What is known about the genetics of wrinkle score in Merino sheep?

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1 Introduction

There has been a long and often heated debate in the Merino sheep breeding community about the merits of wrinkles or folds in the skin. Starting with Belschner(1937) [1] reviewing the negative impact of wrinkle on fleece rot and body strike, the debate was taken up by geneticists who set about declaring that wrinkle was a component of clean wool weight and establishing a scoring method with photographic standards (Carter(1943) [3] , Turner, et al (1953) [16], Turner(1956) [17], Turner(1958) [18]). Two selection experiments, for and against wrinkle, were started, one by the NSW Department of Agriculture, called Folds Plus and Folds Minus lines (Dun(1964) [4]), and one by CSIRO, called the Wrinkle Plus, and Wrinkle Minus lines (Turner, Brooker, and Dolling(1970) [19]). The geneticists concluded that there was a possibility that selection for fleece weight would increase wrinkle, and recommended that some culling against wrinkle be conducted in association with selection for fleece weight. There were also negative impilications of folds for fertility (Drinan and Dun (1965) [5]).

The above paragraph is all about keeping wrinkle at a reasonable level, and controlling its worst side effects with mulesing and chemicals. When the Mules operation and insecticides became politically incorrect in the late 1990's, a new paradigm suddenly arose. A number of attempts were made to breed Merino sheep that were completely wrinkle-free, like to original Merinos that came to Australia from England and Spain, before introduction of the Vermont Merino. One of these attempts is the SRS group of breeders, who assert that it is not just possible, but essential, that all wrinkle be genetically removed from sheep, befor thay can be successfully selected for the SRS criteria which lead to a different skin type with fine primary fibres, a high S/P ratio due to compound follicles having more branches, fine and long secondary fibres which are more soft or pliable than normal wool. The question arises as to why it is necessary to be wrinkle-free, before breeding towards the SRS type of sheep.

To answer this question, we have to work out how wrinkle development impacts on the type of follicle development process which leads to SRS sheep. We know something about the SRS development process. The pre-papilla cell model of Moore etal(1989) [10] and Moore etal(1998) [11] explains why suppression of the size of primary follicles (and therefore suppression of the primary fibre diameter), leads to vastly greater numbers of secondary derived follicles formed as branches to P and So follicles, leading to compound follicles. What we understand far less, is why or these larger compound follicles grow such a different fibre that is fine, long, low crimped, soft, and lustrous. We also know something about why these fibres form smaller staples with a different type of staple crimp (Jackson and Watts(2016) [9].

We know next to nothing about the prenatal development of wrinkle. There is one obscure reference in Fraser and Short(1960) [6]. On page 50, in the section on skin folds it says that body wrinkles appear at around 100 days, first on the dorsal surface and then extending down the sides to the belly. They give an obscure Russian reference (Bogolyubsky(1940)). We should note that 100 days coincides with the period of secondary follicle initiation.

2 Genetic parameters of wrinkle score

2.1 Morley

Morley(1955) analysed folds scores done at weaning from NSW Department of Agriculture Trangie flocks. The correlations of wrinkle scores with other characters are given in Table 1

Table 1: Phenotypic and genetic correlations of wrinkle score with other wool traits from Morley(1955) [12]

Traits	Phenotypic correlation	Genetic correlation
Wr x GFW	0.31	0.42
Wr x Yield	-0.11	0.32
Wr x CWW	0.33	0.12
Wr x Bodywt	-0.07	-0.34
Wr x StapLen	-0.18	-0.47
Wr x Crimp	0.04	0.21

2.2 Brown and Turner

Brown and Turner(1968) [2] analysed wrinkle scores from the CSIRO AB1 experiment. The score analysed was a combination of scores for neck and body wrinkle, done after hogget shearing. Breech wrinkle was not scored as the sheep were mulesed before the scoring took place. The scores were the photographic standards of Turner etal(1953) [16].

Wrinkle had a heritability of 0.38 ± 0.04 . The correlations of wrinkle score with all other wool characteristics are givenin Table 2

2.3 Jackson, Nay, and Turner

Jackson, Nay and Turner (1975) [7] analysed wrinkle scores from the CSIRO AB1 experiment in combination with a number of skin and follicle characteristics. The wrinkle scores were as for Brown and Turner(1968) [2]. The correlations of wrinkle with skin and follicle characteristics are given in Table 3.

These estimates include an enviromental correlation as well as phenotypic and genetic. Environmental correlations should be interpreted as correlations due to all non-genetic effects operating on the two traits.

Note that FibreDensity is a count of fibres per unit area of skin, done on the sheep, not on skin sections.

Table 2: Phenotypic and genetic correlations of wrinkle score with other wool traits from Brown and Turner(1968) [2]

Traits	Phenotypic correlation	Genetic correlation
Wr x GFW	0.27	0.18
Wr x Yield	-0.21	-0.34
Wr x CWW	0.12	-0.06
Wr x Bodywt	-0.09	-0.17
Wr x Facecovcer	0.08	0.14
Wr x FibreDensity	0.04	0.07
Wr x FibreDiam	0.14	0.19
Wr x StapLen	-0.23	-0.52
Wr x Crimp	0.17	0.28

Table 3: Phenotypic and genetic correlations of wrinkle score with other wool traits from Jackson, Nay and Turner(1975) [7]

Traits	Phenotypic correlation	Genetic corelation	Environmental correlation
Wr x Follicle depth	0.06	0.04	0.07
Wr x Follicle curvature	0.36	0.68	0.16
Wr x Follicle density	-0.02	-0.06	0.00
Wr x S/P ratio	0.22	0.29	0.18

2.4 AB32 Jackson unpublished

There is a comprehensive genetic analysis of skin characteristics from the CSIRO AB32 follicle selection experiment. These are a different strain of Merino from the AB1 sheep analysed above. It includes wrinkle scores as for Brown and Turner(1968) [2], and a wide range of skin and wool characteristice, including diameters of primary and secondary fibres. There were some prelimary estimates in Table 8 of Jackson etal(1990); these should be disregarded as they do not include all the data and were made using outdated estimation procedures. The full analysis of these data, using modern maximum likelihood estimation procedures and a full relationship matrix, is in an incomplete manuscript (Jackson(2015)) [8]. What we shall do here is extract just those correlations involving wrinkle score. These are given in Table 4

The trait symbols in Table 4 are somewhat abbreviated. In Table 5 and Table 6 these are explained in full.

Table 4: Phenotypic , genetic and environmental correlations of wrinkle score with other wool and skin traits from Jackson(2015) [8]

Traits	Phenotypic correlation	Genetic correlation	Environmental correlation
WrT x Stal	-0.16	-0.22	-0.11
WrT x Diam	0.20	0.19	0.21
WrT x Bwt	0.03	-0.34	0.28
WrT x WrN	0.91	0.99	0.85
WrT x WrB	0.91	0.99	0.85
WrT x Face	0.07	0.25	-0.18
WrT x Gfw	0.35	0.33	0.37
WrT x Yld	-0.27	-0.36	-0.20
WrT x Cww	0.23	0.15	0.27
WrT x Staladj	-0.16	-0.19	-0.14
WrT x Gfwadj	0.35	0.36	0.34
WrT x Cwwadj	0.22	0.18	0.25
WrT x Crimp	0.20	0.46	-0.23
WrT x Crwvl	-0.16	-0.49	0.13
WrT x Crst	0.08	0.44	-0.27
WrT x Crstadj	0.08	0.42	-0.24
WrT x Crwvt	-0.07	-0.45	0.20
WrT x Dp	0.11	-0.14	0.37
WrT x Ds	0.21	0.47	-0.00
WrT x Dps	0.21	0.46	0.03
WrT x DpovDs	-0.03	-0.32	0.53
WrT x CVDp	0.14	-0.04	0.27
WrT x CVDs	0.04	-0.32	0.26
WrT x MaxDp	0.14	-0.11	0.39
WrT x MinDp	0.11	0.50	0.02
WrT x MaxDs	0.20	0.27	0.18
WrT x MinDs	0.07	0.45	-0.01
WrT x SDDp	0.16	-0.12	0.43
WrT x SDDs	0.16	0.01	0.28
WrT x SDD	0.17	-0.02	0.33
WrT x CVD	0.05	-0.33	0.30
WrT x Gt30Dp	0.09	-0.10	0.28
WrT x Gt30Ds	0.17	0.19	0.16
WrT x Gt30D	0.17	0.12	0.20
WrT x Fnua	-0.01	-0.13	0.06
WrT x Fr	0.16	0.27	0.10
WrT x Fnt	-0.00	-0.33	0.19
WrT x Sarea	0.03	-0.39	0.30
WrT x Fd	0.20	0.16	0.22
WrT x Fc	0.42	0.69	0.13
WrT x Fu	0.40	0.68	0.21
WrT x Colour	0.03	-0.09	0.08
WrT x Fly	0.03	0.04	0.03
WrT x Flcrot	-0.01	-0.28	0.04
WrT x Bactst	-0.03	-0.16	-0.02
WrT x MycD	-0.01	0.37	-0.10
WrT x Bcts	0.05	-0.20	0.51
WrT x Bctb	0.06	-0.20	0.50
WrT x Weanwt	0.03	-0.15	0.12
WrT x NLB	-0.12	0.14	-0.24
WrT x NLW	-0.12	0.02	-0.19
WrT x Fnpua	-0.14	-0.37	-0.04
WrT x Fnsua	0.00	-0.12	0.07
WrT x Fnpt	-0.13	-0.54	0.07
WrT x Fnst	0.01	-0.32	0.19

Table 5: 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 5 – *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 5 – *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 5 – *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

I have deliberately chosen not to present standard errors. These were between 0.03 and 0.06 for genetic and environmental correlations, and between 0.01 and 0.03 for pphenotypic correlations. In other words any correlation bigger than about 0.10 (or less than -0.10) would be significantly different from zero. The heritability of wrinkle score in these analyses was 0.45 ± 0.01, so there is plenty of genetic variation behind these correlations.

There is a general agreement of these correlations with previous estimates. Theere is no reason not to take these as the best available estimates.

2.5 Summary of correlations

There seem to be a number of groups of relationships

- wrinkle is not strongly genetically correlated with Dp or birthcoat, but there is a positive environmental correlation. This suggests wrinkle may not interfere with primary follicle initiation
- wrinkle is positively genetically correlated with Ds and S/P ratio. This is the relation which suggesta wrinkle may affect prepilla cell dynamics. The correlation with overall diameter was large and positive for diameter measured on skin sections, but small and positive for diameter measured on wool.
- wrinkle is very strongly correlated with follicle curvature, follicle unevenness, crimp frequency , and staple length. This groups of relations suggests wrinkle affects bulb cell development into the cortex strructure
- wrinkle is genetically correlated with GFW and Yield, but not strongly with CWW. It would seem that wrinkled sheep produce more wax, but not a lot more wool, if any.
- wrinkle is negatively associated with bodyweight and surface area. The surface area calculated in these data accounts for body size but not wrinkle. It is therefore suspect, and so are the total follicle counts (Fnt, Fnpt, Fnst)

3 Responses to selection for and against wrinkle

We can check on genetic correlations by seeing what happens to other traits if we select for or against wrinkle.

3.1 CSIRO wrinkle plus and minus groups

These lines are reported in Turner, Brooker, and Dolling(1970) [19]. The selectioe led to a difference in GFW, Yield, Bodyweight, Face score, Staple Length and Crimp Frequency. There was little or no difference in CWW, Fibre Number, or Fibre diameter. There was of course a difference in wrinkle.

Table 6: 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	$Crwvt = \frac{365}{Crstadj}$

3.2 NSWDA folds plus and folds minus groups

These groups were selected for and against wrinkle scored at weaning. There are reported correlated responses in reproduction, but I can find nothing on wool or skin characteristics.

4 Search for nonadditive genetic variance

The CSIRO AB1 dataset was used to examine whether for wrinkle score there was evidence of any genetic variance other than individual additive genetic. There was a suggestion of some maternal additive genetic variance (about 10 percent) and also some individual sexlinked additive genetic variance (again about 10 percent). So most of the variation in wrinkle was environmental or individual additive genetic.

What this means is that the genetic correlations reported above, which are all for individual additive genetic (co)variances, are likely to cover all the important large genetic relationships.

5 How might wrinkle development affect the dynamics of pre-papilla cell growth?

Given that the effect of wrinkle on follicle development seems to be at the secondary follicle initiation stage, the following mechanisms are possible

- wrinkles make space for more So sites to form - this contradicts what Philip Moore has demonstrated - that sites for P and So follicles are definite positions, not just empty space.
- wrinkles lead to more pre-papilla cells being used at each So site, leading to larger So follicles and fibres and fewer leftover cells.
- wrinkles lead to earlier So initiation so the pre-papilla cell bank is raided earlier leaving fewer cells left to form Sd follicles.
- wrinkles lead to reduced or early terminated pre-papilla cell division
- wrinkles and sites are genetically correlated

We really have no idea whether any of the above mechanisms operate

6 Discussion

As summarized above there would seem to be several groups of relationships involving wrinkle. Only the correlations with Ds and S/P suggest involvement of wrinkle in the pre-papilla cell dynamics.

The correlation with follicle curvature and crimp suggest something else. Follicle curvture is the same thing as intrinsic fibre curvature, which in turn depends on the structure of the fibre cortex. Cortex structure is determined by what happens to bulb cells as they differentiate and form the fibre. If the fibres are more curved, staple length is shorter, but fibre length is not necessarily less. So this group of correlations probably has nothing to do with pre-papilla cell dynamics, unles, of cource, the cells in the papilla somehow direct how bulb cells differentiate.

Wrinkled sheep make more wax in the fleece. So they have more sebacious glands. That relatesd to higher S/P ratio, and probably to larger compound follicles. Because compound follicles are the endpoint of pre-papilla-cell dynamics, the lower Yield of wrinkled sheep may also indicate that wrinkle interferes with pre-papilla cell development.

References

[1] Belschner H.G. (1937) "A review of the sheep blowfly problem in New South Wales and observations on fleece rot and body strike in sheep, particularly in regards to their incidence, type of sheep susceptible, and economic importance". NSW Department of Agriculture, Science Bulletin No 54, 1937, pp 1-95

[2] Brown, G.H., and Turner, Helen Newton. (1968) Response to selection in Australian Merino sheep. II. Estimates of phenotypic and genetic parameters for some production traits in Merino ewes and an analysis of the possible effects of selection on them. Aust. J. Agric. Res. 19:303-22

[3] Carter, H.B. (1943) Studies in the biology of the skin and fleece of sheep. CSIRO (Aust) Bull. No. 164

[4] Dun, R.B. (1964) Skin folds and Merino breeding. 1. The net reproductive rates of flocks se;lected for and against skin fold. Aust J. Exp. Agric. Anim. Husb. 4:376-385

[5] Drinan, J.P. and Dun, R.B. (1965) Skins folds and Merino breeding. 3. The association between skin fold and productivity of Merino ewes in fourteen NSW flocks. Aust.J.Exp.Agric.Anim.Husb. 5(19): 345-352

[6] Fraser A.S and Short B.F. (1960) The Biology of the Fleece. Animal Research Laboratories Technical Paper No 3. CSIRO Melbourne 1960.

[7] Jackson, N., Nay, T, and Turner, Helen Newton (1975) Response to selection in Australian Merino sheep. VII Phenotypic and genetic parameters for some wool follicle characteristics and their correlation with wool and body traits. Aust. J. Agric. Res. 26:937-57

[8] Jackson, N. (2015) Genetic relationship betweeen skin and wool traits in Merino sheep. Incomplete manuscript.

[9] Jackson, N. and Watts, J.E. (2016) Staple crimp formation in the fleece of Merino sheep. Unpublished manuscript, 18 May 2016.

[10] Moore G.P.M., Jackson, N., and Lax, J. (1989) Evidence of a unique developmental mechanism specifying bot wool follicle density and fibre size in sheep selected for single skin and fleece characters. Genet. Res. Camb. 53:57-62

[11] Moore, G.P.M., Jackson, N., Isaacs, K., and Brown, G (1998) J. Theoretical Biology 191:87-94

[12] Morley F.H.W (1955) Selection for economic characters in Merino sheep. V. Further estimates of phenotypic and genetic parameters. Aust. J. Agric. Res. 6:77-90

[13] Nay, T. and Jackson, N. (1973) Effect of changes in nutritional level on the depth and curvature of wool follicles in Australian Merino sheep. Aust. J. Agric. Res. 24:439-447

[14] Onions, W.J. (1962) Wool: an introduction to its properties, varieties, uses and production. Ernest Benn limited, London, 1962

[15] R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

[16] Turner, Helen Newton, Hayman, R.H., Riches, J.H., Roberts, N.F., and Wilson, L.T. (1953) Physical definition of sheep and their fleece for breeding and husbandry studies: with particular reference to Merino sheep. CSIRO Div. Anim. Hlth. Prod. Div. Rept. No. 4 (Ser SW-2 mimeo)

[17] Turner, Helen Newton (1956) Anim Breed Abstr. 24:87-118

[18] Turner, Helen Newton (1958) Aust J. Agric. Res. 9:521-552

[19] Turner, Helen Newton, Brooker M.G. and Dolling, C.H.S (1970) Response to selection in Australian Merino sheep. III Single character selection for high and low values of wool weight and its components. Aust.J.Agric.Res. 21:955-84