85 (meaning 1974 to 1985). Line (l) is as follows

0 unselected base animals (years 74 and 75 only)

1 selection line 1, selected for high follicle depth

2 selection line 2, selected for large number of follicles per head

3 selection line 3, selected for both large follicle depth and high number of follicles per head

4 unselected control line

Table 9: Fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 1/7.

	Stal	Diam	Bwt	WrN	WrB	WrT	Face	Gfw
C(Sex, sum)1	-1.38	-0.53	2.42	-0.12	-0.13	-0.25	0.30	-0.06
C(YbxLi, sum)749	-0.41	0.12	-0.25	0.12	0.08	0.21	0.44	-0.13
C(YbxLi, sum)750	-0.85	1.38	-0.37	0.01	-0.09	-0.07	0.05	-0.09
C(YbxLi, sum)759	13.71	-1.63	-1.92	0.31	-0.37	-0.05	0.80	-0.47
C(YbxLi, sum)761	17.26	-0.43	-1.31	0.17	-0.62	-0.44	0.29	-0.51
C(YbxLi, sum)762	27.11	0.43	1.06	0.00	0.06	0.07	-0.14	1.09
C(YbxLi, sum)763	25.15	0.36	0.10	0.03	-0.03	0.01	0.22	0.94
C(YbxLi, sum)769	21.83	0.82	1.05	0.21	0.09	0.32	-0.42	1.07
C(YbxLi, sum)771	28.84	1.16	-1.13	0.09	-0.11	-0.02	0.01	1.04
C(YbxLi, sum)772	-4.41	-0.82	-4.14	0.50	0.56	0.79	0.87	-0.69
C(YbxLi, sum)773	-9.39	-1.51	-2.01	0.08	-0.02	0.07	1.39	-0.77
C(YbxLi, sum)779	-4.48	-0.66	-3.94	0.16	0.20	0.37	0.60	-0.60
C(YbxLi, sum)781	5.30	0.12	2.83	-0.20	-0.17	-0.36	-0.46	0.34
C(YbxLi, sum)782	4.86	1.77	3.39	0.12	0.14	0.27	-0.23	0.55
C(YbxLi, sum)783	4.01	-0.48	4.85	0.17	0.50	0.67	-0.08	0.39
C(YbxLi, sum)789	-2.30	-0.82	7.16	-0.15	0.12	-0.02	0.17	0.27
C(YbxLi, sum)791	3.24	-0.67	6.07	0.09	0.32	0.41	-0.13	0.43
C(YbxLi, sum)792	3.61	0.99	6.39	0.04	0.20	0.26	-0.26	0.51
C(YbxLi, sum)793	-0.81	0.63	0.05	-0.02	0.06	0.05	-0.34	-0.14
C(YbxLi, sum)799	-6.61	-1.05	2.20	-0.28	-0.23	-0.51	-0.06	-0.20
C(YbxLi, sum)801	-3.65	-0.33	0.16	-0.38	-0.37	-0.74	-0.53	-0.10
C(YbxLi, sum)802	-1.73	1.43	3.03	-0.13	-0.17	-0.30	-0.39	-0.00
C(YbxLi, sum)803	-12.34	-1.61	-5.84	0.25	0.58	0.84	0.29	-0.87
C(YbxLi, sum)809	-15.02	-2.55	-4.58	-0.23	-0.00	-0.23	0.18	-1.01
C(YbxLi, sum)821	-12.39	-2.10	-4.98	-0.02	0.28	0.26	0.06	-0.84
C(YbxLi, sum)822	-7.40	-0.30	-0.70	-0.26	-0.26	-0.51	-0.19	-0.17
C(YbxLi, sum)823	-3.92	-0.17	-1.33	-0.17	-0.07	-0.23	-0.57	-0.04
C(YbxLi, sum)829	1.29	0.36	-3.27	-0.05	-0.07	-0.11	0.52	-0.63
C(YbxLi, sum)831	-1.84	1.49	-0.39	-0.16	-0.30	-0.45	-0.29	-0.08
C(YbxLi, sum)832	5.06	0.59	1.00	0.03	0.08	0.12	-0.10	0.28
C(YbxLi, sum)833	1.42	-0.35	2.77	-0.21	-0.14	-0.34	-0.25	0.25
C(YbxLi, sum)839	-6.34	0.65	2.98	0.30	0.31	0.62	-0.05	0.34
C(YbxLi, sum)841	-6.24	0.08	3.57	-0.16	-0.25	-0.40	-0.18	0.14
C(YbxLi, sum)842	-7.81	1.70	3.25	0.51	0.33	0.85	-0.37	0.44
C(YbxLi, sum)843	-4.86	2.09	2.99	0.35	0.05	0.41	-0.48	0.39
C(YbxLi, sum)849	-6.09	0.06	-4.21	-0.20	-0.13	-0.33	-0.14	0.01
C(YbxLi, sum)851	-12.48	-1.20	-2.69	-0.42	-0.31	-0.72	0.62	-0.18
C(YbxLi, sum)852	-7.78	-0.24	-3.80	-0.37	-0.31	-0.68	-0.27	-0.06
C(YbxLi, sum)853	-7.60	0.71	-2.98	-0.39	-0.42	-0.80	-0.23	-0.05
C(YbxLi, sum)859	-5.25	0.54	-1.05	0.11	0.23	0.34	-0.10	-0.11
(Intercept)	81.40	19.29	35.15	2.49	1.64	4.12	3.66	3.20

Table 10: Fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 2/7.

	Yld	Cww	Staladj	Gfwadj	Cwwadj	Crimp	Crwvl	Crst
C(Sex, sum)1	-1.03	-0.08	-2.18	-0.10	-0.11	-0.22	0.04	-0.99
C(YbxLi, sum)749	-0.31	-0.10	-0.62	-0.09	-0.07	-2.14	0.39	-6.74
C(YbxLi, sum)750	-1.73	-0.11	-1.04	-0.04	-0.09	0.02	-0.03	7.13
C(YbxLi, sum)759	2.11	-0.26	-10.97	-1.40	-0.90	-1.49	0.25	3.28
C(YbxLi, sum)761	1.77	-0.30	-8.89	-1.47	-0.96	-1.39	0.25	7.39
C(YbxLi, sum)762	-1.02	0.71	-1.63	-0.09	-0.10	-0.10	-0.00	12.24
C(YbxLi, sum)763	-1.10	0.60	-2.15	-0.19	-0.16	-0.67	0.14	8.05
C(YbxLi, sum)769	-1.77	0.66	-4.32	-0.06	-0.10	-2.09	0.41	5.50
C(YbxLi, sum)771	-0.59	0.69	1.62	-0.10	-0.08	0.65	-0.08	0.07
C(YbxLi, sum)772	1.06	-0.44	6.02	-0.48	-0.29	0.66	-0.12	-2.33
C(YbxLi, sum)773	1.15	-0.49	-1.26	-0.60	-0.36	-0.46	0.10	-3.33
C(YbxLi, sum)779	2.17	-0.35	5.95	-0.37	-0.17	-2.08	0.46	-5.89
C(YbxLi, sum)781	0.68	0.27	11.94	0.55	0.42			
C(YbxLi, sum)782	-3.07	0.26	11.64	0.82	0.43			
C(YbxLi, sum)783	0.71	0.30	6.61	0.51	0.39			
C(YbxLi, sum)789	3.12	0.29	-1.51	0.34	0.36			
C(YbxLi, sum)791	2.68	0.39	6.14	0.54	0.49			
C(YbxLi, sum)792	0.08	0.35	6.29	0.62	0.42			
C(YbxLi, sum)793	1.07	-0.06	6.58	0.15	0.14			
C(YbxLi, sum)799	3.65	-0.02	0.73	0.08	0.19			
C(YbxLi, sum)801	3.60	0.04	2.83	0.20	0.28			
C(YbxLi, sum)802	-0.37	-0.01	5.40	0.33	0.21			
C(YbxLi, sum)803	0.18	-0.58	-8.96	-0.87	-0.58			
C(YbxLi, sum)809	3.28	-0.61	-12.36	-1.04	-0.61			
C(YbxLi, sum)821	2.45	-0.51	-9.00	-0.83	-0.49			
C(YbxLi, sum)822	-0.85	-0.15	-2.77	0.15	0.06			
C(YbxLi, sum)823	0.02	-0.03	1.24	0.30	0.19			
C(YbxLi, sum)829	2.64	-0.36	13.09	-0.44	-0.20	-1.70	0.31	-3.04
C(YbxLi, sum)831	-2.00	-0.12	3.63	0.21	0.06			
C(YbxLi, sum)832	-1.02	0.16	11.86	0.49	0.30			
C(YbxLi, sum)833	1.27	0.22	7.34	0.45	0.37			
C(YbxLi, sum)839	-0.02	0.23	-2.04	0.65	0.44	-0.01	-0.01	2.32
C(YbxLi, sum)841	1.40	0.14	-2.19	0.40	0.33	-0.91	0.24	-2.88
C(YbxLi, sum)842	0.92	0.33	-4.20	0.78	0.57	0.18	-0.05	-1.62
C(YbxLi, sum)843	-1.47	0.22	-0.38	0.72	0.43	-1.47	0.28	-6.13
C(YbxLi, sum)849	-5.52	-0.17	-3.99	0.14	-0.11	-2.03	0.39	-6.78
C(YbxLi, sum)851	-4.05	-0.23	-11.75	-0.07	-0.18	0.37	-0.09	-4.83
C(YbxLi, sum)852	-4.49	-0.17	-5.95	0.07	-0.12	0.28	-0.09	-6.22
C(YbxLi, sum)853	-4.35	-0.16	-5.42	0.10	-0.09	-0.52	0.05	-7.08
C(YbxLi, sum)859	-2.71	-0.16	-0.67	0.21	0.03	-0.87	0.12	-7.33
(Intercept)	68.33	2.18	98.82	3.74	2.55	12.57	2.10	39.80

Table 11: Fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 3/7.

	Crstadj	Crwvt	Dp	Ds	Dps	DpovDs	CVDp	CVDs
C(Sex, sum)1	-1.36	0.02	-0.91	-0.20	-0.25	-0.03	1.11	0.76
C(YbxLi, sum)749	-8.20	0.14						
C(YbxLi, sum)750	-4.91	0.08						
C(YbxLi, sum)759	-8.98	0.18						
C(YbxLi, sum)761	-5.99	0.10						
C(YbxLi, sum)762	-1.06	0.02						
C(YbxLi, sum)763	-4.42	0.08						
C(YbxLi, sum)769	-6.97	0.13						
C(YbxLi, sum)771	5.92	-0.08						
C(YbxLi, sum)772	2.57	-0.03						
C(YbxLi, sum)773	1.38	-0.01						
C(YbxLi, sum)779	-2.32	0.06						
C(YbxLi, sum)781								
C(YbxLi, sum)782								
C(YbxLi, sum)783								
C(YbxLi, sum)789								
C(YbxLi, sum)791								
C(YbxLi, sum)792								
C(YbxLi, sum)793								
C(YbxLi, sum)799								
C(YbxLi, sum)801								
C(YbxLi, sum)802								
C(YbxLi, sum)803								
C(YbxLi, sum)809								
C(YbxLi, sum)821								
C(YbxLi, sum)822			-2.55	-1.08	-1.16	-0.07	-0.93	-0.87
C(YbxLi, sum)823			0.71	-0.69	-0.64	0.08	0.57	0.35
C(YbxLi, sum)829	-1.18	0.02						
C(YbxLi, sum)831			-1.75	-0.76	-0.83	-0.05	-3.39	-1.55
C(YbxLi, sum)832			-2.94	-0.80	-0.91	-0.09	-3.70	-3.49
C(YbxLi, sum)833			-1.60	-1.17	-1.23	-0.01	-2.56	-1.76
C(YbxLi, sum)839	3.55	-0.06	0.63	0.55	0.53	0.00	-3.40	-0.51
C(YbxLi, sum)841	0.03	0.03	2.16	2.44	2.41	-0.03	-2.09	-2.14
C(YbxLi, sum)842	1.69	-0.03	-1.25	0.52	0.42	-0.09	-4.52	-3.12
C(YbxLi, sum)843	-4.24	0.08	0.22	-0.11	-0.13	0.02	-4.17	-2.41
C(YbxLi, sum)849	-5.06	0.10						
C(YbxLi, sum)851	-2.78	0.04	1.32	-0.64	-0.57	0.10	-3.55	-0.96
C(YbxLi, sum)852	-4.54	0.07	-2.48	-1.36	-1.44	-0.04	-6.05	-2.25
C(YbxLi, sum)853	-5.66	0.10	0.72	-1.16	-1.10	0.10	-3.43	-1.48
C(YbxLi, sum)859	-5.95	0.10	0.10	0.83	0.80	-0.04	-3.07	-1.16
(Intercept)	48.25	0.79	24.49	21.11	21.28	1.16	20.18	17.66

Table 12: Fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 4/7.

	MaxDp	MinDp	MaxDs	MinDs	SDDp	SDDs	SDD	CVD
C(Sex, sum)1	-1.03	-1.24	0.02	-0.59	0.07	0.12	0.11	0.75
C(YbxLi, sum)749								
C(YbxLi, sum)750								
C(YbxLi, sum)759								
C(YbxLi, sum)761								
C(YbxLi, sum)762								
C(YbxLi, sum)763								
C(YbxLi, sum)769								
C(YbxLi, sum)771								
C(YbxLi, sum)772								
C(YbxLi, sum)773								
C(YbxLi, sum)779								
C(YbxLi, sum)781								
C(YbxLi, sum)782								
C(YbxLi, sum)783								
C(YbxLi, sum)789								
C(YbxLi, sum)791								
C(YbxLi, sum)792								
C(YbxLi, sum)793								
C(YbxLi, sum)799								
C(YbxLi, sum)801								
C(YbxLi, sum)802								
C(YbxLi, sum)803								
C(YbxLi, sum)809								
C(YbxLi, sum)821								
C(YbxLi, sum)822	-3.86	-0.57	-3.26	-0.78	-0.75	-0.37	-0.40	-0.93
C(YbxLi, sum)823	1.98	0.17	-0.46	-0.41	0.26	-0.05	-0.03	0.42
C(YbxLi, sum)829								
C(YbxLi, sum)831	-3.69	2.05	-1.76	0.84	-1.08	-0.46	-0.51	-1.70
C(YbxLi, sum)832	-5.59	1.62	-4.37	0.48	-1.34	-0.84	-0.88	-3.57
C(YbxLi, sum)833	-3.35	1.92	-3.34	0.31	-0.87	-0.54	-0.57	-1.87
C(YbxLi, sum)839	-0.50	3.89	-0.48	2.33	-0.76	-0.02	-0.07	-0.77
C(YbxLi, sum)841	3.76	5.17	1.45	-0.40	0.01	-0.01	-0.01	-2.15
C(YbxLi, sum)842	-3.43	2.80	-2.35	-0.72	-1.26	-0.56	-0.61	-3.29
C(YbxLi, sum)843	-0.92	3.67	-2.82	0.39	-0.92	-0.51	-0.55	-2.56
C(YbxLi, sum)849								
C(YbxLi, sum)851	1.20	4.56	-1.45	-0.03	-0.57	-0.32	-0.33	-1.08
C(YbxLi, sum)852	-5.26	2.81	-4.86	-0.53	-1.80	-0.67	-0.75	-2.53
C(YbxLi, sum)853	0.62	3.53	-3.49	-0.75	-0.62	-0.49	-0.50	-1.53
C(YbxLi, sum)859	-0.39	2.82	-0.78	0.58	-0.71	-0.11	-0.14	-1.30
(Intercept)	35.11	12.85	37.92	8.54	4.93	3.71	3.80	17.92

Table 13: Fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 5/7.

	Gt30Dp	Gt30Ds	Gt30D	Fnua	Fr	Fnt	Sarea	Fd
C(Sex, sum)1	-2.54	0.06	-0.09	2.27	0.94	4.78	0.04	-0.03
C(YbxLi, sum)749								
C(YbxLi, sum)750				1.83	-1.64	-0.24	-0.03	-0.05
C(YbxLi, sum)759				-3.81	-4.48	-5.41	-0.03	-0.01
C(YbxLi, sum)761				-3.46	0.36	-1.89	0.03	0.04
C(YbxLi, sum)762				-2.07	-0.94	-1.48	0.01	-0.03
C(YbxLi, sum)763				-4.10	-0.09	-2.43	0.02	-0.04
C(YbxLi, sum)769				-3.23	-0.84	-4.12	-0.02	0.03
C(YbxLi, sum)771				-1.03	0.02	-5.67	-0.08	0.16
C(YbxLi, sum)772				3.52	1.49	1.28	-0.03	0.15
C(YbxLi, sum)773				1.19	0.24	-3.18	-0.07	0.13
C(YbxLi, sum)779				-4.70	-3.38	-7.85	-0.06	0.25
C(YbxLi, sum)781				-2.56	1.98	1.23	0.06	0.24
C(YbxLi, sum)782				1.34	1.75	5.67	0.07	0.11
C(YbxLi, sum)783				-1.22	1.14	2.79	0.07	0.22
C(YbxLi, sum)789				-4.92	-0.21	-1.46	0.06	0.32
C(YbxLi, sum)791				3.04	1.22	-1.81	-0.07	0.07
C(YbxLi, sum)792				9.47	4.91	6.09	-0.04	-0.08
C(YbxLi, sum)793				7.30	2.32	2.51	-0.07	0.07
C(YbxLi, sum)799				0.16	-0.59	-2.98	-0.05	-0.02
C(YbxLi, sum)801				-2.19	1.61	-2.77	-0.01	0.19
C(YbxLi, sum)802				3.23	1.99	2.91	-0.01	0.05
C(YbxLi, sum)803				7.04	3.09	5.71	-0.02	0.14
C(YbxLi, sum)809				-3.72	-0.16	-3.81	-0.00	0.11
C(YbxLi, sum)821				0.42	1.14	2.01	0.02	0.12
C(YbxLi, sum)822	-8.41	-1.76	-2.14	12.74	3.84	17.22	0.06	-0.05
C(YbxLi, sum)823	2.83	-0.86	-0.72	8.61	2.36	12.45	0.06	0.02
C(YbxLi, sum)829								
C(YbxLi, sum)831	-7.24	-1.49	-1.86	4.19	4.18	11.47	0.11	0.05
C(YbxLi, sum)832	-9.18	-2.14	-2.55	14.21	6.39	27.14	0.16	-0.10
C(YbxLi, sum)833	-8.90	-1.65	-2.10	16.04	6.76	25.68	0.13	0.04
C(YbxLi, sum)839	-0.64	0.94	0.79	6.93	1.58	12.22	0.08	
C(YbxLi, sum)841	3.85	3.26	3.24	-4.30	2.64	-2.87	0.02	
C(YbxLi, sum)842	-7.79	-0.98	-1.38	16.53	8.95	21.86	0.06	
C(YbxLi, sum)843	-3.51	-1.28	-1.50	14.35	5.52	14.65	0.01	
C(YbxLi, sum)849								
C(YbxLi, sum)851	2.83	-1.02	-0.91	13.53	2.32	5.42	-0.11	
C(YbxLi, sum)852	-12.45	-2.01	-2.60	26.19	3.46	17.92	-0.09	
C(YbxLi, sum)853	0.94	-1.69	-1.66	24.78	4.11	16.37	-0.09	
C(YbxLi, sum)859	-2.32	0.89	0.78	10.28	-0.34	5.27	-0.07	
(Intercept)	15.80	2.81	3.49	61.43	18.86	60.60	0.99	1.57

Table 14: Fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 6/7.

	Fc	Fu	Colour	Fly	Flcrot	Bactst	MycD	Bcts
C(Sex, sum)1	-0.11	-0.05	-0.04	-0.04	0.02	-0.04	-0.03	-0.13
C(YbxLi, sum)749			-0.01	-0.90	0.26			
C(YbxLi, sum)750	-0.56	-0.50	-0.36	-1.10	-0.06			
C(YbxLi, sum)759	-0.68	-0.49	-0.19	-0.90	0.01			0.18
C(YbxLi, sum)761	-0.81	-0.87	0.01	-1.52	0.03			-0.55
C(YbxLi, sum)762	-0.89	-0.88	-0.06	-1.02	0.29			-1.09
C(YbxLi, sum)763	-0.30	-0.69	-0.15	0.44	0.07			0.07
C(YbxLi, sum)769	-0.83	-0.30	-0.09	-0.91	-0.39			-0.55
C(YbxLi, sum)771	-0.02	-0.84						0.40
C(YbxLi, sum)772	-0.33	-0.87						-0.23
C(YbxLi, sum)773	-0.27	-0.89						-0.09
C(YbxLi, sum)779	-0.34	-0.89	0.99	0.50	-0.25			0.16
C(YbxLi, sum)781	-0.19	-0.78	-2.82	-4.57	-4.33			-1.27
C(YbxLi, sum)782	-1.10	-1.28	-3.25	-4.57	-4.31	-0.01	-0.01	-1.35
C(YbxLi, sum)783	-0.03	-0.53	-2.91	-4.58	-4.23	-0.01	-0.01	-0.61
C(YbxLi, sum)789	-0.63	-0.78	-2.70	-4.58	-4.37	0.03	-0.01	-0.33
C(YbxLi, sum)791	-0.28	-0.66	-2.68	-4.61	-4.48	-0.02	-0.00	0.22
C(YbxLi, sum)792	-0.79	-1.11	-2.99	-4.61	-4.46	-0.01	0.00	-1.90
C(YbxLi, sum)793	-0.65	-0.87	-2.72	-4.62	-4.47	-0.02	-0.01	-0.92
C(YbxLi, sum)799	-0.52	-0.86	-2.30	-4.61	-4.48	-0.01	0.04	-0.65
C(YbxLi, sum)801	0.67	0.00	-2.41	-4.60	-4.48	-0.02	-0.00	-1.13
C(YbxLi, sum)802	-0.30	-0.75	-2.52	-4.62	-4.45	-0.02	0.14	-1.34
C(YbxLi, sum)803	-0.18	-0.58	-2.44	-4.61	-4.47	-0.02	0.09	-0.33
C(YbxLi, sum)809	0.31	-0.12	-2.00	-4.61	-4.48	-0.01	0.15	-0.72
C(YbxLi, sum)821	0.14	-0.42	-1.88	-4.48	-3.73	0.27	0.36	-1.08
C(YbxLi, sum)822	-0.83	-1.22	-1.94	-4.57	-3.78	0.29	0.25	-1.38
C(YbxLi, sum)823	-0.35	-0.97	-1.88	-4.55	-3.85	0.40	0.58	-0.29
C(YbxLi, sum)829			-1.45	-4.51	-3.94	0.32	0.64	-0.52
C(YbxLi, sum)831	0.03	-0.78	-2.60	-4.61	-4.07	-0.00	0.01	-0.81
C(YbxLi, sum)832	-0.64	-1.43	-2.53	-4.60	-4.18	-0.02	-0.00	-1.58
C(YbxLi, sum)833	-0.47	-1.21	-2.76	-4.62	-3.78	0.01	-0.01	-0.27
C(YbxLi, sum)839			-2.25	-4.58	-4.06	0.01	0.05	-0.56
C(YbxLi, sum)841			-2.91	-4.62	-3.99	0.03	0.15	-1.18
C(YbxLi, sum)842			-2.56	-4.55	-3.24	0.06	0.58	-1.60
C(YbxLi, sum)843			-2.60	-4.55	-3.52	0.18	0.58	-0.67
C(YbxLi, sum)849			-2.34	-4.54	-3.80	0.10	0.58	-0.99
C(YbxLi, sum)851			-2.37	-4.61	-4.40	-0.02	0.02	-0.19
C(YbxLi, sum)852			-2.17	-4.59	-4.43	-0.03	-0.01	-1.75
C(YbxLi, sum)853			-2.49	-4.56	-4.36	-0.02	0.13	-0.68
C(YbxLi, sum)859			-2.53	-4.62	-4.44	-0.02	0.09	-1.06
(Intercept)	3.87	3.62	5.99	4.61	4.47	0.02	0.00	4.61

Table 15: Fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 7/7.

	Bctb	Weanwt	NLB	NLW	Fnpua	Fnsua	Fnpt	Fnst
C(Sex, sum)1	-0.14	0.73	0.00	0.00	-0.03	2.30	0.09	4.69
C(YbxLi, sum)749			0.12	0.06				
C(YbxLi, sum)750			0.13	0.06	0.38	1.45	0.26	-0.50
C(YbxLi, sum)759	0.51	-0.36	-0.05	-0.13	0.72	-4.53	0.56	-5.97
C(YbxLi, sum)761	-0.34	7.18	0.11	-0.08	-0.21	-3.25	-0.13	-1.75
C(YbxLi, sum)762	-0.78	6.15	-0.32	-0.24	0.06	-2.13	0.10	-1.57
C(YbxLi, sum)763	0.54	7.34	-0.13	-0.07	-0.21	-3.89	-0.12	-2.30
C(YbxLi, sum)769	-0.18	6.04	-0.23	-0.18	-0.04	-3.20	-0.08	-4.03
C(YbxLi, sum)771	0.64	0.55	-0.00	-0.04	-0.06	-0.97	-0.28	-5.40
C(YbxLi, sum)772	-0.27	0.47	-0.08	-0.10	-0.05	3.58	-0.14	1.42
C(YbxLi, sum)773	0.05	-0.46	0.06	0.05	0.04	1.15	-0.18	-3.00
C(YbxLi, sum)779	0.35	0.13	0.01	0.06	0.37	-5.07	0.17	-8.02
C(YbxLi, sum)781	-0.27	7.18	-0.05	-0.04	-0.41	-2.15	-0.22	1.46
C(YbxLi, sum)782	-0.38	7.56	0.09	0.05	-0.19	1.53	0.01	5.66
C(YbxLi, sum)783	0.34	7.01	0.23	0.23	-0.21	-1.01	-0.01	2.81
C(YbxLi, sum)789	0.45	6.58	0.20	0.23	-0.21	-4.71	-0.02	-1.44
C(YbxLi, sum)791	0.88	7.45	0.03	0.06	-0.03	3.08	-0.25	-1.55
C(YbxLi, sum)792	-1.56	7.86	0.19	0.18	-0.21	9.68	-0.33	6.42
C(YbxLi, sum)793	-0.53	6.06	0.16	0.16	-0.01	7.31	-0.21	2.71
C(YbxLi, sum)799	-0.19	6.91	0.03	0.04	0.10	0.05	-0.05	-2.93
C(YbxLi, sum)801	-0.80	0.32	0.08	0.14	-0.35	-1.84	-0.37	-2.40
C(YbxLi, sum)802	-1.07	0.43	0.11	0.08	-0.16	3.38	-0.16	3.07
C(YbxLi, sum)803	0.10	-0.04	0.26	0.19	-0.07	7.11	-0.13	5.84
C(YbxLi, sum)809	-0.30	-0.14	0.22	0.18	-0.15	-3.57	-0.15	-3.66
C(YbxLi, sum)821	-0.68	-1.02	0.14	0.02	-0.16	0.58	-0.07	2.09
C(YbxLi, sum)822	-0.99	-0.43	-0.07	-0.05	0.13	12.61	0.34	16.88
C(YbxLi, sum)823	0.15	-0.86	-0.18	-0.14	0.29	8.32	0.47	11.98
C(YbxLi, sum)829	-0.19	-0.81	0.23	0.17				
C(YbxLi, sum)831	-0.34	6.60	-0.13	-0.08	-0.35	4.54	-0.04	11.51
C(YbxLi, sum)832	-0.94	7.49	0.02	-0.04	-0.23	14.44	0.24	26.88
C(YbxLi, sum)833	0.22	7.27	0.08	0.04	-0.14	16.18	0.23	25.45
C(YbxLi, sum)839	-0.16	6.47	-0.16	-0.15	0.08	6.84	0.36	11.87
C(YbxLi, sum)841	-0.18	7.07	-0.17	-0.09	-0.52	-3.78	-0.45	-2.43
C(YbxLi, sum)842	-0.56	8.74	-0.21	-0.14	-0.34	16.88	-0.17	22.02
C(YbxLi, sum)843	0.26	6.52	-0.10	-0.10	-0.09	14.45	-0.08	14.73
C(YbxLi, sum)849	-0.14	8.75	-0.25	-0.19				
C(YbxLi, sum)851	0.77	4.91	-0.22	-0.17	0.29	13.24	-0.07	5.49
C(YbxLi, sum)852	-0.54	5.63	-0.19	-0.14	0.68	25.51	0.33	17.59
C(YbxLi, sum)853	0.36	4.79	-0.05	0.02	0.52	24.26	0.17	16.20
C(YbxLi, sum)859	-0.09	5.41	-0.19	-0.12	0.63	9.65	0.36	4.92
(Intercept)	3.93	14.38	1.32	1.24	3.13	58.29	3.08	57.52

These *C(YbxLi, sum)yyl* effects allow calculation of differences between selected and control lines within a particular year, simply by differencing the appropriate constants. For example we can get the difference between Line 3 and Control in 1985 as *C(YbxLi, sum)853 - C(YbxLi, sum)859* for any any trait.

The standard errors of the above constant estimates are reported in Tables 16 to 22.

If one calculates some linear combination of the constants, the standard error of the combination can be approximated as the geometric mean of the standard errors of the constants involved. This is approximate as it does not allow for any covariances between the constants due to unequal subclass numbers. These covariances are available, but are not reported here.

5.2 Direct responses to selection

For each of the traits selected for (Fnt and Fd), we plotted fixed effects for each Year-of-birth for the selected line and the control line. The difference between selected and control lines represents the amount of genetic change. This is a very elementary way of analysing response to selection in sheep flocks with overlapping generations. It shows what has happened to successive drops of animals. Figure 1 shows the direct response plot for Line 1 and the control line.

Line 1 starts out with a smaller Fd than the Control Line, but changes from 1979 onward to having a larger Fd than the Control Line. There are a lot of data points missing. I am still waiting for CSIRO to complete the Fd measurements on Line 1 in 1984-85 and on the Control Line in 1981-85. Nevertheless we can conclude that there has been genetic change in Fd in Line 1 due to selection for Fd.

Figure 2 shows the direct response plot for Line 2 and the Control Line.

Line 2 starts out with a larger number of follicles than the Control Line, and this difference increases with time. We can conclude that there has been genetic change in Fnt in Line 2 due to selection for Fnt. There is also a considerable environmental shift between years 80 and 82, both Line 2 and the Control Line have increased follicle numnber and this jump is manintained thereafter. The cause of this jump is unknown. It may be significant that there was a change of techniwue from manual counting to semi-automatic image processing in 1982.

Figure 3 shows the direct response plot for follicle depth for Line 3 and the Control Line. Figure 4 shows the direct response plot for follicle number per head for Line 3 and the Control Line.

Line 3 has achieved genetic change in both follicle depth and follicle number per head. The shift in follicle number between years 80 and 82 is again present.

5.3 Indirect responses to selection

We will just look at indirect responses in clean wool weight, fibre diameter and staple length.

Figure 5 shows the indirect or correlated changes in clean wool weight (*Cwwadj*) in all three lines. There is no obvious change in clean wool weight in

Table 16: Standard errors of fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 1/7.

	Stal	Diam	Bwt	WrN	WrB	WrT	Face	Gfw
C(Sex, sum)1	0.16	0.02	0.07	0.01	0.01	0.02	0.02	0.01
C(YbxLi, sum)749	0.48	0.07	0.22	0.04	0.04	0.07	0.05	0.03
C(YbxLi, sum)750	1.16	0.17	0.53	0.09	0.10	0.18	0.13	0.06
C(YbxLi, sum)759	0.56	0.08	0.25	0.05	0.05	0.08	0.06	0.03
C(YbxLi, sum)761	1.29	0.19	0.59	0.10	0.11	0.20	0.14	0.07
C(YbxLi, sum)762	1.66	0.25	0.76	0.13	0.14	0.25	0.19	0.09
C(YbxLi, sum)763	1.32	0.20	0.60	0.11	0.11	0.20	0.15	0.07
C(YbxLi, sum)769	1.58	0.24	0.72	0.13	0.13	0.24	0.18	0.08
C(YbxLi, sum)771	1.18	0.18	0.54	0.10	0.10	0.18	0.13	0.06
C(YbxLi, sum)772	1.05	0.16	0.48	0.09	0.09	0.16	0.12	0.06
C(YbxLi, sum)773	1.00	0.15	0.45	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)779	1.01	0.15	0.46	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)781	1.02	0.15	0.47	0.08	0.09	0.15	0.11	0.05
C(YbxLi, sum)782	1.03	0.16	0.47	0.08	0.09	0.16	0.12	0.05
C(YbxLi, sum)783	1.08	0.16	0.49	0.09	0.09	0.16	0.12	0.06
C(YbxLi, sum)789	1.11	0.17	0.51	0.09	0.09	0.17	0.12	0.06
C(YbxLi, sum)791	1.14	0.17	0.52	0.09	0.10	0.17	0.13	0.06
C(YbxLi, sum)792	0.95	0.14	0.43	0.08	0.08	0.14	0.11	0.05
C(YbxLi, sum)793	0.91	0.14	0.42	0.07	0.08	0.14	0.10	0.05
C(YbxLi, sum)799	1.06	0.16	0.48	0.09	0.09	0.16	0.12	0.06
C(YbxLi, sum)801	1.04	0.16	0.47	0.08	0.09	0.16	0.12	0.06
C(YbxLi, sum)802	1.02	0.15	0.47	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)803	0.96	0.15	0.44	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)809	1.11	0.17	0.51	0.09	0.09	0.17	0.12	0.06
C(YbxLi, sum)821	0.98	0.15	0.45	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)822	1.06	0.16	0.49	0.09	0.09	0.16	0.12	0.06
C(YbxLi, sum)823	1.04	0.16	0.48	0.08	0.09	0.16	0.12	0.06
C(YbxLi, sum)829	0.84	0.13	0.38	0.07	0.07	0.13	0.09	0.04
C(YbxLi, sum)831	0.99	0.15	0.45	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)832	1.13	0.17	0.52	0.09	0.09	0.17	0.13	0.06
C(YbxLi, sum)833	0.97	0.15	0.44	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)839	1.10	0.17	0.50	0.09	0.09	0.17	0.12	0.06
C(YbxLi, sum)841	1.02	0.15	0.47	0.08	0.09	0.16	0.11	0.05
C(YbxLi, sum)842	1.02	0.15	0.47	0.08	0.09	0.15	0.11	0.05
C(YbxLi, sum)843	0.91	0.14	0.42	0.07	0.08	0.14	0.10	0.05
C(YbxLi, sum)849	1.06	0.16	0.48	0.09	0.09	0.16	0.12	0.06
C(YbxLi, sum)851	1.01	0.15	0.46	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)852	1.03	0.16	0.47	0.08	0.09	0.16	0.12	0.05
C(YbxLi, sum)853	0.97	0.15	0.44	0.08	0.08	0.15	0.11	0.05
C(YbxLi, sum)859	1.03	0.16	0.47	0.08	0.09	0.16	0.12	0.05
(Intercept)	0.17	0.03	0.08	0.01	0.01	0.03	0.02	0.01

Table 17: Standard errors of fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 2/7.

	Yld	Cww	Staladj	Gfwadj	Cwwadj	Crimp	Crwvl	Crst
C(Sex, sum)1	0.08	0.01	0.19	0.01	0.01	0.05	0.01	0.16
C(YbxLi, sum)749	0.24	0.02	0.58	0.03	0.02	0.30	0.06	1.01
C(YbxLi, sum)750	0.58	0.04	1.39	0.07	0.05	0.17	0.03	0.56
C(YbxLi, sum)759	0.28	0.02	0.67	0.04	0.02	0.33	0.07	1.10
C(YbxLi, sum)761	0.64	0.05	1.54	0.08	0.06	0.42	0.08	1.41
C(YbxLi, sum)762	0.83	0.06	2.00	0.11	0.07	0.34	0.07	1.13
C(YbxLi, sum)763	0.66	0.05	1.58	0.08	0.06	0.40	0.08	1.33
C(YbxLi, sum)769	0.80	0.06	1.90	0.10	0.07	0.31	0.06	1.03
C(YbxLi, sum)771	0.59	0.04	1.42	0.08	0.05	0.28	0.06	0.93
C(YbxLi, sum)772	0.53	0.04	1.27	0.07	0.05	0.26	0.05	0.88
C(YbxLi, sum)773	0.50	0.04	1.19	0.06	0.04	0.27	0.05	0.90
C(YbxLi, sum)779	0.50	0.04	1.22	0.06	0.04	0.23	0.05	0.78
C(YbxLi, sum)781	0.51	0.04	1.23	0.07	0.04			
C(YbxLi, sum)782	0.52	0.04	1.27	0.07	0.05			
C(YbxLi, sum)783	0.54	0.04	1.33	0.07	0.05			
C(YbxLi, sum)789	0.56	0.04	1.33	0.07	0.05			
C(YbxLi, sum)791	0.57	0.04	1.39	0.07	0.05			
C(YbxLi, sum)792	0.48	0.04	1.19	0.06	0.04			
C(YbxLi, sum)793	0.46	0.03	1.10	0.06	0.04			
C(YbxLi, sum)799	0.53	0.04	1.73	0.09	0.06			
C(YbxLi, sum)801	0.52	0.04	1.25	0.07	0.05			
C(YbxLi, sum)802	0.51	0.04	1.23	0.07	0.04			
C(YbxLi, sum)803	0.48	0.04	1.17	0.06	0.04			
C(YbxLi, sum)809	0.55	0.04	1.33	0.07	0.05			
C(YbxLi, sum)821	0.49	0.04	1.18	0.06	0.04			
C(YbxLi, sum)822	0.54	0.04	1.28	0.07	0.05			
C(YbxLi, sum)823	0.52	0.04	1.26	0.07	0.05			
C(YbxLi, sum)829	0.42	0.03	1.02	0.05	0.04	0.28	0.06	0.93
C(YbxLi, sum)831	0.50	0.04	1.20	0.06	0.04			
C(YbxLi, sum)832	0.57	0.04	1.36	0.07	0.05			
C(YbxLi, sum)833	0.48	0.04	1.16	0.06	0.04			
C(YbxLi, sum)839	0.55	0.04	1.33	0.07	0.05	0.26	0.05	0.88
C(YbxLi, sum)841	0.52	0.04	1.23	0.07	0.04	0.25	0.05	0.82
C(YbxLi, sum)842	0.51	0.04	1.23	0.07	0.04	0.36	0.07	1.22
C(YbxLi, sum)843	0.45	0.03	1.09	0.06	0.04	0.27	0.05	0.91
C(YbxLi, sum)849	0.53	0.04	1.27	0.07	0.05	0.27	0.05	0.89
C(YbxLi, sum)851	0.51	0.04	1.22	0.06	0.04	0.26	0.05	0.87
C(YbxLi, sum)852	0.52	0.04	1.24	0.07	0.05	0.29	0.06	0.97
C(YbxLi, sum)853	0.49	0.04	1.17	0.06	0.04	0.26	0.05	0.87
C(YbxLi, sum)859	0.52	0.04	1.24	0.07	0.05	0.26	0.05	0.88
(Intercept)	0.09	0.01	0.21	0.01	0.01	0.11	0.02	0.37

Table 18: Standard errors of fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 3/7.

	Crstadj	Crwvt	Dp	Ds	Dps	DpovDs	CVDp	CVDs
C(Sex, sum)1	0.19	0.00	0.14	0.08	0.08	0.01	0.19	0.11
C(YbxLi, sum)749	1.20	0.02						
C(YbxLi, sum)750	0.68	0.01						
C(YbxLi, sum)759	1.32	0.03						
C(YbxLi, sum)761	1.68	0.03						
C(YbxLi, sum)762	1.36	0.03						
C(YbxLi, sum)763	1.59	0.03						
C(YbxLi, sum)769	1.23	0.02						
C(YbxLi, sum)771	1.12	0.02						
C(YbxLi, sum)772	1.06	0.02						
C(YbxLi, sum)773	1.08	0.02						
C(YbxLi, sum)779	0.93	0.02						
C(YbxLi, sum)781								
C(YbxLi, sum)782								
C(YbxLi, sum)783								
C(YbxLi, sum)789								
C(YbxLi, sum)791								
C(YbxLi, sum)792								
C(YbxLi, sum)793								
C(YbxLi, sum)799								
C(YbxLi, sum)801								
C(YbxLi, sum)802								
C(YbxLi, sum)803								
C(YbxLi, sum)809								
C(YbxLi, sum)821								
C(YbxLi, sum)822			0.55	0.32	0.32	0.03	0.73	0.44
C(YbxLi, sum)823			0.56	0.33	0.33	0.03	0.75	0.45
C(YbxLi, sum)829	1.12	0.02						
C(YbxLi, sum)831			0.65	0.39	0.38	0.03	0.87	0.52
C(YbxLi, sum)832			0.72	0.42	0.42	0.03	0.96	0.57
C(YbxLi, sum)833			0.68	0.40	0.40	0.03	0.91	0.55
C(YbxLi, sum)839	1.05	0.02	0.66	0.39	0.38	0.03	0.88	0.52
C(YbxLi, sum)841	0.98	0.02	0.71	0.42	0.42	0.03	0.95	0.57
C(YbxLi, sum)842	1.46	0.03	0.73	0.43	0.42	0.03	0.97	0.58
C(YbxLi, sum)843	1.09	0.02	0.61	0.36	0.36	0.03	0.82	0.49
C(YbxLi, sum)849	1.07	0.02						
C(YbxLi, sum)851	1.04	0.02	0.55	0.32	0.32	0.03	0.73	0.44
C(YbxLi, sum)852	1.16	0.02	0.58	0.34	0.34	0.03	0.78	0.47
C(YbxLi, sum)853	1.04	0.02	0.55	0.32	0.32	0.03	0.73	0.44
C(YbxLi, sum)859	1.05	0.02	0.65	0.38	0.38	0.03	0.87	0.52
(Intercept)	0.44	0.01	0.42	0.25	0.24	0.02	0.56	0.33

Table 19: Standard errors of fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 4/7.

	MaxDp	MinDp	MaxDs	MinDs	SDDp	SDDs	SDD	CVD
C(Sex, sum)1	0.27	0.15	0.21	0.10	0.06	0.02	0.02	0.11
C(YbxLi, sum)749								
C(YbxLi, sum)750								
C(YbxLi, sum)759								
C(YbxLi, sum)761								
C(YbxLi, sum)762								
C(YbxLi, sum)763								
C(YbxLi, sum)769								
C(YbxLi, sum)771								
C(YbxLi, sum)772								
C(YbxLi, sum)773								
C(YbxLi, sum)779								
C(YbxLi, sum)781								
C(YbxLi, sum)782								
C(YbxLi, sum)783								
C(YbxLi, sum)789								
C(YbxLi, sum)791								
C(YbxLi, sum)792								
C(YbxLi, sum)793								
C(YbxLi, sum)799								
C(YbxLi, sum)801								
C(YbxLi, sum)802								
C(YbxLi, sum)803								
C(YbxLi, sum)809								
C(YbxLi, sum)821								
C(YbxLi, sum)822	1.07	0.58	0.83	0.39	0.22	0.09	0.09	0.43
C(YbxLi, sum)823	1.09	0.59	0.85	0.40	0.23	0.09	0.10	0.44
C(YbxLi, sum)829								
C(YbxLi, sum)831	1.28	0.69	0.99	0.47	0.27	0.11	0.11	0.51
C(YbxLi, sum)832	1.41	0.76	1.09	0.51	0.29	0.12	0.12	0.56
C(YbxLi, sum)833	1.34	0.72	1.03	0.49	0.28	0.12	0.12	0.54
C(YbxLi, sum)839	1.28	0.69	0.99	0.47	0.27	0.11	0.11	0.52
C(YbxLi, sum)841	1.39	0.75	1.08	0.51	0.29	0.12	0.12	0.56
C(YbxLi, sum)842	1.42	0.77	1.10	0.52	0.29	0.12	0.12	0.57
C(YbxLi, sum)843	1.20	0.65	0.93	0.44	0.25	0.10	0.10	0.48
C(YbxLi, sum)849								
C(YbxLi, sum)851	1.07	0.58	0.83	0.39	0.22	0.09	0.09	0.43
C(YbxLi, sum)852	1.14	0.62	0.88	0.42	0.24	0.10	0.10	0.46
C(YbxLi, sum)853	1.07	0.58	0.83	0.39	0.22	0.09	0.09	0.43
C(YbxLi, sum)859	1.28	0.69	0.99	0.47	0.27	0.11	0.11	0.51
(Intercept)	0.81	0.44	0.63	0.30	0.17	0.07	0.07	0.33

Table 20: Standard errors of fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 5/7.

	Gt30Dp	Gt30Ds	Gt30D	Fnua	Fr	Fnt	Sarea	Fd
C(Sex, sum)1	0.68	0.11	0.13	0.23	0.07	0.23	0.00	0.00
C(YbxLi, sum)749								
C(YbxLi, sum)750				0.93	0.29	0.91	0.01	0.01
C(YbxLi, sum)759				2.20	0.70	2.16	0.01	0.03
C(YbxLi, sum)761				2.32	0.74	2.28	0.02	0.03
C(YbxLi, sum)762				1.85	0.59	1.81	0.01	0.02
C(YbxLi, sum)763				2.19	0.70	2.15	0.01	0.03
C(YbxLi, sum)769				1.67	0.53	1.64	0.01	0.02
C(YbxLi, sum)771				1.51	0.48	1.48	0.01	0.02
C(YbxLi, sum)772				1.46	0.46	1.43	0.01	0.02
C(YbxLi, sum)773				1.46	0.46	1.43	0.01	0.02
C(YbxLi, sum)779				1.26	0.40	1.24	0.01	0.02
C(YbxLi, sum)781				1.58	0.50	1.55	0.01	0.02
C(YbxLi, sum)782				1.48	0.47	1.45	0.01	0.02
C(YbxLi, sum)783				1.48	0.47	1.45	0.01	0.02
C(YbxLi, sum)789				1.36	0.43	1.34	0.01	0.02
C(YbxLi, sum)791				1.53	0.48	1.50	0.01	0.02
C(YbxLi, sum)792				1.47	0.47	1.44	0.01	0.02
C(YbxLi, sum)793				1.49	0.47	1.46	0.01	0.02
C(YbxLi, sum)799				1.41	0.45	1.38	0.01	0.02
C(YbxLi, sum)801				1.49	0.47	1.46	0.01	0.02
C(YbxLi, sum)802				1.53	0.48	1.50	0.01	0.02
C(YbxLi, sum)803				1.49	0.47	1.46	0.01	0.02
C(YbxLi, sum)809				1.43	0.45	1.40	0.01	0.02
C(YbxLi, sum)821				1.61	0.51	1.59	0.01	0.02
C(YbxLi, sum)822	2.66	0.45	0.49	1.41	0.45	1.39	0.01	0.02
C(YbxLi, sum)823	2.72	0.46	0.50	1.47	0.47	1.45	0.01	0.02
C(YbxLi, sum)829								
C(YbxLi, sum)831	3.19	0.54	0.59	1.89	0.60	1.85	0.01	0.03
C(YbxLi, sum)832	3.50	0.59	0.65	2.14	0.68	2.10	0.01	0.03
C(YbxLi, sum)833	3.33	0.56	0.62	2.03	0.64	1.99	0.01	0.03
C(YbxLi, sum)839	3.20	0.54	0.59	1.88	0.60	1.84	0.01	
C(YbxLi, sum)841	3.47	0.59	0.64	1.88	0.60	1.84	0.01	
C(YbxLi, sum)842	3.53	0.60	0.65	2.02	0.64	1.98	0.01	
C(YbxLi, sum)843	2.99	0.51	0.55	1.70	0.54	1.67	0.01	
C(YbxLi, sum)849								
C(YbxLi, sum)851	2.66	0.45	0.49	1.40	0.44	1.38	0.01	
C(YbxLi, sum)852	2.84	0.48	0.52	1.59	0.51	1.57	0.01	
C(YbxLi, sum)853	2.68	0.45	0.49	1.43	0.45	1.40	0.01	
C(YbxLi, sum)859	3.18	0.54	0.59	1.86	0.59	1.83	0.01	
(Intercept)	2.03	0.34	0.38	0.59	0.19	0.58	0.00	0.01

Table 21: Standard errors of fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 6/7.

	Fc	Fu	Colour	Fly	Flcrot	Bactst	MycD	Bcts
C(Sex, sum)1	0.02	0.02	0.01	0.02	0.03	0.01	0.02	0.03
C(YbxLi, sum)749			0.10	0.18	0.24			
C(YbxLi, sum)750	0.08	0.06	0.06	0.10	0.13			
C(YbxLi, sum)759	0.20	0.14	0.11	0.20	0.26			0.21
C(YbxLi, sum)761	0.21	0.15	0.15	0.26	0.33			0.27
C(YbxLi, sum)762	0.17	0.12	0.12	0.21	0.27			0.22
C(YbxLi, sum)763	0.20	0.14	0.14	0.25	0.32			0.26
C(YbxLi, sum)769	0.15	0.11	0.11	0.19	0.24			0.20
C(YbxLi, sum)771	0.14	0.10						0.18
C(YbxLi, sum)772	0.13	0.10						0.18
C(YbxLi, sum)773	0.13	0.10						0.18
C(YbxLi, sum)779	0.11	0.08	0.08	0.14	0.18			0.15
C(YbxLi, sum)781	0.14	0.10	0.10	0.18	0.23			0.19
C(YbxLi, sum)782	0.13	0.10	0.09	0.17	0.21	0.06	0.12	0.18
C(YbxLi, sum)783	0.13	0.10	0.09	0.16	0.21	0.06	0.12	0.18
C(YbxLi, sum)789	0.12	0.09	0.08	0.15	0.19	0.05	0.11	0.16
C(YbxLi, sum)791	0.14	0.10	0.10	0.17	0.22	0.06	0.12	0.18
C(YbxLi, sum)792	0.13	0.10	0.09	0.16	0.21	0.06	0.12	0.18
C(YbxLi, sum)793	0.13	0.10	0.09	0.17	0.21	0.06	0.12	0.18
C(YbxLi, sum)799	0.13	0.09	0.09	0.16	0.20	0.05	0.12	0.17
C(YbxLi, sum)801	0.13	0.10	0.09	0.17	0.21	0.06	0.12	0.18
C(YbxLi, sum)802	0.14	0.10	0.10	0.17	0.22	0.06	0.12	0.18
C(YbxLi, sum)803	0.13	0.10	0.09	0.17	0.21	0.06	0.12	0.18
C(YbxLi, sum)809	0.13	0.09	0.09	0.16	0.21	0.05	0.12	0.17
C(YbxLi, sum)821	0.15	0.11	0.10	0.18	0.23	0.06	0.13	0.19
C(YbxLi, sum)822	0.13	0.09	0.09	0.16	0.20	0.05	0.12	0.17
C(YbxLi, sum)823	0.13	0.10	0.09	0.16	0.21	0.06	0.12	0.18
C(YbxLi, sum)829			0.09	0.17	0.21	0.06	0.12	0.18
C(YbxLi, sum)831	0.19	0.14	0.10	0.17	0.22	0.06	0.12	0.19
C(YbxLi, sum)832	0.19	0.14	0.10	0.18	0.23	0.06	0.13	0.19
C(YbxLi, sum)833	0.22	0.16	0.10	0.18	0.23	0.06	0.13	0.20
C(YbxLi, sum)839			0.09	0.15	0.20	0.05	0.12	0.17
C(YbxLi, sum)841			0.09	0.15	0.19	0.05	0.11	0.16
C(YbxLi, sum)842			0.10	0.17	0.22	0.06	0.12	0.18
C(YbxLi, sum)843			0.09	0.17	0.21	0.06	0.12	0.18
C(YbxLi, sum)849			0.09	0.16	0.21	0.06	0.12	0.18
C(YbxLi, sum)851			0.09	0.16	0.20	0.05	0.12	0.17
C(YbxLi, sum)852			0.10	0.18	0.23	0.06	0.13	0.19
C(YbxLi, sum)853			0.09	0.16	0.20	0.05	0.12	0.17
C(YbxLi, sum)859			0.09	0.16	0.20	0.05	0.12	0.17
(Intercept)	0.05	0.04	0.04	0.07	0.09	0.04	0.09	0.08

Table 22: Standard errors of fixed effects for Sex and Year-born-in-x-Line obtained from fitting model 7 for all 56 measured traits: Part 7/7.

	Bctb	Weanwt	NLB	NLW	Fnpua	Fnsua	Fnpt	Fnst
C(Sex, sum)1	0.03	0.05	0.01	0.01	0.01	0.23	0.01	0.22
C(YbxLi, sum)749			0.02	0.02				
C(YbxLi, sum)750			0.06	0.05	0.05	0.91	0.05	0.89
C(YbxLi, sum)759	0.22	0.44	0.03	0.02	0.11	2.15	0.11	2.11
C(YbxLi, sum)761	0.28	0.56	0.06	0.06	0.12	2.27	0.12	2.23
C(YbxLi, sum)762	0.23	0.46	0.08	0.07	0.10	1.80	0.09	1.77
C(YbxLi, sum)763	0.27	0.53	0.06	0.06	0.11	2.14	0.11	2.10
C(YbxLi, sum)769	0.21	0.42	0.08	0.07	0.09	1.63	0.09	1.60
C(YbxLi, sum)771	0.19	0.38	0.06	0.05	0.08	1.48	0.08	1.45
C(YbxLi, sum)772	0.18	0.36	0.05	0.05	0.08	1.42	0.07	1.40
C(YbxLi, sum)773	0.18	0.37	0.05	0.04	0.08	1.42	0.07	1.40
C(YbxLi, sum)779	0.16	0.32	0.05	0.04	0.06	1.23	0.06	1.21
C(YbxLi, sum)781	0.20	0.39	0.05	0.05	0.08	1.55	0.08	1.52
C(YbxLi, sum)782	0.19	0.37	0.05	0.05	0.08	1.44	0.08	1.42
C(YbxLi, sum)783	0.19	0.37	0.05	0.05	0.08	1.44	0.08	1.42
C(YbxLi, sum)789	0.17	0.33	0.05	0.05	0.07	1.33	0.07	1.31
C(YbxLi, sum)791	0.19	0.38	0.06	0.05	0.08	1.49	0.08	1.47
C(YbxLi, sum)792	0.18	0.37	0.05	0.04	0.08	1.44	0.07	1.41
C(YbxLi, sum)793	0.19	0.37	0.04	0.04	0.08	1.45	0.08	1.43
C(YbxLi, sum)799	0.18	0.36	0.05	0.05	0.07	1.38	0.07	1.35
C(YbxLi, sum)801	0.19	0.37	0.05	0.05	0.08	1.45	0.08	1.43
C(YbxLi, sum)802	0.19	0.38	0.05	0.04	0.08	1.49	0.08	1.47
C(YbxLi, sum)803	0.19	0.37	0.05	0.04	0.08	1.45	0.08	1.43
C(YbxLi, sum)809	0.18	0.36	0.05	0.05	0.07	1.40	0.07	1.37
C(YbxLi, sum)821	0.20	0.40	0.05	0.04	0.08	1.58	0.08	1.55
C(YbxLi, sum)822	0.18	0.35	0.05	0.05	0.07	1.38	0.07	1.36
C(YbxLi, sum)823	0.18	0.37	0.05	0.05	0.08	1.44	0.07	1.41
C(YbxLi, sum)829	0.19	0.37	0.04	0.04				
C(YbxLi, sum)831	0.19	0.39	0.05	0.04	0.10	1.84	0.10	1.81
C(YbxLi, sum)832	0.20	0.40	0.06	0.05	0.11	2.09	0.11	2.06
C(YbxLi, sum)833	0.20	0.41	0.05	0.04	0.10	1.98	0.10	1.95
C(YbxLi, sum)839	0.17	0.35	0.05	0.05	0.10	1.83	0.10	1.80
C(YbxLi, sum)841	0.17	0.34	0.05	0.05	0.10	1.83	0.10	1.80
C(YbxLi, sum)842	0.19	0.38	0.05	0.05	0.10	1.97	0.10	1.94
C(YbxLi, sum)843	0.19	0.37	0.04	0.04	0.09	1.66	0.09	1.63
C(YbxLi, sum)849	0.18	0.37	0.05	0.05				
C(YbxLi, sum)851	0.18	0.35	0.05	0.04	0.07	1.37	0.07	1.34
C(YbxLi, sum)852	0.20	0.39	0.05	0.05	0.08	1.56	0.08	1.53
C(YbxLi, sum)853	0.18	0.36	0.05	0.04	0.07	1.39	0.07	1.37
C(YbxLi, sum)859	0.18	0.35	0.05	0.05	0.10	1.82	0.09	1.78
(Intercept)	0.09	0.17	0.01	0.01	0.03	0.58	0.03	0.57

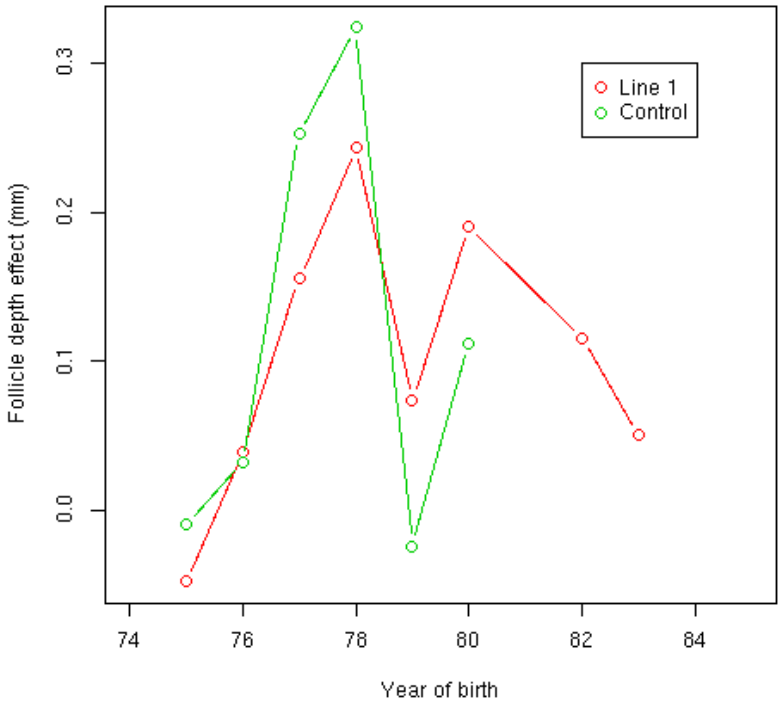

Figure 1: Direct response to selection for follicle depth in Line 1. Shifts in the difference between Line 1 and Control Line represent genetic change.

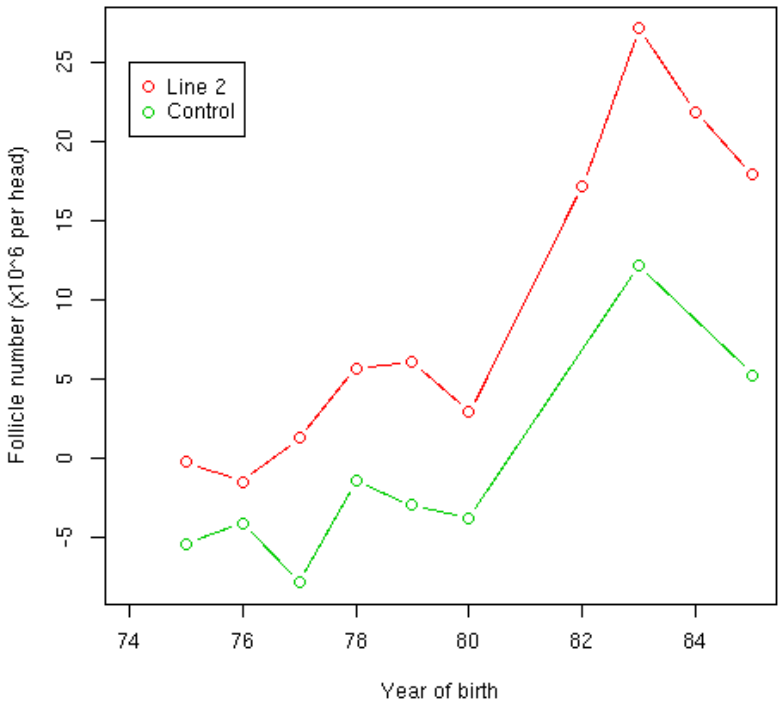

Figure 2: Direct response to selection for follicle number per head in Line 2. Shifts in the difference between Line 2 and Control Line represent genetic change.

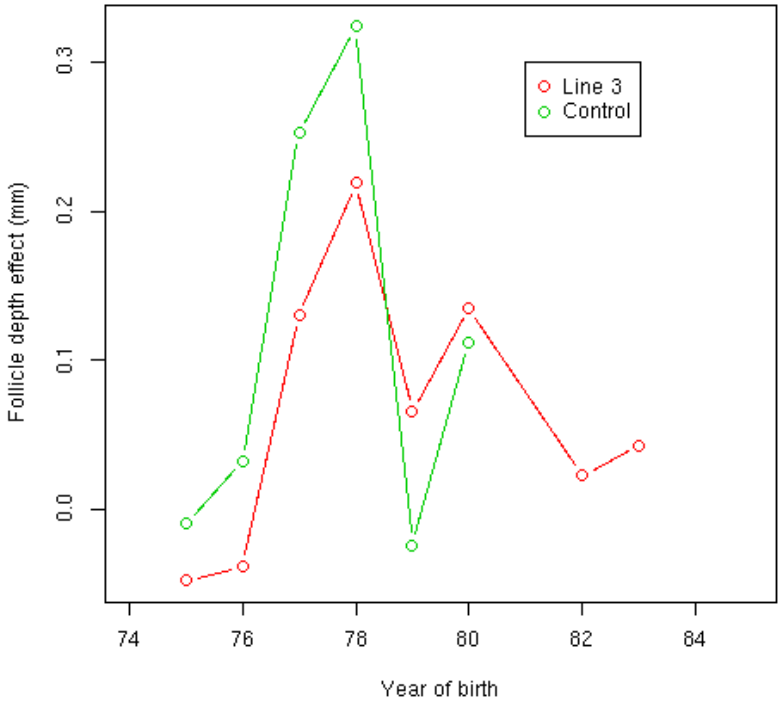

Figure 3: Direct response in follicle depth, to selection for follicle depth and follicle number per head in Line 3. Shifts in the difference between Line 3 and Control Line represent genetic change.

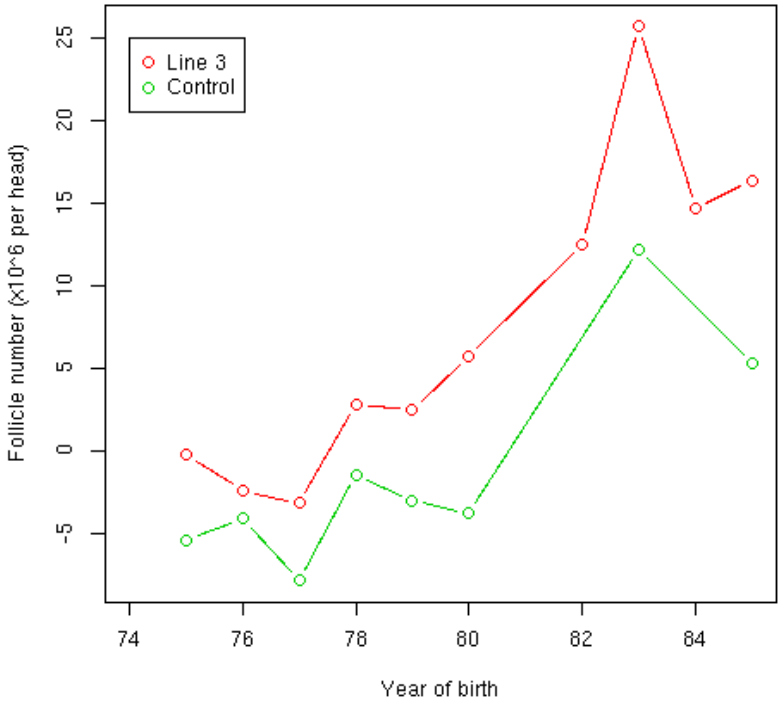

Figure 4: Direct response in follicle number per head, to selection for follicle depth and follicle number per head in Line 3. Shifts in the difference between Line 3 and Control Line represent genetic change.

any of the three lines. There is a slight suggestion that the selected line might average out above the control line in both Line 2 and Line 3. This is not what was expected. The original thinking behind this experiment was that if one wanted to engineer a change in wool weight one had to put selection pressure on all of its components. The components of wool weight in this scenario were considred to be follicle size (measured as follicle depth) and number of follicles (measured as follicle number per head). It was expected that there would be a change in wool weight in Line 3 only. This did not occur. Possible explanations are

- the experiment did not continue for long enough
- the two components (follicle size and number) are in some way not an adequate representation of the biology of wool growth
- the concept of components is somehow flawed

We can look into this a little more thoroughly by seeing if there were any correlated changes in fibre diameter or in fibre length growth rate (measured as staple length).

Figure 7 and Figure 6 show the correlated changes in average fibre diameter and staple length.

There are no obvious correlated changes in staple length or fibre diameter in any of the 3 lines. There is a slight suggestion that staple length might average out higher than the Control line in Lines 2 and 3, as was observeed for clean wool weight. It is becoming clear that the experiment simply did not continue for enough years for correlated responses to be studied. Correlated genetic change is almost always smaller than direct responses to selection, and will therefore take more generations to detect.

In view of the above, the experiment was simply not carried on for long enough to fulfil its original aim. The hypothesis that one can 'engineer' a genetic improvement in wool weight by changing its components in a coordinated way, is still open. A more detailed analysis of responses against amount of selection applied, is not warranted, and would be difficult to carry out because of the missing observations.

The experiment does however provide an important pedigreed data set with some interesting measurements not available elsewhere. We now proceed to an analysis of the pedigree data.

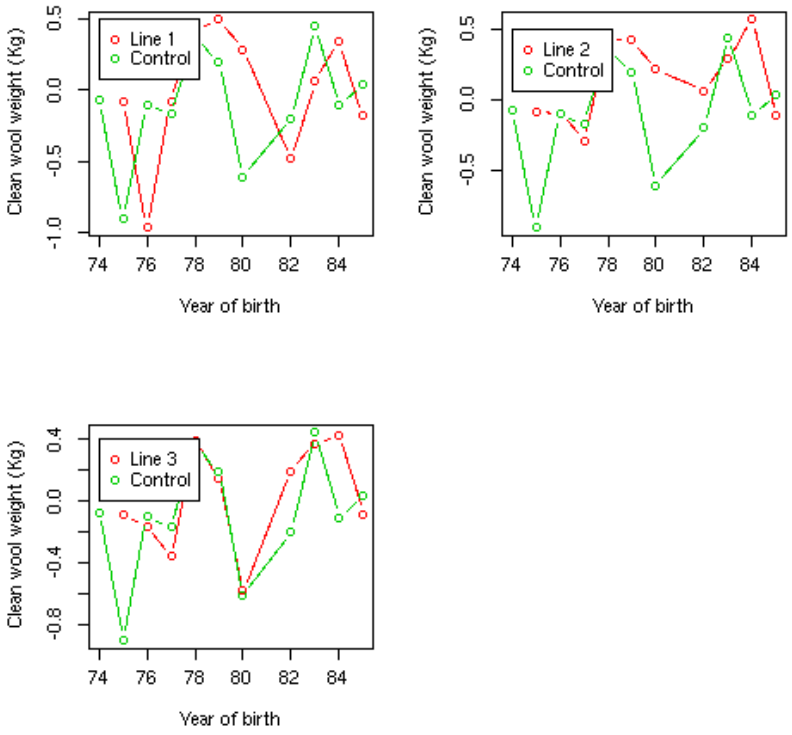

Figure 5: Indirect response in clean wool weight, to selection for follicle depth in Line 1, follicle number per head in Line 2, and follicle depth and follicle number per head in Line 3. Shifts in the difference between each Line and the Control Line represent genetic change.

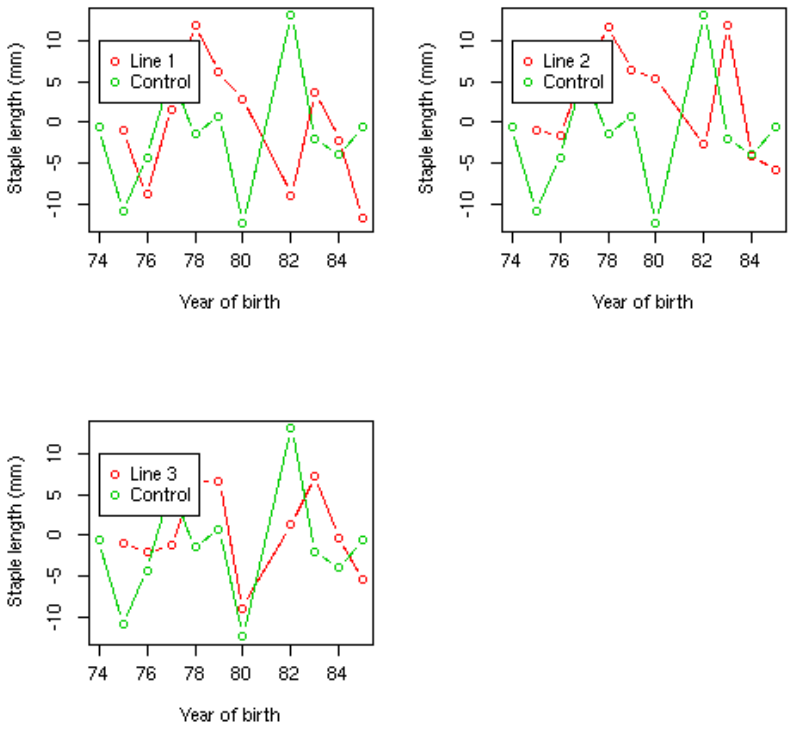

Figure 6: Indirect response in staple length, to selection for follicle depth in Line 1, follicle number per head in Line 2, and follicle depth and follicle number per head in Line 3. Shifts in the difference between each Line and the Control Line represent genetic change.

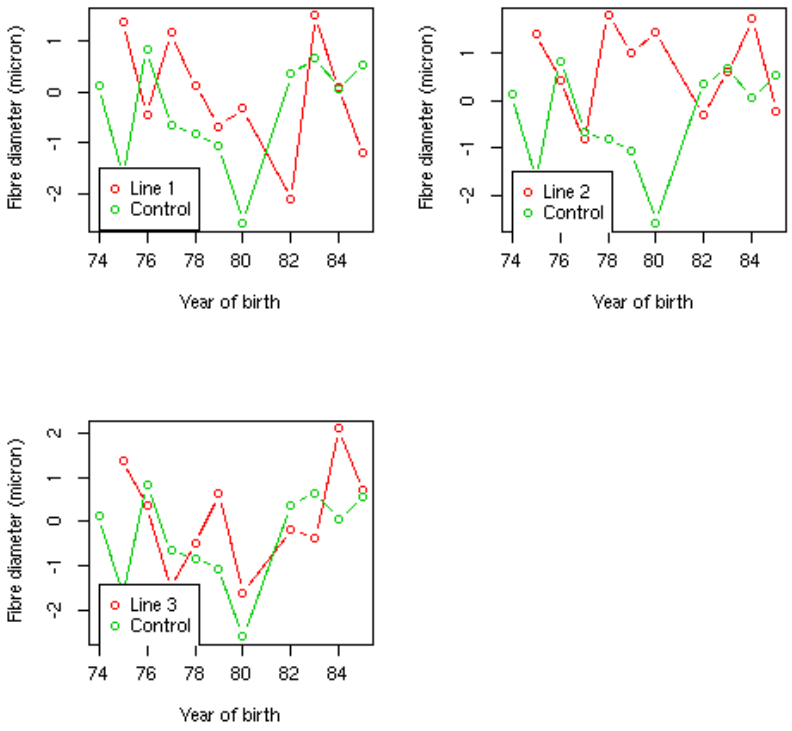

Figure 7: Indirect response in fibre diameter, to selection for follicle depth in Line 1, follicle number per head in Line 2, and follicle depth and follicle number per head in Line 3. Shifts in the difference between each Line and the Control Line represent genetic change.

5.4 Phenotypic parameters

5.4.1 Phenotypic variance

5.4.2 Phenotypic correlation

5.5 Genetic parameters

5.5.1 Proportion of variance which is genetic

5.5.2 Genetic correlation

5.6 Multivariate analysis

6 Discussion

7 Conclusions

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