Genetics of primary and secondary fibre diameters and densities in Merino sheep

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Contents

1 Introduction

In the document Jackson etal(1990) [12] some genetic parameter estimates were presented (see Table 8 of Jackson etal(1990) [12]) for diameters of primary and secondary fibres and a number of other important wool characteristics. These were preliminary estimates obtained by the now outdated analysis of variance method for partitioning variances between and within half-sib families.

A modern method of obtaining these parameters would be to estimate additive genetic variance components using maximum likelihood methods and incorating the full additive genetic relationship matrix among all individuals, computed from a pedigree going back to the base generation of the flock.

This analysis has been done on the exact same dataset for a comprehensive set of 48 traits (Jackson (2015) [7]). What we present here is parameter estimates for a small subset of these traits which are relevant to the issues of Merino evolution and atavism.

2 Materials and methods

The sheep and measurements were as described in Jackson (2015) [7].

2.1 Traits

The subset of traits covered here are summarized in Table 1

Table 1: Definition of traits measured

Trait name	Abbreviation	Units	Age measured	Description
Clean wool weight	Cww	Kg	14 months	Weight of clean fibre at 16% regain
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
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
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
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
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

2.2 Statistical Methods

The statistical techniques used for estimation of parameters for these data are covered in Jackson (2015) [7]. The software used is called *dmm*, which runs as a package under the R statistical language [18]. *dmm* is documented in a user's guide (Jackson(2015b) [8]).

3 Results

All parameter estimates are presented with a standard error estimate and the upper and lower bounds of a 95 percent confidence interval.

3.1 Heritabilities

Estimates of heritability for the 13 traits are given in Table 2

Table 2: Heritability estimates with standard errors and 95 percent confidence limits for 13 skin and wool traits

Trait	Estimate	StdErr	CI95lo	CI95hi
Cww	0.34	0.01	0.32	0.37
Fnua	0.29	0.01	0.27	0.32
Fr	0.31	0.01	0.28	0.33
Bctb	0.76	0.02	0.72	0.79
NLB	0.20	0.01	0.18	0.22
NLW	0.21	0.01	0.19	0.23
Dp	0.52	0.03	0.45	0.58
Ds	0.41	0.03	0.35	0.47
Dps	0.38	0.03	0.33	0.44
DpovDs	0.81	0.04	0.74	0.88
SDDp	0.49	0.03	0.43	0.55
SDDs	0.41	0.03	0.35	0.47
SDD	0.43	0.03	0.37	0.48

The heritability estimates for density and ratio are somewhat different from those of Jackson, Nay, and Turner (1975) [6]. Estimates for Fnua and Fr are lower than previous estimates. However for Cww and Dps estimates agree with other published values (see Turner and Young (1969) [24]). The high estimates for Bctb and DpovDs are surprising, but given that estimates for other traits are reasonable , we have to accept them. The estimates for Dp and Ds and their standard deviations are new - there are no other published values, but their magnitude looks reasonable given that most wool traits have about a 40 perent heritability. We would expect lower values for NLB and NLW so the 20 percent values are quite acceptable.

3.2 Genetic correlations

The additive genetic correlation estimates for all pairs of the 13 traits are presented in Table 3.

Table 3: Genetic correlation estimates with standard errors and 95 percent confidence limits for 13 skin and wool traits

Traits	Estimate	StdErr	CI95lo	CI95hi
Cww:Cww	1.00	0.00	1.00	1.00
Cww:Fnua	0.01	0.04	-0.07	0.08
Cww:Fr	0.06	0.04	-0.01	0.13
Cww:Bctb	-0.12	0.03	-0.18	-0.07
Cww:NLB	0.15	0.04	0.07	0.24
Cww:NLW	0.10	0.04	0.02	0.18
Cww:Dp	-0.01	0.06	-0.12	0.10
Cww:Ds	0.63	0.06	0.50	0.75
Cww:Dps	0.63	0.06	0.50	0.75
Cww:DpovDs	-0.31	0.04	-0.40	-0.22
Cww:SDDp	-0.07	0.06	-0.18	0.04
Cww:SDDs	0.30	0.06	0.18	0.43
Cww:SDD	0.27	0.06	0.14	0.39
Fnua:Cww	0.01	0.04	-0.07	0.08
Fnua:Fnua	1.00	0.00	1.00	1.00
Fnua:Fr	0.49	0.03	0.43	0.56
Fnua:Bctb	0.07	0.03	0.02	0.13
Fnua:NLB	0.15	0.05	0.05	0.25
Fnua:NLW	0.22	0.05	0.11	0.32
Fnua:Dp	0.00	1.34	-2.63	2.63
Fnua:Ds	-0.73	0.06	-0.85	-0.61
Fnua:Dps	-0.74	0.06	-0.86	-0.62
Fnua:DpovDs	0.36	0.06	0.26	0.47
Fnua:SDDp	-0.06	0.07	-0.19	0.08
Fnua:SDDs	-0.37	0.07	-0.52	-0.23
Fnua:SDD	-0.36	0.07	-0.51	-0.22
Fr:Cww	0.06	0.04	-0.01	0.13
Fr:Fnua	0.49	0.03	0.43	0.56
Fr:Fr	1.00	0.00	1.00	1.00
Fr:Bctb	0.02	0.03	-0.04	0.07
Fr:NLB	0.08	0.05	-0.02	0.18
Fr:NLW	0.12	0.05	0.02	0.22
Fr:Dp	-0.13	0.07	-0.27	0.01

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Traits	Estimate	StdErr	CI95lo	CI95hi
Fr:Ds	-0.12	0.08	-0.28	0.03
Fr:Dps	-0.15	0.08	-0.31	0.01
Fr:DpovDs	-0.03	0.06	-0.15	0.08
Fr:SDDp	-0.12	0.07	-0.27	0.02
Fr:SDDs	-0.27	0.08	-0.43	-0.11
Fr:SDD	-0.28	0.08	-0.44	-0.12
Bctb:Cww	-0.12	0.03	-0.18	-0.07
Bctb:Fnua	0.07	0.03	0.02	0.13
Bctb:Fr	0.02	0.03	-0.04	0.07
Bctb:Bctb	1.00	0.00	1.00	1.00
Bctb:NLB	0.06	0.03	0.00	0.12
Bctb:NLW	0.17	0.03	0.12	0.23
Bctb:Dp	0.70	0.03	0.65	0.76
Bctb:Ds	-0.14	0.04	-0.22	-0.07
Bctb:Dps	-0.08	0.04	-0.16	-0.00
Bctb:DpovDs	0.65	0.02	0.61	0.69
Bctb:SDDp	0.85	0.03	0.79	0.91
Bctb:SDDs	0.31	0.04	0.24	0.38
Bctb:SDD	0.43	0.04	0.36	0.50
NLB:Cww	0.15	0.04	0.07	0.24
NLB:Fnua	0.15	0.05	0.05	0.25
NLB:Fr	0.08	0.05	-0.02	0.18
NLB:Bctb	0.06	0.03	0.00	0.12
NLB:NLB	1.00	0.00	1.00	1.00
NLB:NLW	0.98	0.03	0.93	1.03
NLB:Dp	0.41	0.08	0.26	0.55
NLB:Ds	-0.16	0.09	-0.33	0.02
NLB:Dps	-0.12	0.09	-0.30	0.06
NLB:DpovDs	0.42	0.06	0.30	0.54
NLB:SDDp	0.38	0.08	0.22	0.54
NLB:SDDs	0.06	0.09	-0.10	0.23
NLB:SDD	0.14	0.08	-0.03	0.30
NLW:Cww	0.10	0.04	0.02	0.18
NLW:Fnua	0.22	0.05	0.11	0.32
NLW:Fr	0.12	0.05	0.02	0.22
NLW:Bctb	0.17	0.03	0.12	0.23
NLW:NLB	0.98	0.03	0.93	1.03
NLW:NLW	1.00	0.00	1.00	1.00
NLW:Dp	0.42	0.07	0.28	0.57
NLW:Ds	-0.23	0.09	-0.40	-0.06
NLW:Dps	-0.19	0.09	-0.36	-0.02
NLW:DpovDs	0.47	0.06	0.36	0.59
NLW:SDDp	0.42	0.08	0.27	0.57

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Traits	Estimate	StdErr	CI95lo	CI95hi
NLW:SDDs	0.22	0.08	0.06	0.38
NLW:SDD	0.28	0.08	0.12	0.44
Dp:Cww	-0.01	0.06	-0.12	0.10
Dp:Fnua	0.00	1.34	-2.63	2.63
Dp:Fr	-0.13	0.07	-0.27	0.01
Dp:Bctb	0.70	0.03	0.65	0.76
Dp:NLB	0.41	0.08	0.26	0.55
Dp:NLW	0.42	0.07	0.28	0.57
Dp:Dp	1.00	0.00	1.00	1.00
Dp:Ds	-0.09	0.06	-0.22	0.03
Dp:Dps	-0.00	0.15	-0.30	0.29
Dp:DpovDs	0.87	0.02	0.82	0.91
Dp:SDDp	0.85	0.03	0.78	0.92
Dp:SDDs	0.34	0.05	0.24	0.45
Dp:SDD	0.47	0.05	0.38	0.57
Ds:Cww	0.63	0.06	0.50	0.75
Ds:Fnua	-0.73	0.06	-0.85	-0.61
Ds:Fr	-0.12	0.08	-0.28	0.03
Ds:Bctb	-0.14	0.04	-0.22	-0.07
Ds:NLB	-0.16	0.09	-0.33	0.02
Ds:NLW	-0.23	0.09	-0.40	-0.06
Ds:Dp	-0.09	0.06	-0.22	0.03
Ds:Ds	1.00	0.00	1.00	1.00
Ds:Dps	1.00	0.00	0.99	1.00
Ds:DpovDs	-0.58	0.04	-0.66	-0.49
Ds:SDDp	-0.06	0.06	-0.18	0.07
Ds:SDDs	0.60	0.06	0.48	0.71
Ds:SDD	0.54	0.06	0.42	0.65
Dps:Cww	0.63	0.06	0.50	0.75
Dps:Fnua	-0.74	0.06	-0.86	-0.62
Dps:Fr	-0.15	0.08	-0.31	0.01
Dps:Bctb	-0.08	0.04	-0.16	-0.00
Dps:NLB	-0.12	0.09	-0.30	0.06
Dps:NLW	-0.19	0.09	-0.36	-0.02
Dps:Dp	-0.00	0.15	-0.30	0.29
Dps:Ds	1.00	0.00	0.99	1.00
Dps:Dps	1.00	0.00	1.00	1.00
Dps:DpovDs	-0.50	0.05	-0.59	-0.41
Dps:SDDp	0.02	0.06	-0.10	0.14
Dps:SDDs	0.63	0.06	0.51	0.75
Dps:SDD	0.59	0.06	0.47	0.70
DpovDs:Cww	-0.31	0.04	-0.40	-0.22
DpovDs:Fnua	0.36	0.06	0.26	0.47

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Traits	Estimate	StdErr	CI95lo	CI95hi
DpovDs:Fr	-0.03	0.06	-0.15	0.08
DpovDs:Bctb	0.65	0.02	0.61	0.69
DpovDs:NLB	0.42	0.06	0.30	0.54
DpovDs:NLW	0.47	0.06	0.36	0.59
DpovDs:Dp	0.87	0.02	0.82	0.91
DpovDs:Ds	-0.58	0.04	-0.66	-0.49
DpovDs:Dps	-0.50	0.05	-0.59	-0.41
DpovDs:DpovDs	1.00	0.00	1.00	1.00
DpovDs:SDDp	0.74	0.03	0.68	0.80
DpovDs:SDDs	-0.04	0.05	-0.13	0.06
DpovDs:SDD	0.10	0.05	0.01	0.19
SDDp:Cww	-0.07	0.06	-0.18	0.04
SDDp:Fnua	-0.06	0.07	-0.19	0.08
SDDp:Fr	-0.12	0.07	-0.27	0.02
SDDp:Bctb	0.85	0.03	0.79	0.91
SDDp:NLB	0.38	0.08	0.22	0.54
SDDp:NLW	0.42	0.08	0.27	0.57
SDDp:Dp	0.85	0.03	0.78	0.92
SDDp:Ds	-0.06	0.06	-0.18	0.07
SDDp:Dps	0.02	0.06	-0.10	0.14
SDDp:DpovDs	0.74	0.03	0.68	0.80
SDDp:SDDp	1.00	0.00	1.00	1.00
SDDp:SDDs	0.37	0.06	0.26	0.48
SDDp:SDD	0.52	0.05	0.42	0.61
SDDs:Cww	0.30	0.06	0.18	0.43
SDDs:Fnua	-0.37	0.07	-0.52	-0.23
SDDs:Fr	-0.27	0.08	-0.43	-0.11
SDDs:Bctb	0.31	0.04	0.24	0.38
SDDs:NLB	0.06	0.09	-0.10	0.23
SDDs:NLW	0.22	0.08	0.06	0.38
SDDs:Dp	0.34	0.05	0.24	0.45
SDDs:Ds	0.60	0.06	0.48	0.71
SDDs:Dps	0.63	0.06	0.51	0.75
SDDs:DpovDs	-0.04	0.05	-0.13	0.06
SDDs:SDDp	0.37	0.06	0.26	0.48
SDDs:SDDs	1.00	0.00	1.00	1.00
SDDs:SDD	0.99	0.01	0.97	1.00
SDD:Cww	0.27	0.06	0.14	0.39
SDD:Fnua	-0.36	0.07	-0.51	-0.22
SDD:Fr	-0.28	0.08	-0.44	-0.12
SDD:Bctb	0.43	0.04	0.36	0.50
SDD:NLB	0.14	0.08	-0.03	0.30
SDD:NLW	0.28	0.08	0.12	0.44

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Traits	Estimate	StdErr	CI95lo	CI95hi
SDD:Dp	0.47	0.05	0.38	0.57
SDD:Ds	0.54	0.06	0.42	0.65
SDD:Dps	0.59	0.06	0.47	0.70
SDD:DpovDs	0.10	0.05	0.01	0.19
SDD:SDDp	0.52	0.05	0.42	0.61
SDD:SDDs	0.99	0.01	0.97	1.00
SDD:SDD	1.00	0.00	1.00	1.00

The genetic correlations involving Dp are most relevent. Dp is not genetically correlated with either Ds or Cww or Fnua. This indicates that Dp and Ds can be changed independently. Dp is strongly genetically correlated with Bcts, SDDp, and DpovDs. Dp also has a moderate genetic correlation with the fertility traits NLB and NLW. This supports the argument that Dp is in some way related to fitness.

The genetic correlations involving Ds are different to those involving Dp. Ds has a strong positive genetic correlation with Cww, and a strong negative genetic correlation with Fnua. Selection for Cww will increase Ds, but not Dp. Ds has weak negative genetic correlations with Bctb and the fertility traits (NLB and NLW). Ds is positively correlated with its standard deviation (SDDs).

The other correlations of interest are between Cww and SDDp, which is close to zero, and between Cww and SDDs which is medium positive. So Cww selection will change both the mean (Ds) and standard deviation(SDDs) of the secondary fibres, but the primary fibres will not be affected in either mean (Dp) or standard deviation (SDDp). This goes against what has been said (Jackson et al (1990) [12]) about Cww selection possibly being one of the factors which can cause primitive individuals to appear in a flock. What the parameters say is that Cww selection without amendments will lead to coarse fibres and a broader distribution of diameter, but this will come from the secondary fibres getting coarser, not the primaries. Other factors must be involved when we observe individuals with coarse primary fibres. It would seem, from the parameters, that these other factors might be fitness related, because the present genetic correlations suggest that sheep with coarse primaries are more fertile and better survivors.

We can summarize the Cww selection issue as follows. There are two ways wool quality can be allowed to deteriorate while selecting a Fine Merino flock for Cww

- failing to put sufficient counter-selection pressure on Ds and SDDs (or D and SDD which is nearly the same thing). This leads to sheep becoming like Btritish Longwools - all fibres coarser. This is the components issue. The South Australian Merino is a good example.

- failing to put sufficient counter-selection pressure on Dp to counter the fitness effect of Dp, and allowing density to decline (see below). This leads to sheep becoming like primitive 2-coated domestic sheep with Dp coarser than Ds.

So the genetic correlations between Cww and Ds (and between Cww and SDDs) are simply the positive correlations between Cww and and two of its components. Nothing else is involved, it is purely a physical part/whole situation.

But the genetic correlation between Cww and Dp is more complicated. First there is the part/whole components situation, which would tend to make the correlation positive. Second there is the fact that another component of Cww - density or Ns/Np ratio - has a strong negative correlation with Dp because the pre-papilla cell theory (Moore et al (1998) [15]) shows that small primary follicles conserve pre-papilla cell numbers so that they can multiply more and form more secondary follicles. So this situation would tend to make the correlation between Cww and Dp negative, to the extent that variation in Cww involves variation in density. Third Dp is a fitness component because it is strongly correlated with birthcoat and fertility. If Cww is related to fitness (one would expect low Cww to be fitter in a non-domestic environment) this would also lead to a negative correlation between Cww and Dp. The balance between these three effects is what we see as the genetic correlation between Cww and Dp. In our flock the balance was close to zero. In other flocks the balance could be different.

The net result of situations like the above where genetic correlations depend on a balancing of forces, is that predictions made using such genetic correlations are not likely to be very useful. The balance can change in a population under selection.

3.3 Phenotypic variances and covariances

To use genetic parameters for predicting selection response requires phenotypic (co)variances in addition to heritabilities and genetic correlations. We present these here for completeness in Table 4

Table 4: Phenotypic variance and covariance estimates with standard errors and 95 percent confidence limits for 13 skin and wool traits

Traitpair	Estimate	StdErr	CI95lo	CI95hi
Cww:Cww	0.12	0.00	0.12	0.12
Cww:Fnua	-0.13	0.07	-0.27	0.01
Cww:Fr	0.20	0.02	0.15	0.24
Cww:Bctb	0.03	0.01	0.01	0.05
Cww:NLB	-0.02	0.00	-0.03	-0.02

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Table 4 – *Continued from previous page*

Traitpair	Estimate	StdErr	CI95lo	CI95hi
Cww:NLW	-0.02	0.00	-0.02	-0.01
Cww:Dp	0.10	0.04	0.03	0.17
Cww:Ds	0.14	0.02	0.09	0.18
Cww:Dps	0.13	0.02	0.09	0.18
Cww:DpovDs	-0.00	0.00	-0.01	0.00
Cww:SDDp	0.01	0.01	-0.02	0.04
Cww:SDDs	0.01	0.01	-0.00	0.02
Cww:SDD	0.01	0.01	-0.00	0.02
Fnua:Cww	-0.13	0.07	-0.27	0.01
Fnua:Fnua	148.64	2.63	143.50	153.79
Fnua:Fr	24.10	0.83	22.47	25.74
Fnua:Bctb	-0.49	0.34	-1.16	0.18
Fnua:NLB	-0.46	0.10	-0.65	-0.27
Fnua:NLW	-0.27	0.09	-0.45	-0.10
Fnua:Dp	-11.54	1.63	-14.73	-8.35
Fnua:Ds	-14.62	0.95	-16.48	-12.76
Fnua:Dps	-14.71	0.94	-16.55	-12.86
Fnua:DpovDs	0.26	0.08	0.11	0.41
Fnua:SDDp	-3.19	0.66	-4.49	-1.89
Fnua:SDDs	-1.68	0.28	-2.22	-1.14
Fnua:SDD	-1.86	0.28	-2.41	-1.32
Fr:Cww	0.20	0.02	0.15	0.24
Fr:Fnua	24.10	0.83	22.47	25.74
Fr:Fr	15.00	0.26	14.49	15.52
Fr:Bctb	-0.16	0.11	-0.38	0.05
Fr:NLB	-0.18	0.03	-0.24	-0.12
Fr:NLW	-0.13	0.03	-0.18	-0.07
Fr:Dp	-1.70	0.52	-2.71	-0.69
Fr:Ds	-1.74	0.30	-2.33	-1.15
Fr:Dps	-1.86	0.30	-2.45	-1.28
Fr:DpovDs	0.02	0.02	-0.03	0.06
Fr:SDDp	-0.49	0.21	-0.90	-0.08
Fr:SDDs	-0.20	0.09	-0.37	-0.03
Fr:SDD	-0.28	0.09	-0.45	-0.11
Bctb:Cww	0.03	0.01	0.01	0.05
Bctb:Fnua	-0.49	0.34	-1.16	0.18
Bctb:Fr	-0.16	0.11	-0.38	0.05
Bctb:Bctb	2.27	0.04	2.20	2.35
Bctb:NLB	-0.02	0.01	-0.05	0.00
Bctb:NLW	-0.02	0.01	-0.04	-0.00
Bctb:Dp	2.79	0.18	2.44	3.14
Bctb:Ds	-0.20	0.11	-0.41	0.01
Bctb:Dps	-0.07	0.11	-0.28	0.13

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Table 4 – *Continued from previous page*

Traitpair	Estimate	StdErr	CI95lo	CI95hi
Bctb:DpovDs	0.15	0.01	0.14	0.17
Bctb:SDDp	1.12	0.07	0.98	1.26
Bctb:SDDs	0.10	0.03	0.04	0.16
Bctb:SDD	0.17	0.03	0.11	0.23
NLB:Cww	-0.02	0.00	-0.03	-0.02
NLB:Fnua	-0.46	0.10	-0.65	-0.27
NLB:Fr	-0.18	0.03	-0.24	-0.12
NLB:Bctb	-0.02	0.01	-0.05	0.00
NLB:NLB	0.21	0.00	0.20	0.22
NLB:NLW	0.15	0.00	0.14	0.16
NLB:Dp	0.30	0.06	0.18	0.41
NLB:Ds	0.07	0.03	-0.00	0.13
NLB:Dps	0.08	0.03	0.01	0.14
NLB:DpovDs	0.01	0.00	0.01	0.02
NLB:SDDp	0.05	0.02	0.01	0.10
NLB:SDDs	0.02	0.01	0.00	0.04
NLB:SDD	0.02	0.01	0.00	0.04
NLW:Cww	-0.02	0.00	-0.02	-0.01
NLW:Fnua	-0.27	0.09	-0.45	-0.10
NLW:Fr	-0.13	0.03	-0.18	-0.07
NLW:Bctb	-0.02	0.01	-0.04	-0.00
NLW:NLB	0.15	0.00	0.14	0.16
NLW:NLW	0.17	0.00	0.17	0.18
NLW:Dp	0.29	0.05	0.18	0.39
NLW:Ds	0.04	0.03	-0.02	0.10
NLW:Dps	0.05	0.03	-0.01	0.12
NLW:DpovDs	0.01	0.00	0.01	0.02
NLW:SDDp	0.05	0.02	0.00	0.09
NLW:SDDs	0.03	0.01	0.01	0.05
NLW:SDD	0.03	0.01	0.01	0.05
Dp:Cww	0.10	0.04	0.03	0.17
Dp:Fnua	-11.54	1.63	-14.73	-8.35
Dp:Fr	-1.70	0.52	-2.71	-0.69
Dp:Bctb	2.79	0.18	2.44	3.14
Dp:NLB	0.30	0.06	0.18	0.41
Dp:NLW	0.29	0.05	0.18	0.39
Dp:Dp	11.81	0.39	11.04	12.57
Dp:Ds	2.60	0.23	2.15	3.05
Dp:Dps	3.03	0.23	2.59	3.48
Dp:DpovDs	0.43	0.02	0.39	0.47
Dp:SDDp	3.16	0.16	2.85	3.47
Dp:SDDs	0.80	0.07	0.67	0.93
Dp:SDD	0.97	0.07	0.84	1.10

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Table 4 – *Continued from previous page*

Traitpair	Estimate	StdErr	CI95lo	CI95hi
Ds:Cww	0.14	0.02	0.09	0.18
Ds:Fnua	-14.62	0.95	-16.48	-12.76
Ds:Fr	-1.74	0.30	-2.33	-1.15
Ds:Bctb	-0.20	0.11	-0.41	0.01
Ds:NLB	0.07	0.03	-0.00	0.13
Ds:NLW	0.04	0.03	-0.02	0.10
Ds:Dp	2.60	0.23	2.15	3.05
Ds:Ds	4.06	0.14	3.79	4.32
Ds:Dps	4.01	0.13	3.75	4.27
Ds:DpovDs	-0.10	0.01	-0.13	-0.08
Ds:SDDp	0.44	0.09	0.25	0.62
Ds:SDDs	0.43	0.04	0.36	0.51
Ds:SDD	0.44	0.04	0.36	0.51
Dps:Cww	0.13	0.02	0.09	0.18
Dps:Fnua	-14.71	0.94	-16.55	-12.86
Dps:Fr	-1.86	0.30	-2.45	-1.28
Dps:Bctb	-0.07	0.11	-0.28	0.13
Dps:NLB	0.08	0.03	0.01	0.14
Dps:NLW	0.05	0.03	-0.01	0.12
Dps:Dp	3.03	0.23	2.59	3.48
Dps:Ds	4.01	0.13	3.75	4.27
Dps:Dps	3.99	0.13	3.73	4.25
Dps:DpovDs	-0.08	0.01	-0.10	-0.06
Dps:SDDp	0.56	0.09	0.38	0.74
Dps:SDDs	0.45	0.04	0.38	0.53
Dps:SDD	0.46	0.04	0.39	0.54
DpovDs:Cww	-0.00	0.00	-0.01	0.00
DpovDs:Fnua	0.26	0.08	0.11	0.41
DpovDs:Fr	0.02	0.02	-0.03	0.06
DpovDs:Bctb	0.15	0.01	0.14	0.17
DpovDs:NLB	0.01	0.00	0.01	0.02
DpovDs:NLW	0.01	0.00	0.01	0.02
DpovDs:Dp	0.43	0.02	0.39	0.47
DpovDs:Ds	-0.10	0.01	-0.13	-0.08
DpovDs:Dps	-0.08	0.01	-0.10	-0.06
DpovDs:DpovDs	0.03	0.00	0.03	0.03
DpovDs:SDDp	0.13	0.01	0.12	0.15
DpovDs:SDDs	0.01	0.00	0.01	0.02
DpovDs:SDD	0.02	0.00	0.02	0.03
SDDp:Cww	0.01	0.01	-0.02	0.04
SDDp:Fnua	-3.19	0.66	-4.49	-1.89
SDDp:Fr	-0.49	0.21	-0.90	-0.08
SDDp:Bctb	1.12	0.07	0.98	1.26

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Table 4 – *Continued from previous page*

Traitpair	Estimate	StdErr	CI95lo	CI95hi
SDDp:NLB	0.05	0.02	0.01	0.10
SDDp:NLW	0.05	0.02	0.00	0.09
SDDp:Dp	3.16	0.16	2.85	3.47
SDDp:Ds	0.44	0.09	0.25	0.62
SDDp:Dps	0.56	0.09	0.38	0.74
SDDp:DpovDs	0.13	0.01	0.12	0.15
SDDp:SDDp	1.95	0.06	1.83	2.08
SDDp:SDDs	0.27	0.03	0.22	0.33
SDDp:SDD	0.39	0.03	0.34	0.44
SDDs:Cww	0.01	0.01	-0.00	0.02
SDDs:Fnua	-1.68	0.28	-2.22	-1.14
SDDs:Fr	-0.20	0.09	-0.37	-0.03
SDDs:Bctb	0.10	0.03	0.04	0.16
SDDs:NLB	0.02	0.01	0.00	0.04
SDDs:NLW	0.03	0.01	0.01	0.05
SDDs:Dp	0.80	0.07	0.67	0.93
SDDs:Ds	0.43	0.04	0.36	0.51
SDDs:Dps	0.45	0.04	0.38	0.53
SDDs:DpovDs	0.01	0.00	0.01	0.02
SDDs:SDDp	0.27	0.03	0.22	0.33
SDDs:SDDs	0.34	0.01	0.31	0.36
SDDs:SDD	0.33	0.01	0.31	0.36
SDD:Cww	0.01	0.01	-0.00	0.02
SDD:Fnua	-1.86	0.28	-2.41	-1.32
SDD:Fr	-0.28	0.09	-0.45	-0.11
SDD:Bctb	0.17	0.03	0.11	0.23
SDD:NLB	0.02	0.01	0.00	0.04
SDD:NLW	0.03	0.01	0.01	0.05
SDD:Dp	0.97	0.07	0.84	1.10
SDD:Ds	0.44	0.04	0.36	0.51
SDD:Dps	0.46	0.04	0.39	0.54
SDD:DpovDs	0.02	0.00	0.02	0.03
SDD:SDDp	0.39	0.03	0.34	0.44
SDD:SDDs	0.33	0.01	0.31	0.36
SDD:SDD	0.34	0.01	0.32	0.36

These are only of interest to someone wanting to calculate predicted responses.

3.4 Phenotypic correlations

These are the correlation one observes in a flock. They are made up of a genetic and environmental component, so they may differ from a genetic correlation if the environmental correlation differsa. They are presented in Table 5

Table 5: Phenotypic correlation estimates with standard errors and 95 percent confidence limits for 13 skin and wool traits

Traits	Estimate	StdErr	CI95lo	CI95hi
Cww:Cww	1.00	0.00	1.00	1.00
Cww:Fnua	-0.03	0.02	-0.07	0.00
Cww:Fr	0.15	0.02	0.12	0.18
Cww:Bctb	0.06	0.02	0.02	0.09
Cww:NLB	-0.15	0.02	-0.18	-0.12
Cww:NLW	-0.13	0.02	-0.16	-0.10
Cww:Dp	0.09	0.03	0.03	0.15
Cww:Ds	0.20	0.03	0.14	0.27
Cww:Dps	0.20	0.03	0.14	0.26
Cww:DpovDs	-0.06	0.03	-0.12	0.00
Cww:SDDp	0.01	0.03	-0.05	0.08
Cww:SDDs	0.06	0.03	-0.00	0.12
Cww:SDD	0.06	0.03	-0.01	0.12
Fnua:Cww	-0.03	0.02	-0.07	0.00
Fnua:Fnua	1.00	0.00	1.00	1.00
Fnua:Fr	0.51	0.01	0.48	0.54
Fnua:Bctb	-0.03	0.02	-0.06	0.01
Fnua:NLB	-0.08	0.02	-0.12	-0.05
Fnua:NLW	-0.06	0.02	-0.09	-0.02
Fnua:Dp	-0.24	0.03	-0.30	-0.17
Fnua:Ds	-0.52	0.03	-0.57	-0.46
Fnua:Dps	-0.52	0.03	-0.58	-0.47
Fnua:DpovDs	0.11	0.03	0.05	0.18
Fnua:SDDp	-0.16	0.03	-0.23	-0.10
Fnua:SDDs	-0.20	0.03	-0.27	-0.14
Fnua:SDD	-0.23	0.03	-0.29	-0.16
Fr:Cww	0.15	0.02	0.12	0.18
Fr:Fnua	0.51	0.01	0.48	0.54
Fr:Fr	1.00	0.00	1.00	1.00
Fr:Bctb	-0.03	0.02	-0.06	0.01
Fr:NLB	-0.10	0.02	-0.14	-0.07
Fr:NLW	-0.08	0.02	-0.12	-0.05
Fr:Dp	-0.11	0.03	-0.18	-0.05
Fr:Ds	-0.19	0.03	-0.26	-0.13

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Table 5 – *Continued from previous page*

Traits	Estimate	StdErr	CI95lo	CI95hi
Fr:Dps	-0.21	0.03	-0.27	-0.15
Fr:DpovDs	0.02	0.03	-0.04	0.09
Fr:SDDp	-0.08	0.03	-0.14	-0.01
Fr:SDDs	-0.08	0.03	-0.14	-0.01
Fr:SDD	-0.11	0.03	-0.17	-0.04
Bctb:Cww	0.06	0.02	0.02	0.09
Bctb:Fnua	-0.03	0.02	-0.06	0.01
Bctb:Fr	-0.03	0.02	-0.06	0.01
Bctb:Bctb	1.00	0.00	1.00	1.00
Bctb:NLB	-0.03	0.02	-0.07	0.00
Bctb:NLW	-0.04	0.02	-0.07	-0.00
Bctb:Dp	0.42	0.02	0.37	0.47
Bctb:Ds	-0.05	0.03	-0.10	0.00
Bctb:Dps	-0.02	0.03	-0.07	0.03
Bctb:DpovDs	0.48	0.02	0.43	0.52
Bctb:SDDp	0.41	0.02	0.37	0.46
Bctb:SDDs	0.09	0.03	0.04	0.14
Bctb:SDD	0.15	0.03	0.10	0.20
NLB:Cww	-0.15	0.02	-0.18	-0.12
NLB:Fnua	-0.08	0.02	-0.12	-0.05
NLB:Fr	-0.10	0.02	-0.14	-0.07
NLB:Bctb	-0.03	0.02	-0.07	0.00
NLB:NLB	1.00	0.00	1.00	1.00
NLB:NLW	0.79	0.01	0.77	0.81
NLB:Dp	0.17	0.03	0.11	0.24
NLB:Ds	0.07	0.03	0.00	0.13
NLB:Dps	0.08	0.03	0.01	0.14
NLB:DpovDs	0.14	0.03	0.07	0.20
NLB:SDDp	0.08	0.03	0.01	0.14
NLB:SDDs	0.07	0.03	0.00	0.13
NLB:SDD	0.08	0.03	0.02	0.15
NLW:Cww	-0.13	0.02	-0.16	-0.10
NLW:Fnua	-0.06	0.02	-0.09	-0.02
NLW:Fr	-0.08	0.02	-0.12	-0.05
NLW:Bctb	-0.04	0.02	-0.07	-0.00
NLW:NLB	0.79	0.01	0.77	0.81
NLW:NLW	1.00	0.00	1.00	1.00
NLW:Dp	0.17	0.03	0.11	0.24
NLW:Ds	0.04	0.03	-0.02	0.11
NLW:Dps	0.06	0.03	-0.01	0.12
NLW:DpovDs	0.15	0.03	0.09	0.21
NLW:SDDp	0.07	0.03	0.00	0.13
NLW:SDDs	0.10	0.03	0.03	0.16

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Table 5 – *Continued from previous page*

Traits	Estimate	StdErr	CI95lo	CI95hi
NLW:SDD	0.11	0.03	0.04	0.17
Dp:Cww	0.09	0.03	0.03	0.15
Dp:Fnua	-0.24	0.03	-0.30	-0.17
Dp:Fr	-0.11	0.03	-0.18	-0.05
Dp:Bctb	0.42	0.02	0.37	0.47
Dp:NLB	0.17	0.03	0.11	0.24
Dp:NLW	0.17	0.03	0.11	0.24
Dp:Dp	1.00	0.00	1.00	1.00
Dp:Ds	0.38	0.03	0.32	0.43
Dp:Dps	0.44	0.03	0.39	0.50
Dp:DpovDs	0.76	0.02	0.72	0.79
Dp:SDDp	0.66	0.02	0.61	0.70
Dp:SDDs	0.40	0.03	0.34	0.46
Dp:SDD	0.49	0.03	0.43	0.54
Ds:Cww	0.20	0.03	0.14	0.27
Ds:Fnua	-0.52	0.03	-0.57	-0.46
Ds:Fr	-0.19	0.03	-0.26	-0.13
Ds:Bctb	-0.05	0.03	-0.10	0.00
Ds:NLB	0.07	0.03	0.00	0.13
Ds:NLW	0.04	0.03	-0.02	0.11
Ds:Dp	0.38	0.03	0.32	0.43
Ds:Ds	1.00	0.00	1.00	1.00
Ds:Dps	1.00	0.00	0.99	1.00
Ds:DpovDs	-0.31	0.03	-0.37	-0.25
Ds:SDDp	0.15	0.03	0.09	0.22
Ds:SDDs	0.37	0.03	0.31	0.43
Ds:SDD	0.37	0.03	0.31	0.43
Dps:Cww	0.20	0.03	0.14	0.26
Dps:Fnua	-0.52	0.03	-0.58	-0.47
Dps:Fr	-0.21	0.03	-0.27	-0.15
Dps:Bctb	-0.02	0.03	-0.07	0.03
Dps:NLB	0.08	0.03	0.01	0.14
Dps:NLW	0.06	0.03	-0.01	0.12
Dps:Dp	0.44	0.03	0.39	0.50
Dps:Ds	1.00	0.00	0.99	1.00
Dps:Dps	1.00	0.00	1.00	1.00
Dps:DpovDs	-0.24	0.03	-0.31	-0.18
Dps:SDDp	0.20	0.03	0.14	0.26
Dps:SDDs	0.39	0.03	0.33	0.45
Dps:SDD	0.40	0.03	0.34	0.46
DpovDs:Cww	-0.06	0.03	-0.12	0.00
DpovDs:Fnua	0.11	0.03	0.05	0.18
DpovDs:Fr	0.02	0.03	-0.04	0.09

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Table 5 – *Continued from previous page*

Traits	Estimate	StdErr	CI95lo	CI95hi
DpovDs:Bctb	0.48	0.02	0.43	0.52
DpovDs:NLB	0.14	0.03	0.07	0.20
DpovDs:NLW	0.15	0.03	0.09	0.21
DpovDs:Dp	0.76	0.02	0.72	0.79
DpovDs:Ds	-0.31	0.03	-0.37	-0.25
DpovDs:Dps	-0.24	0.03	-0.31	-0.18
DpovDs:DpovDs	1.00	0.00	1.00	1.00
DpovDs:SDDp	0.56	0.02	0.51	0.61
DpovDs:SDDs	0.15	0.03	0.09	0.21
DpovDs:SDD	0.24	0.03	0.17	0.30
SDDp:Cww	0.01	0.03	-0.05	0.08
SDDp:Fnua	-0.16	0.03	-0.23	-0.10
SDDp:Fr	-0.08	0.03	-0.14	-0.01
SDDp:Bctb	0.41	0.02	0.37	0.46
SDDp:NLB	0.08	0.03	0.01	0.14
SDDp:NLW	0.07	0.03	0.00	0.13
SDDp:Dp	0.66	0.02	0.61	0.70
SDDp:Ds	0.15	0.03	0.09	0.22
SDDp:Dps	0.20	0.03	0.14	0.26
SDDp:DpovDs	0.56	0.02	0.51	0.61
SDDp:SDDp	1.00	0.00	1.00	1.00
SDDp:SDDs	0.34	0.03	0.28	0.40
SDDp:SDD	0.48	0.03	0.42	0.53
SDDs:Cww	0.06	0.03	-0.00	0.12
SDDs:Fnua	-0.20	0.03	-0.27	-0.14
SDDs:Fr	-0.08	0.03	-0.14	-0.01
SDDs:Bctb	0.09	0.03	0.04	0.14
SDDs:NLB	0.07	0.03	0.00	0.13
SDDs:NLW	0.10	0.03	0.03	0.16
SDDs:Dp	0.40	0.03	0.34	0.46
SDDs:Ds	0.37	0.03	0.31	0.43
SDDs:Dps	0.39	0.03	0.33	0.45
SDDs:DpovDs	0.15	0.03	0.09	0.21
SDDs:SDDp	0.34	0.03	0.28	0.40
SDDs:SDDs	1.00	0.00	1.00	1.00
SDDs:SDD	0.99	0.00	0.98	0.99
SDD:Cww	0.06	0.03	-0.01	0.12
SDD:Fnua	-0.23	0.03	-0.29	-0.16
SDD:Fr	-0.11	0.03	-0.17	-0.04
SDD:Bctb	0.15	0.03	0.10	0.20
SDD:NLB	0.08	0.03	0.02	0.15
SDD:NLW	0.11	0.03	0.04	0.17
SDD:Dp	0.49	0.03	0.43	0.54

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Table 5 – *Continued from previous page*

Traits	Estimate	StdErr	CI95lo	CI95hi
SDD:Ds	0.37	0.03	0.31	0.43
SDD:Dps	0.40	0.03	0.34	0.46
SDD:DpovDs	0.24	0.03	0.17	0.30
SDD:SDDp	0.48	0.03	0.42	0.53
SDD:SDDs	0.99	0.00	0.98	0.99
SDD:SDD	1.00	0.00	1.00	1.00

The phenotypic correlations are mostly of the same sign as the genetic correlations, but of smaller magnitude. Cww is not correlated with SDDp, SDDs, SDD, and the correlation of Cww with Dp is now slightly positive. Dp and Ds have a phenotypic correlation, but no genetic correlation, so they must therefore have an environmental correlation. We shall see below.

3.5 Environmental correlations

The environmental correlations are correlation caused by any non-genetic factors which traits have in common. They are presented in Table 6

Table 6: Environmental correlation estimates with standard errors and 95 percent confidence limits for 13 skin and wool traits

Traitpair	Estimate	StdErr	CI95lo	CI95hi
Cww:Cww	1.00	0.00	1.00	1.00
Cww:Fnua	-0.05	0.03	-0.11	0.01
Cww:Fr	0.19	0.03	0.13	0.25
Cww:Bctb	0.28	0.05	0.18	0.38
Cww:NLB	-0.26	0.03	-0.31	-0.21
Cww:NLW	-0.22	0.03	-0.27	-0.16
Cww:Dp	0.18	0.08	0.03	0.34
Cww:Ds	-0.11	0.07	-0.25	0.04
Cww:Dps	-0.09	0.07	-0.23	0.05
Cww:DpovDs	0.40	0.13	0.14	0.66
Cww:SDDp	0.09	0.08	-0.06	0.24
Cww:SDDs	-0.12	0.07	-0.26	0.02
Cww:SDD	-0.11	0.07	-0.25	0.04
Fnua:Cww	-0.05	0.03	-0.11	0.01
Fnua:Fnua	1.00	0.00	1.00	1.00
Fnua:Fr	0.52	0.02	0.47	0.56
Fnua:Bctb	-0.14	0.05	-0.25	-0.04
Fnua:NLB	-0.16	0.03	-0.22	-0.11

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Table 6 – *Continued from previous page*

Traitpair	Estimate	StdErr	CI95lo	CI95hi
Fnua:NLW	-0.14	0.03	-0.20	-0.09
Fnua:Dp	-0.42	0.07	-0.56	-0.28
Fnua:Ds	-0.40	0.06	-0.51	-0.29
Fnua:Dps	-0.41	0.05	-0.52	-0.31
Fnua:DpovDs	-0.20	0.12	-0.45	0.04
Fnua:SDDp	-0.24	0.07	-0.37	-0.10
Fnua:SDDs	-0.11	0.06	-0.24	0.02
Fnua:SDD	-0.15	0.07	-0.28	-0.02
Fr:Cww	0.19	0.03	0.13	0.25
Fr:Fnua	0.52	0.02	0.47	0.56
Fr:Fr	1.00	0.00	1.00	1.00
Fr:Bctb	-0.08	0.05	-0.19	0.02
Fr:NLB	-0.17	0.03	-0.22	-0.11
Fr:NLW	-0.15	0.03	-0.21	-0.10
Fr:Dp	-0.11	0.07	-0.25	0.04
Fr:Ds	-0.23	0.06	-0.36	-0.11
Fr:Dps	-0.24	0.06	-0.36	-0.12
Fr:DpovDs	0.11	0.12	-0.12	0.34
Fr:SDDp	-0.05	0.07	-0.19	0.08
Fr:SDDs	0.02	0.07	-0.11	0.15
Fr:SDD	-0.01	0.06	-0.14	0.11
Bctb:Cww	0.28	0.05	0.18	0.38
Bctb:Fnua	-0.14	0.05	-0.25	-0.04
Bctb:Fr	-0.08	0.05	-0.19	0.02
Bctb:Bctb	1.00	0.00	1.00	1.00
Bctb:NLB	-0.14	0.05	-0.23	-0.04
Bctb:NLW	-0.27	0.05	-0.37	-0.17
Bctb:Dp	-0.18	0.15	-0.48	0.11
Bctb:Ds	0.12	0.12	-0.12	0.35
Bctb:Dps	0.09	0.12	-0.13	0.32
Bctb:DpovDs	-0.38	0.25	-0.86	0.11
Bctb:SDDp	-0.52	0.17	-0.85	-0.19
Bctb:SDDs	-0.32	0.13	-0.58	-0.06
Bctb:SDD	-0.39	0.14	-0.66	-0.11
NLB:Cww	-0.26	0.03	-0.31	-0.21
NLB:Fnua	-0.16	0.03	-0.22	-0.11
NLB:Fr	-0.17	0.03	-0.22	-0.11
NLB:Bctb	-0.14	0.05	-0.23	-0.04
NLB:NLB	1.00	0.00	1.00	1.00
NLB:NLW	0.74	0.01	0.72	0.77
NLB:Dp	0.04	0.07	-0.09	0.18
NLB:Ds	0.17	0.06	0.05	0.30
NLB:Dps	0.17	0.06	0.05	0.29

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Table 6 – *Continued from previous page*

Traitpair	Estimate	StdErr	CI95lo	CI95hi
NLB:DpovDs	-0.15	0.12	-0.37	0.08
NLB:SDDp	-0.09	0.07	-0.22	0.04
NLB:SDDs	0.07	0.06	-0.05	0.19
NLB:SDD	0.06	0.06	-0.07	0.18
NLW:Cww	-0.22	0.03	-0.27	-0.16
NLW:Fnua	-0.14	0.03	-0.20	-0.09
NLW:Fr	-0.15	0.03	-0.21	-0.10
NLW:Bctb	-0.27	0.05	-0.37	-0.17
NLW:NLB	0.74	0.01	0.72	0.77
NLW:NLW	1.00	0.00	1.00	1.00
NLW:Dp	0.02	0.07	-0.11	0.16
NLW:Ds	0.18	0.06	0.06	0.31
NLW:Dps	0.18	0.06	0.05	0.30
NLW:DpovDs	-0.20	0.12	-0.43	0.04
NLW:SDDp	-0.14	0.07	-0.27	-0.00
NLW:SDDs	0.04	0.06	-0.08	0.16
NLW:SDD	0.02	0.06	-0.10	0.14
Dp:Cww	0.18	0.08	0.03	0.34
Dp:Fnua	-0.42	0.07	-0.56	-0.28
Dp:Fr	-0.11	0.07	-0.25	0.04
Dp:Bctb	-0.18	0.15	-0.48	0.11
Dp:NLB	0.04	0.07	-0.09	0.18
Dp:NLW	0.02	0.07	-0.11	0.16
Dp:Dp	1.00	0.00	1.00	1.00
Dp:Ds	0.78	0.07	0.65	0.91
Dp:Dps	0.81	0.06	0.69	0.93
Dp:DpovDs	0.65	0.08	0.49	0.80
Dp:SDDp	0.46	0.06	0.34	0.58
Dp:SDDs	0.45	0.07	0.32	0.59
Dp:SDD	0.50	0.06	0.38	0.63
Ds:Cww	-0.11	0.07	-0.25	0.04
Ds:Fnua	-0.40	0.06	-0.51	-0.29
Ds:Fr	-0.23	0.06	-0.36	-0.11
Ds:Bctb	0.12	0.12	-0.12	0.35
Ds:NLB	0.17	0.06	0.05	0.30
Ds:NLW	0.18	0.06	0.06	0.31
Ds:Dp	0.78	0.07	0.65	0.91
Ds:Ds	1.00	0.00	1.00	1.00
Ds:Dps	1.00	0.00	0.99	1.01
Ds:DpovDs	0.06	0.14	-0.21	0.33
Ds:SDDp	0.33	0.07	0.18	0.47
Ds:SDDs	0.22	0.07	0.09	0.34
Ds:SDD	0.25	0.07	0.12	0.38

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Table 6 – *Continued from previous page*

Traitpair	Estimate	StdErr	CI95lo	CI95hi
Dps:Cww	-0.09	0.07	-0.23	0.05
Dps:Fnua	-0.41	0.05	-0.52	-0.31
Dps:Fr	-0.24	0.06	-0.36	-0.12
Dps:Bctb	0.09	0.12	-0.13	0.32
Dps:NLB	0.17	0.06	0.05	0.29
Dps:NLW	0.18	0.06	0.05	0.30
Dps:Dp	0.81	0.06	0.69	0.93
Dps:Ds	1.00	0.00	0.99	1.01
Dps:Dps	1.00	0.00	1.00	1.00
Dps:DpovDs	0.11	0.13	-0.15	0.36
Dps:SDDp	0.34	0.07	0.20	0.48
Dps:SDDs	0.23	0.06	0.11	0.36
Dps:SDD	0.27	0.06	0.15	0.40
DpovDs:Cww	0.40	0.13	0.14	0.66
DpovDs:Fnua	-0.20	0.12	-0.45	0.04
DpovDs:Fr	0.11	0.12	-0.12	0.34
DpovDs:Bctb	-0.38	0.25	-0.86	0.11
DpovDs:NLB	-0.15	0.12	-0.37	0.08
DpovDs:NLW	-0.20	0.12	-0.43	0.04
DpovDs:Dp	0.65	0.08	0.49	0.80
DpovDs:Ds	0.06	0.14	-0.21	0.33
DpovDs:Dps	0.11	0.13	-0.15	0.36
DpovDs:DpovDs	1.00	0.00	1.00	1.00
DpovDs:SDDp	0.31	0.11	0.10	0.52
DpovDs:SDDs	0.51	0.13	0.27	0.76
DpovDs:SDD	0.54	0.12	0.30	0.78
SDDp:Cww	0.09	0.08	-0.06	0.24
SDDp:Fnua	-0.24	0.07	-0.37	-0.10
SDDp:Fr	-0.05	0.07	-0.19	0.08
SDDp:Bctb	-0.52	0.17	-0.85	-0.19
SDDp:NLB	-0.09	0.07	-0.22	0.04
SDDp:NLW	-0.14	0.07	-0.27	-0.00
SDDp:Dp	0.46	0.06	0.34	0.58
SDDp:Ds	0.33	0.07	0.18	0.47
SDDp:Dps	0.34	0.07	0.20	0.48
SDDp:DpovDs	0.31	0.11	0.10	0.52
SDDp:SDDp	1.00	0.00	1.00	1.00
SDDp:SDDs	0.32	0.07	0.18	0.45
SDDp:SDD	0.45	0.06	0.32	0.57
SDDs:Cww	-0.12	0.07	-0.26	0.02
SDDs:Fnua	-0.11	0.06	-0.24	0.02
SDDs:Fr	0.02	0.07	-0.11	0.15
SDDs:Bctb	-0.32	0.13	-0.58	-0.06

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Table 6 – *Continued from previous page*

Traitpair	Estimate	StdErr	CI95lo	CI95hi
SDDs:NLB	0.07	0.06	-0.05	0.19
SDDs:NLW	0.04	0.06	-0.08	0.16
SDDs:Dp	0.45	0.07	0.32	0.59
SDDs:Ds	0.22	0.07	0.09	0.34
SDDs:Dps	0.23	0.06	0.11	0.36
SDDs:DpovDs	0.51	0.13	0.27	0.76
SDDs:SDDp	0.32	0.07	0.18	0.45
SDDs:SDDs	1.00	0.00	1.00	1.00
SDDs:SDD	0.99	0.01	0.97	1.00
SDD:Cww	-0.11	0.07	-0.25	0.04
SDD:Fnua	-0.15	0.07	-0.28	-0.02
SDD:Fr	-0.01	0.06	-0.14	0.11
SDD:Bctb	-0.39	0.14	-0.66	-0.11
SDD:NLB	0.06	0.06	-0.07	0.18
SDD:NLW	0.02	0.06	-0.10	0.14
SDD:Dp	0.50	0.06	0.38	0.63
SDD:Ds	0.25	0.07	0.12	0.38
SDD:Dps	0.27	0.06	0.15	0.40
SDD:DpovDs	0.54	0.12	0.30	0.78
SDD:SDDp	0.45	0.06	0.32	0.57
SDD:SDDs	0.99	0.01	0.97	1.00
SDD:SDD	1.00	0.00	1.00	1.00

We see that Cww has a small positive environmental correlation with Dp, and a small negative environmental correlation with Ds. We also see that Dp and Ds have a strong positive environmental correlation, as predicted above from noting a phenotypic correlation but no genetic correlation. One would expect something like good nutrition to affect all follicles positively.

The other relationship that shows an inversion of sign is Cww with fertility (NLB and NLW) and birthcoat. There is a positive genetic correlation and a negative environmental correlation with fertility, and the other way around with birthcoat. It would seem that there are fitness issues with Cww, but they are complicated and the net effect may be a balance of competing forces.

4 Discussion

The one thing that genetic parameters establish clearly is that D_p and D_s are under independent genetic control. It is possible to change one without the other. That is of course what has happened during evolution of the Merino - D_p has changed substantially while D_s initially increased a small amount, then decreased again. It also means that is is possible to reverse the evolutionary trend and have atavistic individuals occuring.

Genetic parameters are not the final word on what happens in selected flocks. One can use parameters to predict genetic change under selection. For single trait selection and predicting response in the trait selected, they work quite well. You only need a heritability and a phenotypic variance for that. However for multi-trait selection and for responses in traits other than those selected on, the reliability of predictions is less than one would wish. Using genetic parameters to predict long term trends is a bit like using daily fluctuations in the stockmarket to predict longer term time trends. It simply does not work because the factors involved in longterm change are different.

When it comes to the occurrence of rare individuals showing characteristics resembling primitive or ancestral breeds of sheep, genetic parameters tell us nothing useful. Atavism is about what happens when normal quantitative genetics breaks down . Unusual individuals are just that - outside of the normal distribution for one or more traits. The interesting thing is that they always seem to be on the ancestral side of the distribution. Distributions always skew towards the wild type. There is nothing in quantitative genetics about that.

Atavisms will show up most in those traits which have changed most from ancestors to now. This should be obvious. If there is no change in a trait from ancestors to now, it cant show any atavism as there is nothing to revert back to. This is why it was important in Jackson (2017) [10] to determine which fleece traits had changed most during evolution.

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