

Can we convert between observed or *checked*
diameter and potential or *base* diameter?

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1 Introduction

Given that the number of cells in each follicle papilla cell aggregate determines the *base* or potential diameter of each fibre, and given that we have an empirical equation relating dermal papilla cell number to *checked* fibre diameter, we need to see whether we can modify that equation to estimate base or potential fibre diameter.

We need a definition of terms

fibre cross section area A is calculated from measured fibre diameter as $\frac{\pi}{4}D^2$ where D is measured fibre diameter

follicle density is the count of primary and secondary follicles per unit area of skin as measured on skin biopsies

base diameter is the maximum or potential diameter that a fibre can grow to given unlimited nutrients and no sharing with surrounding follicles. It is determined by the number of dermal papilla cells in the follicle bulb. It is actually cross sectional area that is determined, not diameter. The nearest thing to base diameter or cross sectional area which could be observed would be the diameter of fibres in the sickle tips of primary central follicles as seen in the hairy tips of the birthcoat. These sickle tips are grown *in utero* with presumably unrestricted nutrition and are grown from Pc follicles before any other follicles develop around them.

checked diameter is the observed diameter of a fibre under normal conditions of limited nutrients and a certain density of surrounding follicles.

If we call the observed diameter at time i D_i and the base diameter for the same follicle D_B , then the amount of *check* at time i is $\frac{D_B - D_i}{D_B}$. We really should define this in terms of A rather than D , so $\frac{A_B - A_i}{A_B}$ is preferable. So check is the fractional reduction in A_i below A_B

What we are setting out to do is, given A_i can we devise a way of estimating A_B . Clearly some other information such as nutritional level and follicle densities will be needed.

2 Materials and Methods

We utilize data from Carter(1968) [6] specifically breed means for follicle density and fibre cross sectional area estimated as $A = \frac{\pi}{4}Dps^2$. Each mean represents around 20 animals sampled and Dr Carter has stated that all sheep sampled were in good nutritional condition, and the samplings were mostly at around 2 years of age, ie adult sheep. A critical aspect is that the diameters and follicle densities were at the same time, ie at the time the skin biopsies were taken.

We also examine various nutrition experiment data sets, some unpublished, in which we have either

- Sheep subjected to a series of nutritional treatments over time. These types of study are paired comparisons - the same sheep being observed under more than one nutritional regime. They are subject to correlated errors issues because the results for each sheep are a time series. That is unlikely to concern us here.
- Random samples of sheep are subjected to different nutritional regimes. These studies are randomized block experiments. They depend on having sufficient sheep for random samples to be equivalent in mean.

Again the critical requirement was fibre diameter and follicle density measurements at the same time.

We also utilize data from Jackson and Downes(1979) [14] on staple diameter profiles. In these data we only have a follicle density measurement for adult sheep, not at all 10 diameter positions along the staple.

We also utilize data from CSIRO flocks for genetic analysis of fibre diameter and follicle density. Again these had to be either skin section data, or 'cast' technique data, to ensure diameters and follicle densities were concurrent.

3 Results

Our fibre diameters calculated from papilla cell counts (Swan, Jackson and Moore(2021) [30]), and also all observed fibre diameter data, are a *checked* fibre diameter. That is, we have been simulating diameters at the average level of *check* obtaining in the dataset used to estimate the diameter on papilla cell count regression equation. We do not know quantitatively how much this *check* is, but it is substantial - something like 50 percent of the *base* or potential diameter.

3.1 What causes check?

We need to develop some concept of what causes *checks* in fibre diameter. We are trying to model a situation where there is a nominal amount of *skin nutrients* to be shared between a number of follicles. We are not sure whether the sharing depends on follicle density (ie follicles per unit skin area), or whether the sharing is within trio groups and depends on intra-group follicle density or on follicles per group or on group area. We will start with the simple assumption of density dependence regardless of trio groups. For this we can write

$$A = k/N$$

where

A is fibre cross sectional area

N is follicle density

k is a constant of proportion, somehow related to the amount of skin nutrients

We should note that this proposes an hyperbolic relationship between *A* and *N*, ie $AN = k$ is the equation of an hyperbola with asymptotes at the axes.

That is indeed what is observed. We can revisit the Carter(1968) [6] data to verify it. These data are particularly valuable because the diameters (on which cross sectional area is based) and densities were both measured on skin sections and are therefore at the same point in time. Figure 1 shows follicle density plotted against cross sectional area. The data are breed means from around 20 animals per breed sampled.

There is also the study of Scobie *et al*(20..) which demonstrates that the relationship between diameter and density is curvilinear, but does not propose that it is hyperbolic.

The hyperbolic nature of the relationship is apparent. This can be conclusively demonstrated by showing that the data can be linearized with a simple reciprocal transformation of the follicle densities. Figure 2 shows the reciprocal of follicle density plotted against fibre cross sectional area for the same breed means as in Figure 1

There is some spread of points but no evidence of curvature. The linear regression without an intercept was $A = 12689(1/N)$ and had a multiple correlation of 0.87. The linear regression with an intercept was $A = 163 + 10700(1/N)$

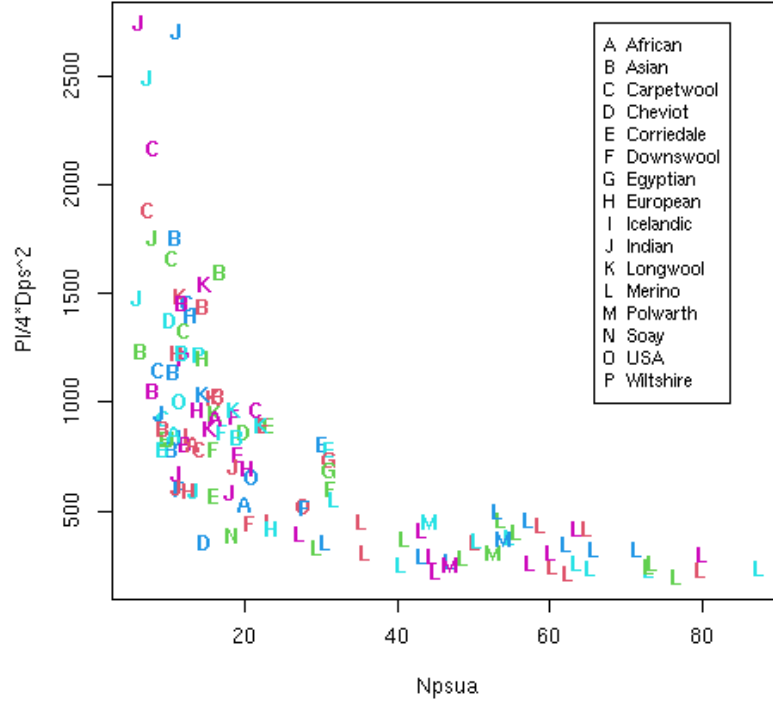


Figure 1: Plot of breed means for follicle density and fibre cross sectional area from Carter(1968) [6]

and had a multiple correlation of 0.61. If there is a nonzero intercept it simply means the hyperbola is asymptotic to $A = 163$ instead of to $A = 0$. There seems to be little case for a non zero asymptote.

However the data in Figure 2 do seem to split into two groups. There may be a case for two regression lines, ie two values of the k constant. This is explored in Figure 3

So these data exhibit a range of values for k from around 8000 to around 15000 with a mean of 12689. There are two possible reasons that k would vary

dermal papilla cell number may vary between breeds. So the maximum potential cross sectional area of fibres may vary. On second thought, this should not affect k . Changes in papilla cell number should simply move the data points along the regression line without changing its slope k .

nutrition of the skin at time of sampling may vary between breeds. So the degree of nutritional check may vary. This is what we are hoping k will

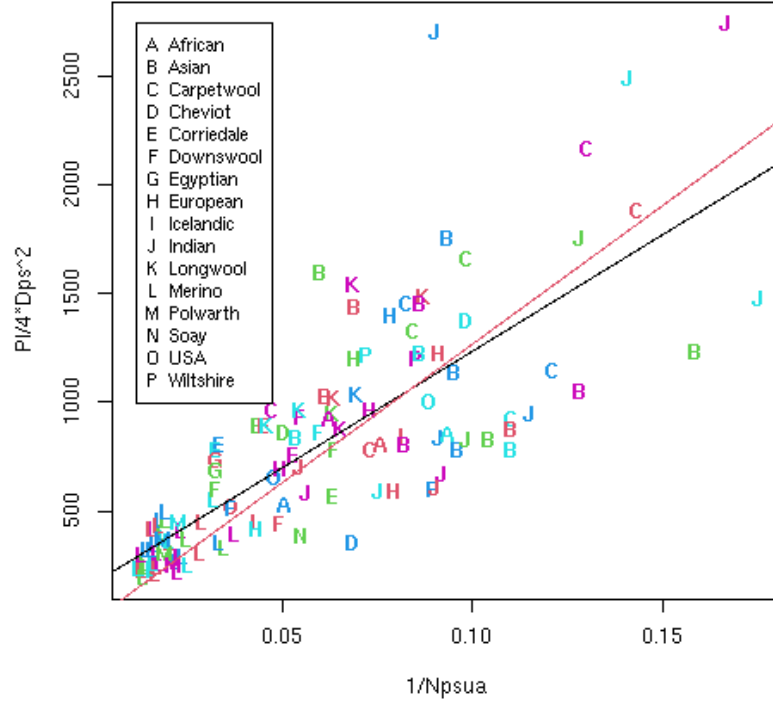


Figure 2: Plot of breed means for reciprocal of follicle density and fibre cross sectional area from Carter(1968) [6]. The black line is a linear regression fitted with an intercept. The red line is a linear regression fitted without an intercept.

be a measure of.

We can even compute an estimate of the value of k for each breed as $k = AN$. This has a physical interpretation - it is the sum of the cross sectional areas of all fibres in a square millimeter. But it is not the physical interpretation that we are interested in. We see k as an index of nutritional status, provided we can find a way to remove the influences of papilla cell number and density from it.

3.2 Identifying the causes of *check*

With the data from Carter(1968) [6] in the previous section we have been able to demonstrate the reciprocal density component of check in terms of its effect on fibre cross sectional area, but we were left with a value k which could be either a skin nutritional component or could reflect some other unidentified factor.

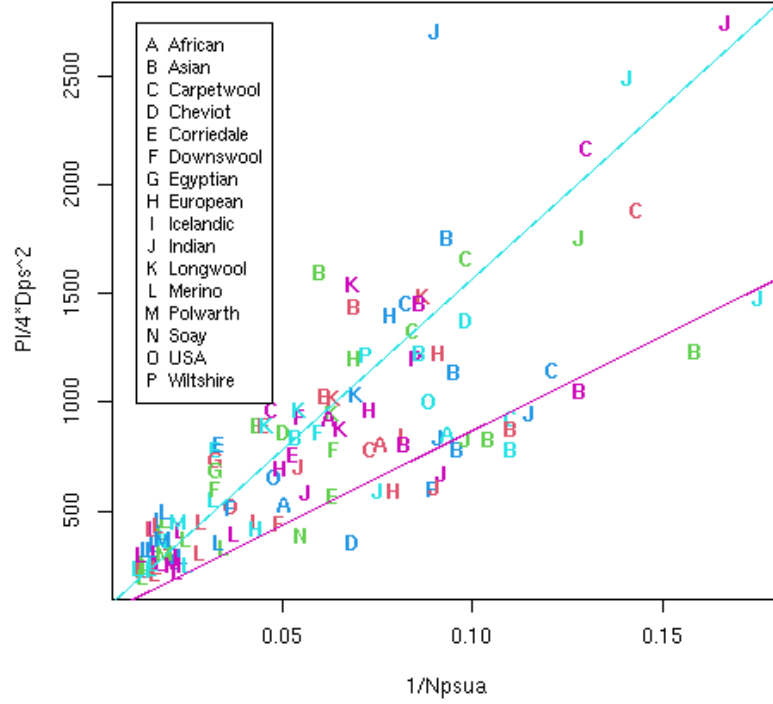


Figure 3: Plot of breed means for reciprocal of follicle density and fibre cross sectional area from Carter(1968) [6]. The blue line is a linear regression fitted with a slope of 15689 and no intercept. The red line is a linear regression fitted with a slope of 8689 and no intercept.

To try and identify these we need data with a controlled systematic nutritional effect, as in an experiment with various levels of nutrition.

3.2.1 Daly and Carter experiments

Daly and Carter(1955) [8] and (1956) [9] conducted a series of 3 experiments with Lincoln, Corriedale, Polwarth and Fine Merino ewes. Experiments 1 and 2 were with hand feeding starting with *ad lib* for a period of 50 weeks in experiment 1, and moving stepwise down to 20percent of *ad lib* over a period of 30 weeks in experiment 2. Experiment 3 was the same breeds at pasture over a period of 40 weeks during which there was a steady gain in liveweight. The raw data are available in the above publications as Breed means at the starting and ending periods of each experiment, representing good nutrition in experiment 1, good

changing to poor nutrition in experiment 2, and the reverse in experiment 3.

The relationship of fibre cross sectional area to the reciprocal of density is shown for experiment 1 in Figure 4

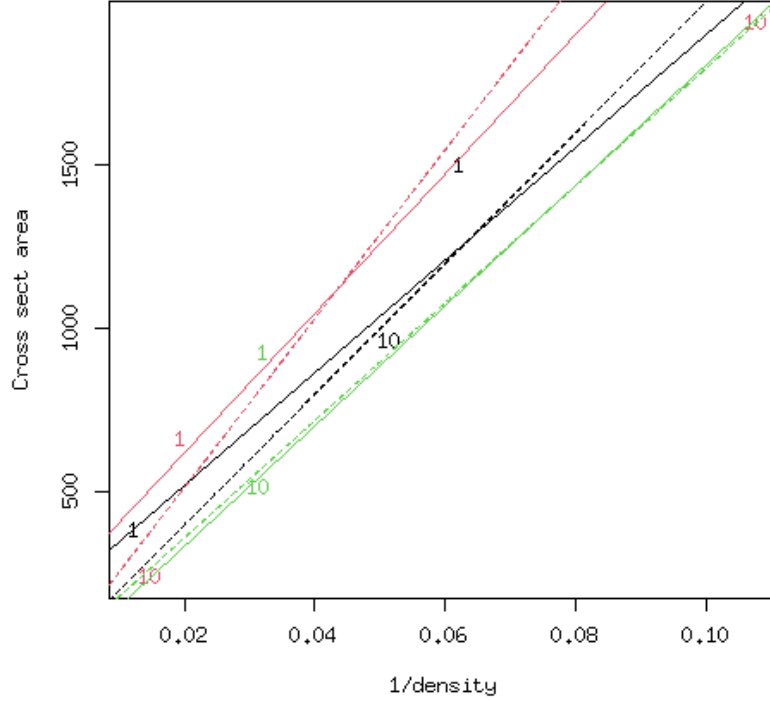


Figure 4: Plot of breed means for reciprocal of follicle density and fibre cross sectional area from Daly and Carter(1955) [8] experiment 1. The black lines are linear regressions fitted to all data, full line with an intercept, dashed line without an intercept. The red lines are linear regressions fitted to breed means for period 1 . The green lines are linear regressions fitted to breed means for period 10 .

There is no case for including an intercept. Analyses of variance show that only the regression slopes are significant. We will only discuss results for regressions thru zero. The estimated slope for Period 1 data was 25837 (units are microns squared x no of follicles per mm squared). The estimate of slope for Period 10 data was 17941. The standard errors for these slopes were 1773 and 302 respectively. The difference is significant. These slopes are our estimates of k for for growing animals on *ad lib* . So k is larger for younger smaller animals .

The relationship of fibre cross sectional area to the reciprocal of density is

shown for experiment 2 in Figure 5

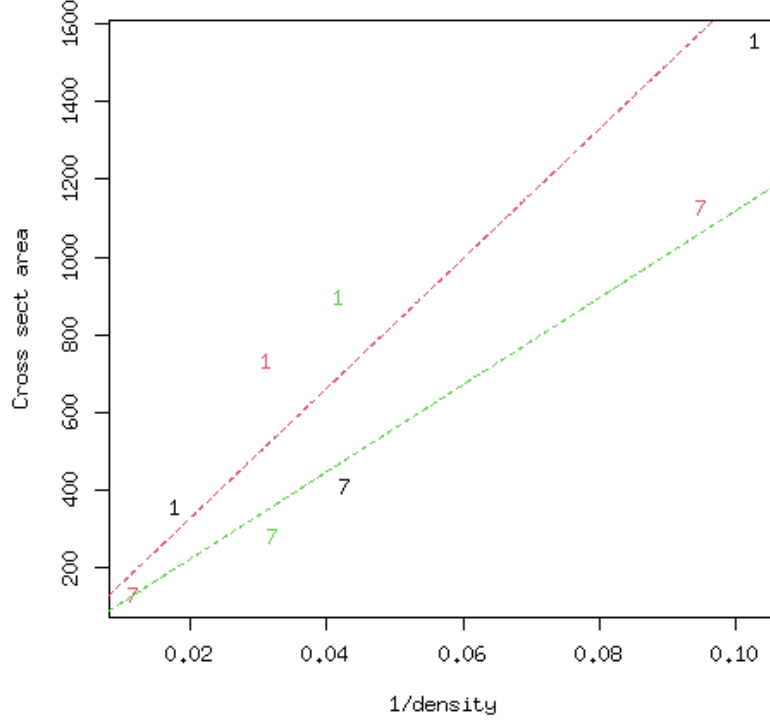


Figure 5: Plot of breed means for reciprocal of follicle density and fibre cross sectional area from Daly and Carter(1955) [8] experiment 2. The red lines are linear regressions with zero intercept fitted to breed means for period 1 (*ad lib* nutrition). The green lines are linear regressions with zero intercept fitted to breed means for period 7 (restricted nutrition).

Here we have a larger difference in slopes but a poorer fit. The red line (good nutrition) is a larger slope than the green line (restricted nutrition). The slopes are 16589 for Period 1 (good nutrition) and 11159 for Period 7 (poor nutrition). The standard errors are 1670 and 2401 respectively. The difference is again significant.

The k values in experiment 2 are lower than those in experiment 1. The diets in the two experiments were similar, but the sheep were older and of considerably larger LiveWeight in experiment 2. So the absolute value of k does not inform us about level of nutrition, for example $k = 17000$ in experiment 1 is a restricted feeding, but $k = 17000$ in experiment 2 is an *ad lib* feeding. Differences in k mean something in relation to nutrition, other things being

equal, but absolute values of k do not indicate level of nutrition.

Another point of concern in experiment 2 is that the fibre diameters may have been on wool samples, not skin biopsies. The fibre cross sectional areas presented do not agree with what we calculate using the formula $A = \frac{\pi}{4}D^2$. They are close but not identical. We used their fibre cross sectional areas.

There was a third experiment by Daly and Carter using the same sheep as in experiments 1 and 2, but grazed at pasture over a period of 40 weeks. Over the 40 weeks Liveweights rose to a peak at about 30 weeks, then declined slightly as the pasture hayed off in Summer. The relationship of fibre cross sectional area to the reciprocal of density is shown for experiment 3 in Figure 6

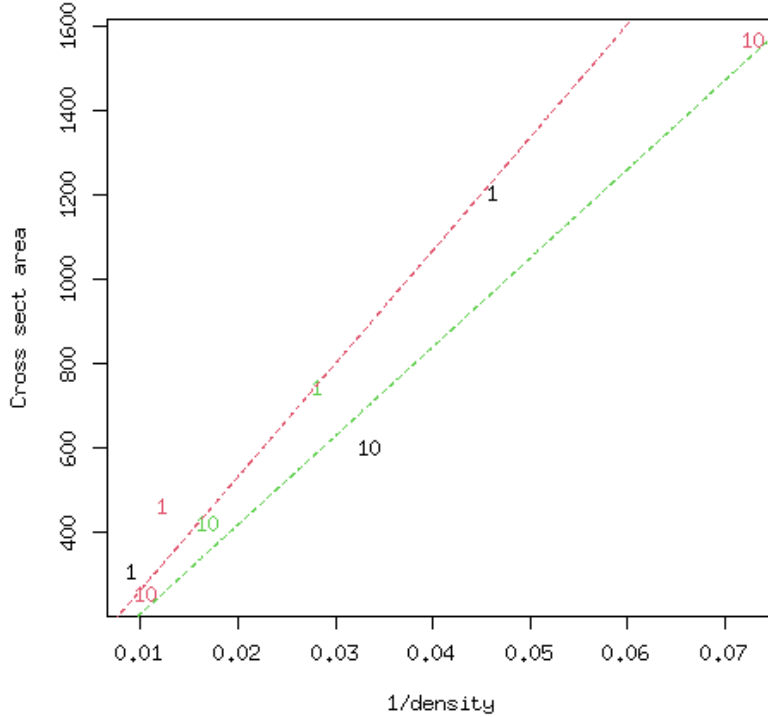


Figure 6: Plot of breed means for reciprocal of follicle density and fibre cross sectional area from Daly and Carter(1956) [9] experiment 3. The red lines are linear regressions with zero intercept fitted to breed means for period 1 (lowest liveweight). The green lines are linear regressions with zero intercept fitted to breed means for period 10 (higher liveweight and older).

Here, the k value for period 1 was 26768 and for period 10 was 21004. Both k values are high compared to experiments 1 and 2, and the difference is small.

Subtle pasture changes do not produce the same dramatic effect as changes in level of hand feeding. The difference is in the expected direction - ie the higher quality pasture of period 1 produced a higher k value than the lower quality pasture of period 10, even though the liveweights increased from period 1 to period 10.

Finally we need to see if shifting scales are an issue by plotting all 3 experiments on one graph. Figure 7 shows this

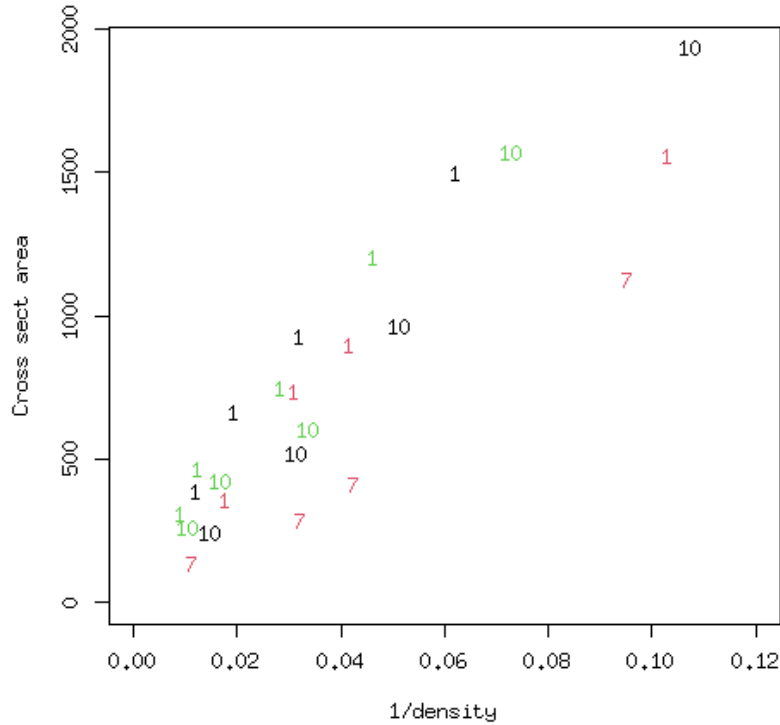


Figure 7: Plot of breed means for reciprocal of follicle density and fibre cross sectional area from Daly and Carter(1956) [9] all 3 experiments . The black points are experiment 1, the red points are experiment 2, the green points are experiment 3.

We can see that there is no shift of scale between experiments. The only really different set of points is period 7 in experiment 2, which had a very low k value of 11159. It seems visually from Figure 7 that k does not vary greatly. That is because it is difficult to judge slopes visually. If we calculate k for each Breed x Period x Experiment combination and do an analysis of variance we get

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Breed	3	80429331	26809777	2.812	0.0751 .
Expt	2	540764086	270382043	28.359	8.01e-06 ***
Expt:Period	3	646855973	215618658	22.615	8.06e-06 ***
Residuals	15	143011782	9534119		

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

So there are large differences in k between Experiments, and between Periods within Experiments, but there are no Breed differences in k . That is what we concluded doing things one experiment at a time above. The Breed differences in diameter are due to the density part of the check effect and/or the dermal papilla cell counts. Differences in diameter due to k are to do with growth and development and nutritional status.

3.2.2 Old unpublished Carter experiments

A further source of such data is again Dr Carter. Figure 8 shows an original data sheet of a very old nutritional experiment obtained from Dr Carter in a personal communication.

This looks promising, there are two planes of nutrition, but the fibre diameter measurement may not be at one point of growth (ie a skin measurement) , and the 'estimated' S/P ratio is the nearest thing we have to a density. There is a second sheet (Figure 9)

where sheep numbers have been written in. So it is a randomised design, not a paired design with the same sheep subjected to different nutritional planes at different times. Paired or time series designs are difficult to interpret for our purpose, because nutritional differences at a series of times are confounded with effects of increasing age and accompanying growth and development of the sheep. For example, if bodyweights increase with age, densities will decrease with age.

For Carters experiment, we can estimate a density from S/P ratio and LiveWeight using $N = 36.7 - 0.714LiveWt(Kg) + 2.72S/P$. This formula was obtained from The Daly and Carter data above. Using this estimated density, and using the 'dubious' fibre diameter to estimate cross sectional area, we obtain the plot of reciprocal density against cross sectional area shown in Figure 10

The High nutrition group has a k (ie slope of regression) of 21481, while the Low nutrition group has a k of 19059. This is in the direction noted previously, ie higher k values indicate better nutrition, but the difference is not large. The High nutrition group has a k (ie slope of regression) of 21481, while the Low nutrition group has a k of 19059. This is in the direction noted previously, ie higher k values indicate better nutrition, but the difference is not large. There is no record of level of feeding in the High and Low nutrition groups, but the bodyweight differences were large, and the fleece weight differences were large. We can at least conclude that the difference in k is due to nutrition, because the design is randomised.

There is a lot of variation around the regressions in Figure 10. We look into this with an analysis of variance of the k values for Strain x Age x Nutrition combinations, as follows

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Strain	1	30539076	30539076	11.695	0.0188	*
NutPlane	1	32654244	32654244	12.505	0.0166	*
Age	2	20132088	10066044	3.855	0.0971	.
NutPlane:Age	2	49939448	24969724	9.562	0.0196	*
Residuals	5	13056235	2611247			

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1						

There is an interaction between NutPlane and Age. This is summarized by the following table of means

NutPlane:Age

	Age		
NutPlane	1	2	3
High	23858	23640	17629
Low	15828	19846	19556

Something happened to the difference between High and Low NutPlanes at Age 3 - the effect is reversed. The differences in k at Ages 1 and 2 are much larger and more in line with those found in the Daly and Carter experiments. We will never find out what happened at Age 3, but both Strains in the High NutPlane group suddenly became finer, while both Strains in the Low Nutplane group increased slightly in diameter?

There is a further old unpublished study by Thompson and Carter(1952) [32]. The result sheets are shown in Figures 11, 12, and 13

The plot of reciprocal density against cross sectional area for these data is shown in Figure 14

This plot is interesting. The unimproved pasture has a higher k value (green line) than the improved pasture (red line). The difference between pasture types is significant , as shown by the following analysis of variance of means

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Breed	3	36749637	12249879	7.708	0.0637 .
Pasture	1	25173778	25173778	15.840	0.0284 *
Residuals	3	4767746	1589249		

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

The residual is actually the interaction sum of squares, but it would not seem there is any interaction between Breeds and Pastures, as in the following set of means for k the difference between Improved and Unimproved Pasture is in the same direction for all Breeds

Breed:Pasture		
	Pasture	
Breed	Improved	Unimproved
Corriedale	14253	20240
FineMerino	14379	16479
MedMerino	17604	21364
Polwarth	12540	14885

We can only suppose that either the unimproved pasture was actually 'better' than the improved, or that some other factor is involved. The two Pastures were at different locations.

SHEEP TYPE AND PLANE OF NUTRITION	Live Weight lb.	Greasy Fleece Weight lb.	Clean Yield per cent	Clean Fleece Weight lb.	Staple Length in cm. per yr.	Fibre Diamet. ^r in microns	Estd. Ratio S/P
<u>Modern Fine Merino</u>							
At 1 yr.	76	9.2	66.0	6.0	9.2	19.7	20.9
<u>High</u> 2 yrs.	100	13.3	63.5	8.5	9.1	20.9	22.4
[70's] 3 yrs.	111	12.5	63.0	7.9	8.3	18.8	23.6
At 1 yr.	41	4.3	65.2	2.8	7.1	15.0	19.5
<u>Low</u> 2 yrs.	61	7.6	62.5	4.6	8.1	17.3	21.6
[80's] 3 yrs.	76	8.5	60.5	5.3	7.7	18.0	21.3
<u>Modern Strong Merino</u>							
At 1 yr.	90	12.9	70.0	9.1	13.9	26.5	14.9
<u>High</u> 2 yrs.	129	18.5	66.5	12.3	13.1	28.3	16.3
[56's/58's] 3 yrs.	141	17.4	69.2	12.0	12.4	25.3	15.7
At 1 yr.	42	5.9	66.0	3.9	10.8	19.6	13.6
<u>Low</u> 2 yrs.	58	8.1	64.5	5.2	11.2	21.8	14.9
[60's/64's] 3 yrs.	75	9.6	60.5	6.7	11.2	23.0	14.2
Reference: Marston, H.R., Pierce A.W., and Carter H.B. (1939-42); unpublished data.							

Figure 8: Data from an old nutritional experiment obtained from Dr Carter

STRAIN AND PLANE OF NUTRITION	Age= years	Nett liveweight in Kg.	Greasy fleece wt. Kg./365 days	Clean fleece wt. Kg./365 days	Food intake as crude protein Kg./365 days	Efficiency per cent(3)/(4) x 100	Clean wool per 100 sq. cm. in g./365 days	Staple length cm./365 days	Fibre diameter in microns	Follicle ratio estd. S/P	Basal area of tattooed patch in sq. cm.	Skin wrinkle area in sq. cm.
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
FINE HIGH <i>n = 10</i>	1	34.2	4.13	2.72	44.5	6.13	17.8	9.18	19.7	20.9	89.8	38.3
		0.41	0.12	0.07	0.47	0.17	0.71	0.20	0.34	1.01	1.53	6.94
	2	45.1	6.00	3.81	54.3	7.01	23.4	9.09	20.9	22.4	109.4	38.9
		0.95	0.25	0.15	0.97	0.23	1.06	0.17	0.38	1.08	2.34	7.29
	3	50.0	5.85	3.56	47.2	7.52	20.7	8.32	18.8	23.6	122.2	31.4
		1.23	0.30	0.17	1.21	0.24	0.64	0.15	0.44	1.35	2.98	6.96
FINE LOW <i>n = 15</i>	1	18.4	1.95	1.27	20.1	6.33	13.0	7.14	15.0	19.5	65.6	5.1
		0.19	0.07	0.04	0.05	0.23	0.82	0.24	0.34	0.98	1.48	1.37
	2	27.5	3.29	2.06	32.2	6.41	18.9	8.07	17.3	21.6	83.4	11.5
		0.32	0.14	0.07	0.02	0.23	0.92	0.16	0.48	0.99	1.58	2.60
	3	34.5	3.82	2.37	38.2	6.20	19.1	7.73	18.0	21.3	98.9	15.0
		0.65	0.19	0.10	0.11	0.26	0.82	0.17	0.46	1.46	2.18	3.63
STRONG HIGH <i>n = 12</i>	1	40.5	5.31	4.07	50.9	8.02	35.1	13.91	26.5	14.9	110.7	5.7
		0.79	0.17	0.12	0.28	0.23	1.46	0.49	0.51	0.50	4.86	8.31
	2	58.2	8.36	5.54	67.4	8.25	41.0	13.13	28.3	16.3	148.5	4.4
		1.28	0.25	0.19	1.03	0.36	1.07	0.33	0.51	0.52	6.44	2.91
	3	63.4	7.85	5.41	55.5	9.78	33.6	12.39	25.3	15.7	161.7	5.3
		1.88	0.31	0.17	1.85	0.21	1.03	0.22	0.43	0.71	6.77	3.69
STRONG LOW <i>n = 13</i>	1	19.1	2.65	1.75	21.8	8.03	20.3	10.82	19.6	13.6	71.4	0.0
		0.29	0.09	0.06	0.09	0.27	0.98	0.42	0.43	0.62	2.95	0.0
	2	26.1	3.62	2.33	32.3	7.22	28.9	11.16	21.8	14.9	89.4	0.0
		0.53	0.09	0.06	0.02	0.19	0.93	0.28	0.36	0.56	4.45	0.0
	3	33.7	4.33	3.01	37.9	7.66	28.9	11.18	23.0	14.2	106.8	0.0
		0.88	0.12	0.08	0.04	0.21	0.76	0.26	0.37	0.66	5.38	0.0

Figure 9: Data from an old nutritional experiment obtained from Dr Carter

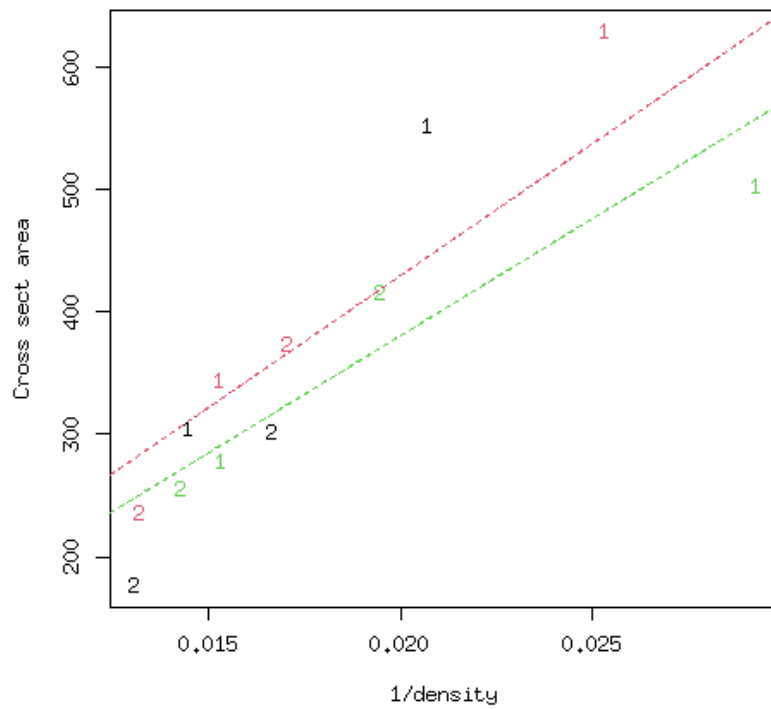


Figure 10: Plot of breed means for reciprocal of follicle density and fibre cross sectional area from Carter(1939) [3]. The red line is a linear regressions with zero intercept fitted to strain x age means for the high nutrition group. The green line is a linear regressions with zero intercept fitted to strain x age means for the Low nutrition group.

BREED AND ENVIRONMENT.	No. of Follicles per sq. mm.		Ratio \bar{n}_s/\bar{n}_p	Mean Fibre Diameter in microns			Ratio \bar{d}_p/\bar{d}_s
	\bar{n}_{p+s}	\bar{n}_p		\bar{d}_p	\bar{d}_s	\bar{d}_{p+s}	
<u>Fine Merino</u>							
(a) Improved [n=10]	64.1 ± 2.29	2.6 0.09	24.3 1.06	17.8 0.62	16.8 0.38	16.9 0.37	1.06 0.039
(b) Unimproved [n=10]	72.8 ± 3.56	3.4 0.26	21.4 1.97	17.7 0.51	16.9 0.29	17.0 0.29	1.05 0.029
<u>Medium Merino</u>							
(a) Improved [n=10]	47.6 ± 1.85	2.2 0.08	20.8 0.61	23.2 0.41	21.6 0.64	21.7 0.61	1.08 0.043
(b) Unimproved [n=9]	64.1 ± 3.40	2.6 0.02	20.2 1.93	22.7 2.81	20.5 1.64	20.6 1.56	1.11 0.053
<u>Polwarth [3/4 Merino]</u>							
(a) Improved [n=10]	26.6 ± 1.87	2.0 0.10	12.9 1.19	21.9 0.68	24.7 1.04	24.5 0.99	0.89 0.034
(b) Unimproved [n=10]	41.0 ± 3.19	2.6 0.18	14.9 1.10	21.3 0.86	21.5 0.86	21.5 0.86	1.00 0.027
<u>Corriedale [1/2 Merino]</u>							
(a) Improved [n=10]	22.5 ± 1.53	2.1 0.13	9.9 0.71	28.3 1.15	28.4 1.16	28.4 1.14	1.00 0.044
(b) Unimproved [n=10]	24.1 ± 1.43	2.3 0.09	9.5 0.68	31.6 0.83	32.8 1.08	32.7 1.02	0.97 0.084

General Skin Characters in Wethers of Four Breeds
run together in Two Environments at Age = 2-3 years.

Tasmania 1951-52

Environment (a) Improved = sown pasture at Wynyard, N.W. Coast.

Environment (b) Unimproved = native pasture ["bush run"] at Tullochgoram, E.Coast.

[Sheep shorn and sampled: mid-November, 1952]

Experiment by: D.S. Thompson, Tasmanian Dept. of Agric., and H.B. Carter, C.S.I.R.O.

Figure 11: Data from an old nutritional experiment obtained from Dr Carter

BREED AND ENVIRONMENT	Greasy Fleece Weight lb.	Clean Yield %	Clean Fleece Weight lb.	Staple Length cm. /365days	No. of Fibres per cm. ²	Fibre Diameter microns	Crimps per cm.
<u>Fine Merino</u>							
(a) Improved [n=19]	7.6 ± 0.24	67.5 0.82	5.1 0.18	8.9 0.18	8.42 0.41	15.0 0.31	6.3 0.24
(c) Improved [n= 7]	9.7 ± 0.49	61.3 1.86	5.9 0.23	9.1 0.43	8.18 0.32	16.4 0.75	6.5 0.20
<u>Medium Merino</u>							
(a) Improved [n=19]	9.9 ± 0.22	70.8 0.88	7.0 0.21	10.0 0.17	6.80 0.28	18.7 0.49	4.2 0.17
(c) Improved [n= 8]	13.1 ± 0.24	66.9 2.01	8.7 0.31	11.4 0.28	7.58 0.67	20.1 0.49	3.9 0.44
<u>Polwarth [3/4 Merino]</u>							
(a) Improved [n=21]	10.5 ± 0.28	71.1 1.09	7.5 0.26	12.2 0.26	3.48 0.20	23.2 0.44	3.6 0.24
(c) Improved [n= 7]	12.3 ± 0.34	68.5 1.59	8.5 0.32	13.1 0.34	4.20 0.28	22.3 0.81	4.0 0.21
<u>Corriedale [1/2 Merino]</u>							
(a) Improved [n=20]	9.6 ± 0.39	73.8 0.90	7.1 0.33	12.3 0.27	2.81 0.13	25.1 0.90	2.7 0.18
(c) Improved [n= 8]	11.2 ± 1.00	69.0 1.84	7.7 0.72	12.6 0.59	2.70 0.34	27.3 0.97	3.0 0.34

General Fleece Characters in Wethers of Four Breeds
run together in Two Environments at Age = 2-3 years.

Tasmania 1951-52

Environment (a) Improved = sown pasture at Wynyard, N.W. Coast.

Environment (c) Improved = sown pasture at Cressy, Midlands.

[Sheep shorn and sampled: mid-November, 1952]

Experiment by D.S. Thompson, Tasmanian Dept. of Agric., and H.B. Carter, C.S.I.R.O.

Figure 12: Data from an old nutritional experiment obtained from Dr Carter

BREED & ENVIRONMENT	Body Weight off-shears lb.		Greasy Fleece Weight lb.		Price per lb. d.		Fleece Value per head s.d.		Fleece Weight per 100lb. B.Wt. s.d.		Fleece Value per 100lb. B.Wt. s.d.	
	1951	1952	1951	1952	1951	1952	1951	1952	1951	1952	1951	1952
<u>Fine Merino</u>												
(a) Improved n = (20)	77.8	82.4	9.5	7.9	93	103	60/1	64/10	12.2	9.6	73/8	78/10
(b)Unimproved n = (14)	59.7	53.7	5.5	5.6	88	109	40/5	50/10	9.3	10.2	64/6	90/7
<u>Medium Merino</u>												
(a) Improved n = (21)	98.2	100.0	10.7	10.1	79	95	70/2	70/8	10.9	10.1	68/6	78/11
(b)Unimproved n = (20)	80.1	66.2	7.6	7.2	88	106	55/7	63/4	8.5	10.9	67/6	87/4
<u>Polwarth[3/4M]</u>												
(a) Improved n = (21)	98.9	111.0	10.9	10.2	70	84	63/6	71/5	11.1	9.8	64/9	65/2
(b)Unimproved n = (18)	75.7	66.7	7.2	6.5	77	102	46/4	45/2	9.5	9.8	62/3	78/5
<u>Corriedale[1/2M]</u>												
(a) Improved n = (21)	100.7	112.4	11.0	9.6	59	62	54/-	49/9	10.9	8.5	49/8	44/-
(b)Unimproved n = (21)	77.8	64.7	8.3	6.4	60	87	41/5	48/3	10.6	9.8	52/6	68/-

Wool Production from Wethers of Four Breeds run together in
Two Environments for Two Consecutive Years from Age=1yr to 3yrs.
Tasmania 1950 - 1952

Environment (a) Improved = sown pasture at Wynyard, N.W.Coast.

Environment (b)Unimproved = native pasture["bush run"] at Tullochgorum, E. Coast.

[Sheep shorn: mid-November, 1950, 1951, 1952.]

Experiment by: D.A. Thompson, Tasmanian Dept. of Agric., and H.B.Carter, C.S.I.R.O.

Figure 13: Data from an old nutritional experiment obtained from Dr Carter

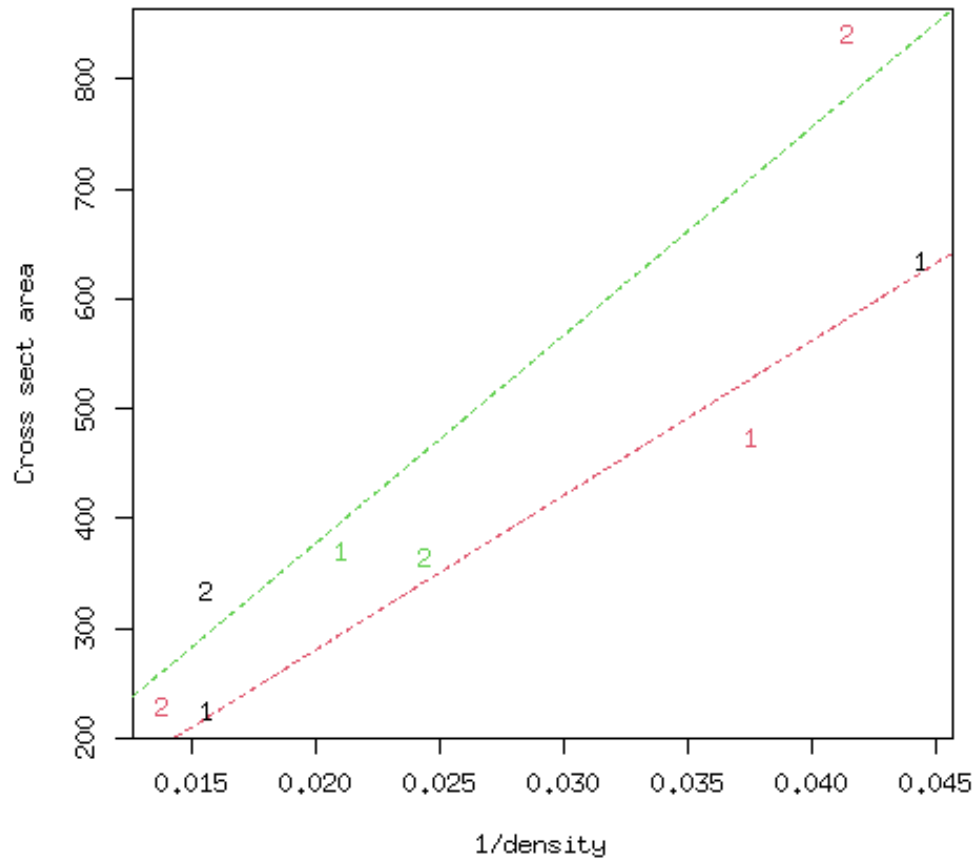


Figure 14: Plot of reciprocal density against cross sectional area for data from Thompson and Carter(1952) [32]. Red line is regression through origin for the Improved Pasture group. Green line is regression through origin for the Unimproved Pasture group.

3.2.3 Trangie Flc+ and Flc- lines feeding experiment

Williams and Winston(1987) [35] conducted a feedings experiment in which ewes from the Trangie Flc+ and Flc- selection lines were randomly allocated to two groups fed a High and Low ration for a period of 100 days. Follicle density and fibre cross sectional area were measured at the end of the treatment period. A plot of reciprocal density against cross sectional area is shown in Figure 15

This looks like an insignificant result but the range of variation is tiny compared to previous graphs and there are only 2 points, one from Flc+ and one from Flc-, for each diet level. The two slopes were 24268 for High Diet and 20976 for Low Diet, so they are within the ranges of previous datasets. An analysis of variance of k values gives

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Line	1	68774420	68774420	24.987	0.126
Diet	1	8857061	8857061	3.218	0.324
Residuals	1	2752389	2752389		

and the Line x Diet means were

Line:Diet		
	Diet	
Line	H	L
Flc+	30125	25490
Flc-	20173	18856

so the Line difference is large and significant, the Diet difference is small and not significant.

We have to conclude k can be changed by intense selection for one trait (in this case fleece weight). We know that k is not just how much the animal eats, but something like nutritional status of a skin area or a follicle group. That could easily be influenced by all sorts of genetic mechanisms in the skin as well as by overall nutritional status.

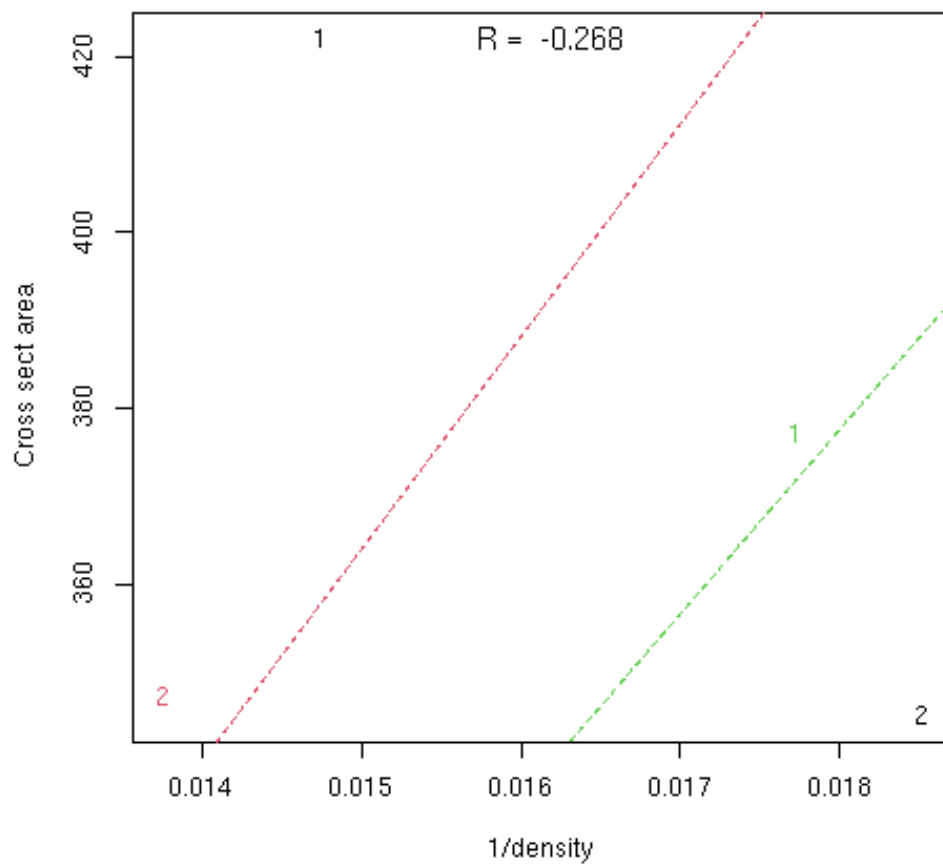


Figure 15: Data from Williams and Winston(1987) [35] showing reciprocal density and cross sectional area for Trangie Flc+ and Fls - sheep under High and Low levels of feeding. Red line is regression thru origin for High level Diet, green line is regression thru origin for Low level of diet

3.2.4 CSIRO selection lines

The experiments reported by Turner, Brooker and Dolling (1970) [33] are single character selection lines with pairs of lines selected up and down for the following traits - Bodyweight, Density, Staple Length, CWW per head, Wrinkle, Fibre Diameter, CWW per unit area, and Clean Scoured Yield of wool. Figures 16 and 17 show plots of the k values of sheep born in years 1947 to 1970.

The result is clearcut. Density and diameter (which make up k) show a small response, as does bodyweight (because surface area contributes to density). CWW per head and per unit area show a larger response in k because they are density and diameter together, ignoring length. Length, wrinkle, and yield are unrelated to k , although there might be a small change in k in the wrinkle plus and minus lines. CWW per unit area is just k with length added.

So the whole thing is purely physical, $k = ND$ being the definition of k . It sheds no light on our interpretation of k as skin nutritional status. There is, however, considerable year to year fluctuation in k within all selection lines. This fluctuation reflects yearly shifts in pasture quality and thus represents the environmental sensitivity of k . The difference between largest and smallest k value is shown for each line in Table 3.2.4.

Table 1: Difference between largest and smallest k value for each of 8 single character selection lines

Line	Range of k
BwtPlus	4509.70
BwtMinus	7404.50
DensPlus	11528.80
DensMinus	5310.40
LengthPlus	7333.10
LengthMinus	7406.30
CWWPlus	6383.40
CWWMinus	5431.10
WrinklePlus	7372.20
WrinkleMinus	5024.20
DiamPlus	7139.40
DiamMinus	8137.50
CWWperuaPlus	7072.10
CWWperuaMinus	6296.10
YieldPlus	8188.30
YieldMinus	6501.90

Most of the ranges are around 5000-7000 but the Density Plus Line has a range of 11000. It may be that having a high Density makes sheep more responsive in Diameter to seasonal changes.

3.2.5 Quantitative genetic analysis of variation in k within a Merino flock

We have a modest amount of CSIRO data (820 sheep) in which fibre diameter and follicle density were measured on skin sections from a pedigreed Merino sheep flock. This permits a quantitative genetic analysis of variation in k among animals within a flock. We obtain the following estimates of heritable and non-heritable variance of k

Proportion of phenotypic var/covariance partitioned by DME:
to each component (OLS-b):

	Trait	Estimate	StdErr	CI95lo	CI95hi
VarE(I)	k	0.798	0.029	0.741	0.855
VarG(Ia)	k	0.202	0.029	0.145	0.259
VarP(I)	k	1.000	0.000	1.000	1.000

So the heritability of k is not zero but is only 0.2, so 80 percent of the variance is non-heritable. That goes along with k being mostly a skin nutritional status indicator.

We can also look at how k is correlated with other variables

	Traitpair	Estimate	StdErr	CI95lo	CI95hi
VarE(I)	k:Cww	-0.0108	0.0394	-0.0880	0.0663
VarG(Ia)	k:Cww	0.4495	0.1002	0.2531	0.6460
VarP(I)	k:Cww	0.0822	0.0240	0.0351	0.1293

	Traitpair	Estimate	StdErr	CI95lo	CI95hi
VarE(I)	k:Bwt	-0.1057	0.3619	-0.815	0.6036
VarG(Ia)	k:Bwt	-0.0521	0.1181	-0.284	0.1794
VarP(I)	k:Bwt	-0.0480	0.0611	-0.168	0.0717

	Traitpair	Estimate	StdErr	CI95lo	CI95hi
VarE(I)	k:Stal	-0.0947	0.0662	-0.225	0.0351
VarG(Ia)	k:Stal	0.0130	0.0945	-0.172	0.1982
VarP(I)	k:Stal	-0.0565	0.0336	-0.122	0.0094

So there is a genetic correlation with Cww, and not much correlation of any type with Bwt or Staple Length. The positive correlation with Cww is just a reflection of the fact that cross sectional area is part of Cww, and also part of k . So there is nothing there to suggest that our interpretation of k as skin nutritional status is questionable. Remember that Staple Length and Cww are not point measures; they are integrations of the preceding year of wool growth. We are viewing k as an instantaneous measure of skin status, not an integrated measure during development.

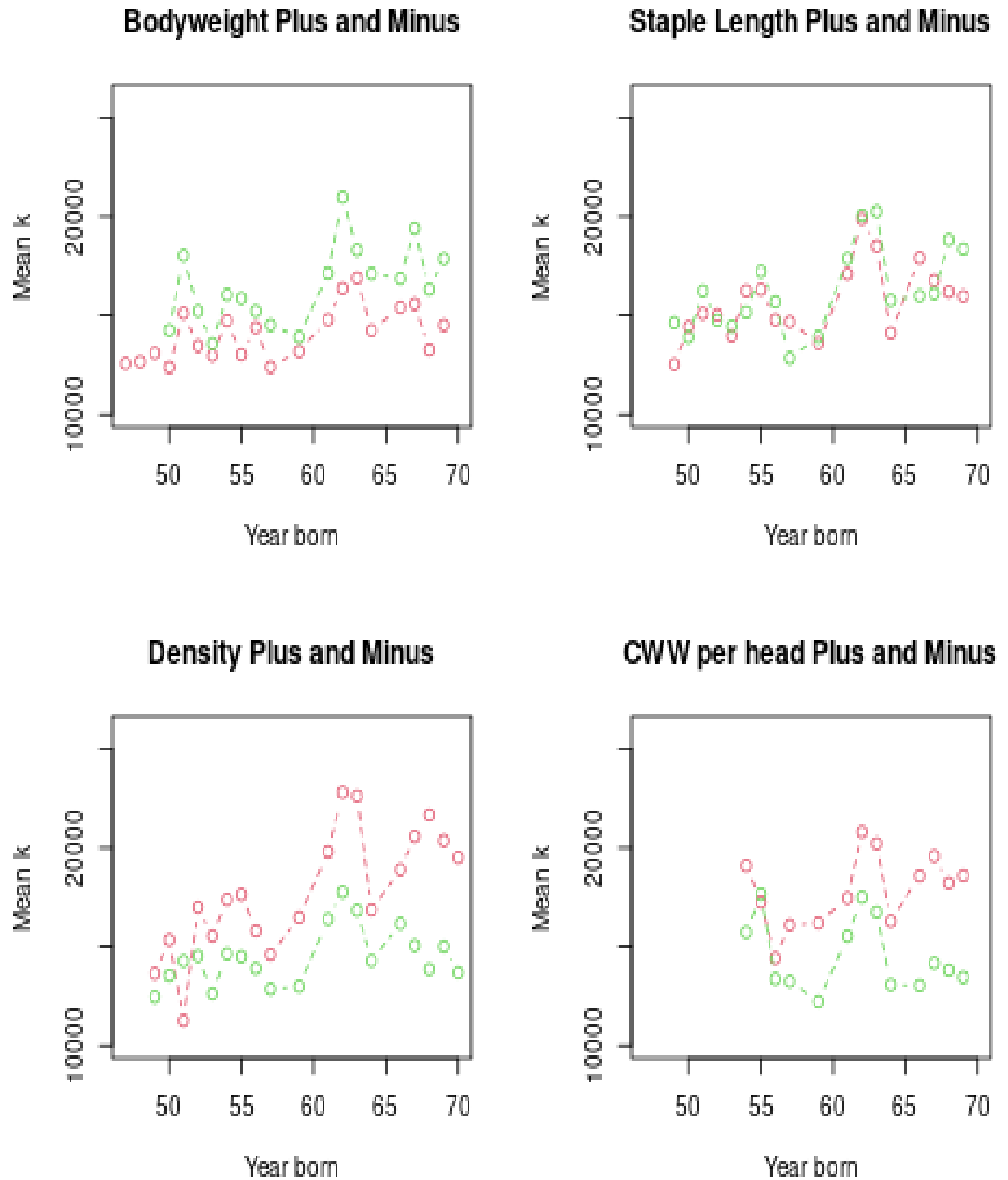


Figure 16: Data from Turner, Brooker, and Dolling (1970) [33] showing the mean k value for sheep born in years 1947 to 1970 of four single trait selection lines with selection up and down for eight wool traits. Red lines are Plus selection. Green lines are Minus selection

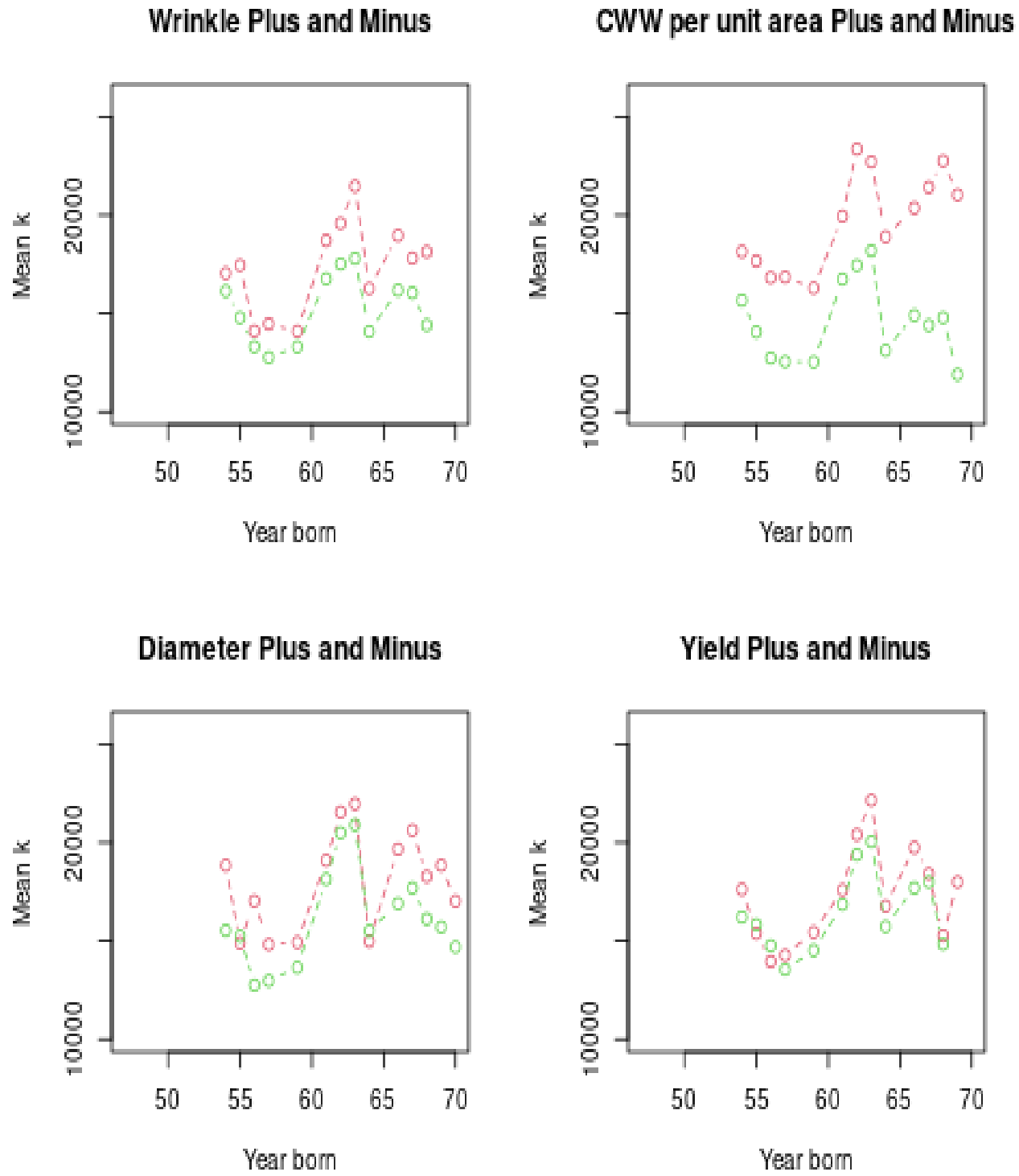


Figure 17: Data from Turner, Brooker, and Dolling (1970) [33] showing the mean k value for sheep born in years 1947 to 1970 of four single trait selection lines with selection up and down for eight wool traits. Red lines are Plus selection. Green lines are Minus selection

3.2.6 Staple diameter profile data

..... This section is not as definitive as I originally thought It needs to be rewritten There are only density measurements at the time of the tenth diameter reading along the profile. This limits what we can do with these data.

..... Varying *check* is what makes staple diameter profiles. Data from Jackson and Downes (1979) [14] has sheep from 4 single character selection lines (L+, L-, D+, D-). There were 5 sheep from each selection line, and 2 staples per sheep. All sheep were rams born in 1972. Each staple was divided into 10 equal length segments, and the mean fibre diameter of each segment was measured with the liquid scintillation counting technique (Downes et al 1975) [10]. Each staple represented wool growth from weaning in January 1973 to hogget shearing in February of 1974. The changes in diameter for each selection line are shown in Figure 18 which is copied from the paper

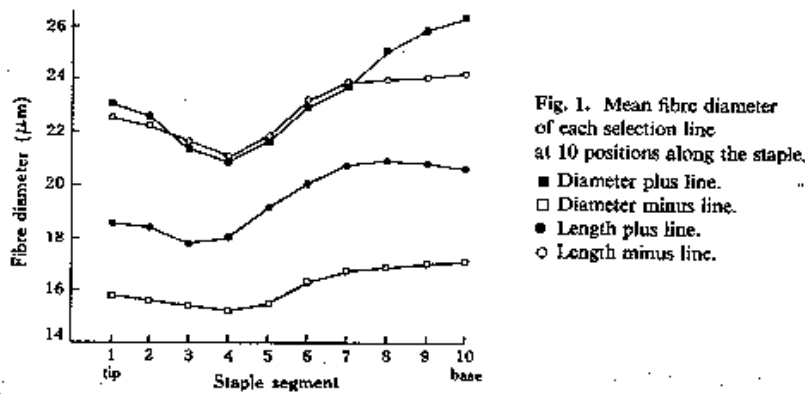


Figure 18: Mean diameter of each selection line at 10 positions along the staple. Taken from Jackson and Downes (1979) [14]

In trying to use these data to study the *check* effect we need to be aware of the changes that are occurring as the wool growth proceeds from segment 1 to segment 10. At segment 1 the sheep are weaners, by segment 10 they are hoggets of about 18 months of age, and almost mature. Over this period the sheep increase in body weight and surface area, but decrease in follicle density. At the same time segment 1 is end of Summer, the pastures in Armidale then go into an Autumn/Winter decline, so segments 3,4, and 5 represent the poorest nutrition, and there is then an increase in pasture quality as we go into Spring and Summer up to segment 10.

So several things are altering simultaneously along the profiles. They are all variations in degree of *check*, but by various mechanisms.

We first examine a plot of reciprocal density against cross sectional area

estimated from diameter of staple segment 10, which is at the same time as the density measurement. Figure 19 shows a separate regression line for each selection line (D+, D-, L+, L-).

The data show a high correlation with some points from the D+ Line (labelled '1' on the graph) being deviant than the remainder. The mean slopes for each line were

Family				
	D+	D-	L+	L-
	19478	18094	17074	18668
rep	10	10	10	6

An analysis of variance of k values shows that Lines and Sheep within Line varied significantly

Analysis of Variance Table

Response: k

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Line	3	30149810	10049937	57.925	1.906e-09 ***
Line:Sheep	14	311176471	22226891	128.110	4.477e-15 ***
Residuals	18	3122968	173498		

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

So the k values (slopes) of the 4 Lines are significantly different. What will be interesting will be to see whether these k values correlate with the staple diameter profiles. Figure 20 shows a positive relationship between k and $D_{10} - D_4$ with a correlation of 0.62

So a larger k means a more responsive diameter profile, or the reverse; a more responsive diameter profile leads to a larger end segment diameter and a larger end segment k . We are unable to sort out causation here, because we do not have densities (and therefore k 's) at the first nine staple segments.

We can see whether the Line means show the same relationship as Figure 20 by plotting them in Figure 21

The relationship is still positive, and in this case the correlation among Line means is 0.79. So whatever applies to Sheep applies to Line means also.

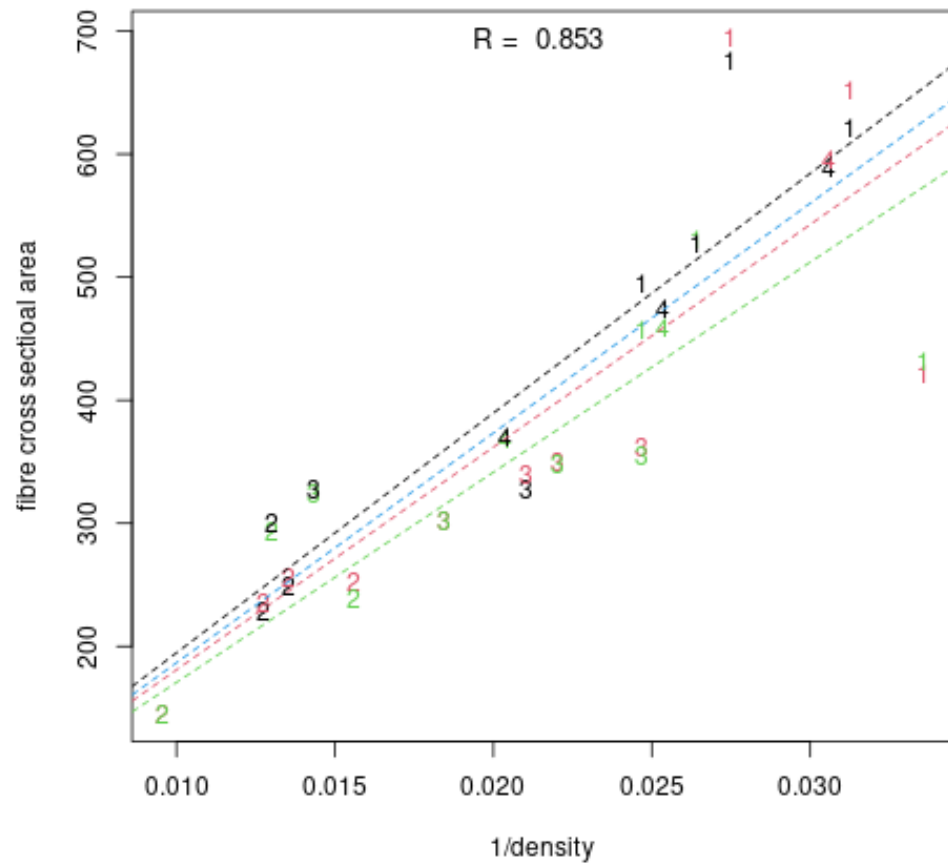


Figure 19: Plot of reciprocal density against cross sectional area of tenth staole segment for data from Jackson and Downes (1979) [14]. Regression lines are through the origin. Black is D+ Line, red is D- Line. Green is L+ Line. Blue is L- Line

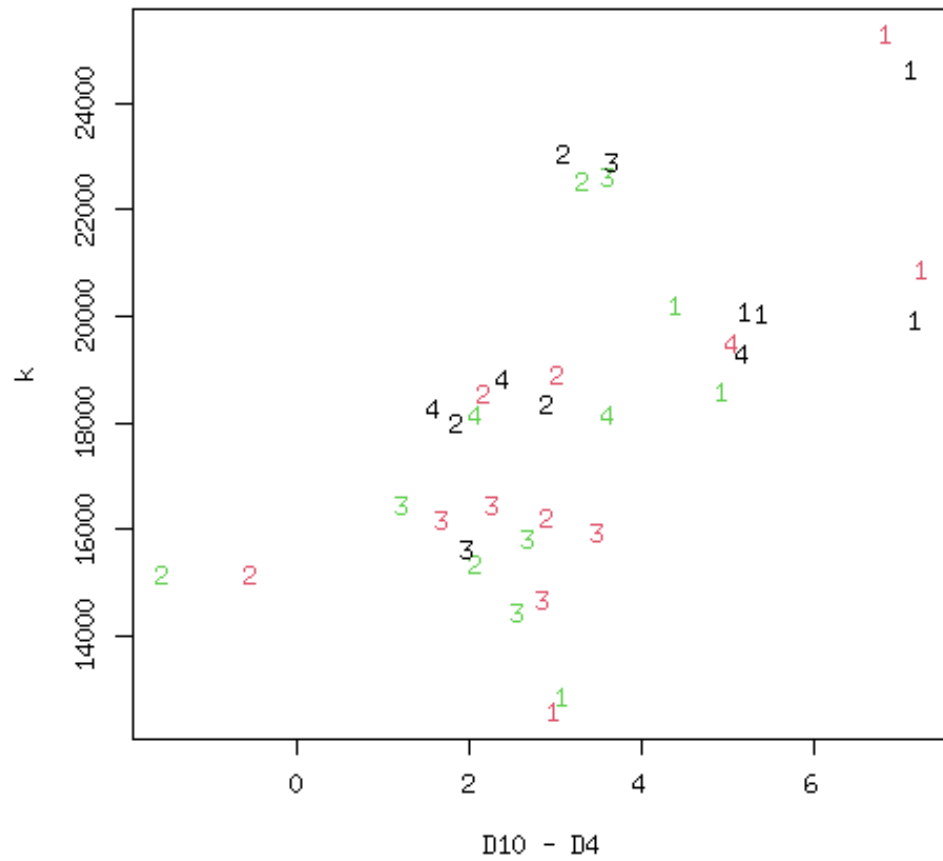


Figure 20: Plot of difference between D10 and D4 against k value for individual sheep x replicate staple data from Jackson and Downes (1979) [14]

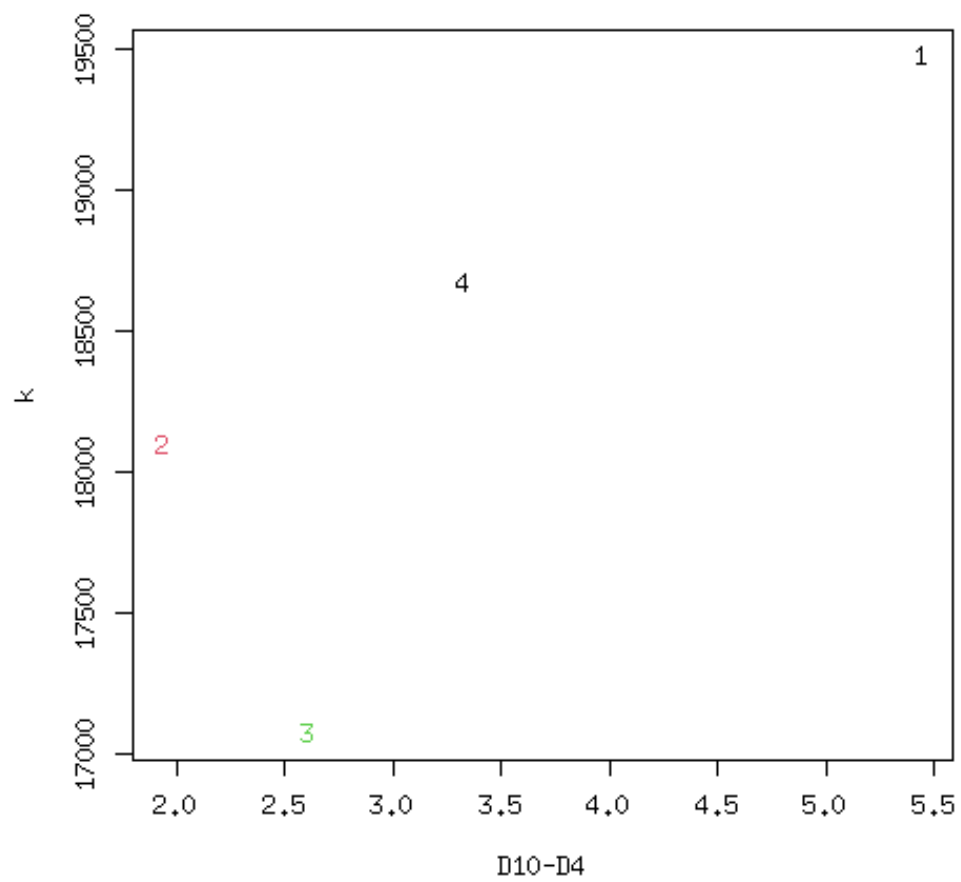


Figure 21: Plot of Line means for difference between D10 and D4 against k value for data from Jackson and Downes (1979) [14]

3.3 Defining *check* by relating it to fibre diameter

We have defined *check* at time i C_i as follows

$$C_i = \frac{A_B - A_i}{A_B}$$

which is just the fractional change in cross sectional area. This definition implies a linear relationship between C and A , as shown in Figure 22

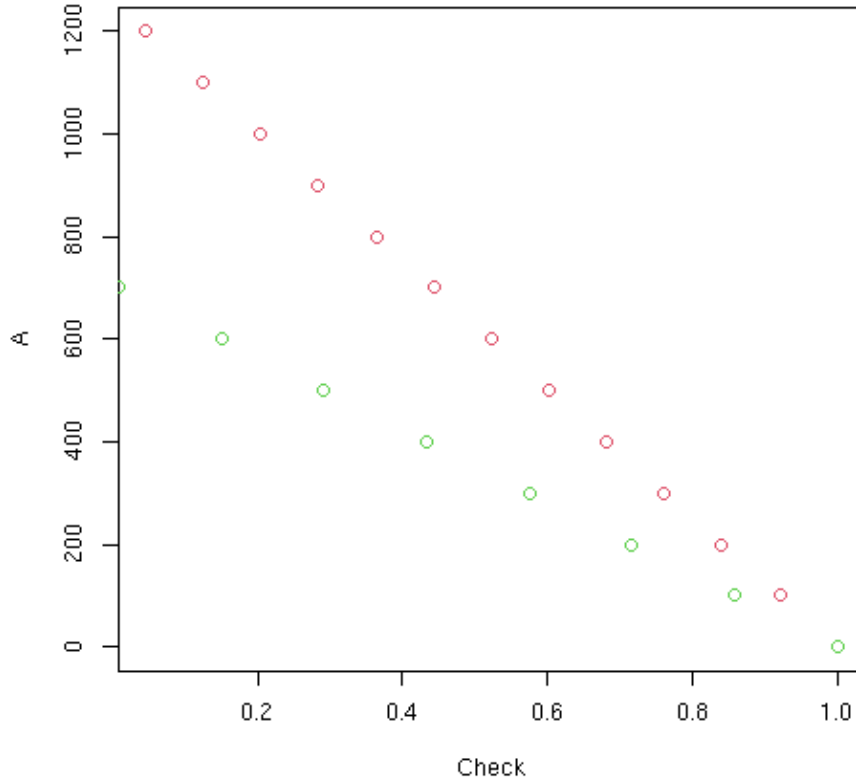


Figure 22: Two relationships between check (C) and cross sectional area (A) implied by defining check as $C = \frac{A_B - A}{A_B}$. For the redline A_B is set to 1256.6 (40 microns diameter), and this corresponds to zero check. For the green line A_B is set to 706. (30 microns diameter), and this corresponds to zero check. Both lines intersect the X-axis at (1,0)

In Figure 22 the Y-axis intercept is A_B and the slope is $-A_B$.

We could define a curved relationship, such as an exponential decay function. This would make the rate of decay (ie check) proportional to the value of A , so that a sequence of checks would encounter diminishing responses in A .

The linear definition has fibres with a larger A_B respond more to a given check than fibres with a smaller A_B , and that is what we observe, but the rate of response does not change along a sequence of checks, so we get a straight line relationship.

We have assumed the A_B is known. This is not the case. The only way one could directly obtain A_B would be estimation from dermal papilla cell counts. We would need a calibration of DPC counts to A_B . We do not have such a calibration. We only have a relationship of DPCC to checked A at an unknown level of check. To get anywhere we need an independent measure of check.

3.4 Measuring *check*

Our hypothesis is that check has two components

developmental component the amount of check is directly proportional to density (N). The more fibres/follicles there are to share resources, the greater the check.

nutritional component the amount of check is inversely proportional to the nutritional status of the skin. The less resources there are to share among a given number of follicles, the greater the check.

The developmental component has been well studied , particularly in relation to birthcoats and prenatal check. Prenatal check is attributed to the sudden increase in number of secondary derived (Sd) follicles which occurs just before birth.

The skin resources component is elusive. We have attempted in the data analyses from nutritional and other experiments to show that k (the constant of a hyperbolic equation relating A to N) is at least an indicator of skin nutritional status - high k indicating more skin nutrients.

So what our hypothesis implies about check C is

$$C \propto \frac{N}{k}$$

but this has problems. k is the sum of the areas of all fibres in a unit area, which can be written $N\bar{A}$, so C becomes $\frac{N}{N\bar{A}}$, which is $\frac{1}{\bar{A}}$. That is true - the smallest fibres have the largest check, but it does not tell us anything useful, and the logic is circular.

We need to take a different approach. Go back to the original Carter(1968) graph (Figure 1) and draw the family of hyperbolas implied by a set of k values. The result is shown in Figure 23

The red and green 'lines of equal k value' are quite close, but follow the data points closely. We have got it right - k reflects the position of the hyperbola - ie its distance ifrom the origin along the 45 degree axis of the hyperbola.

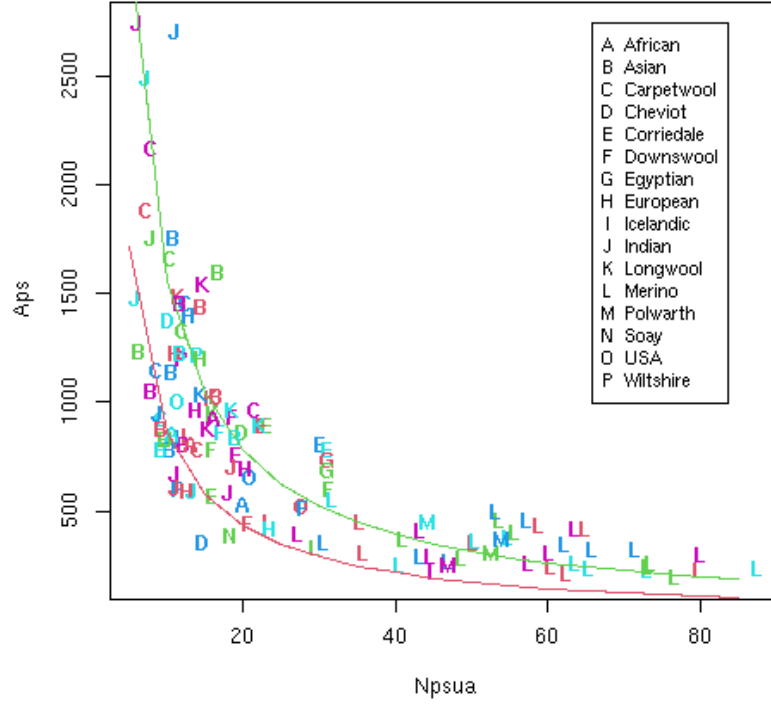


Figure 23: Plot of breed means for follicle density and fibre cross sectional area from Carter(1968) [6]. Red line shows points with a k value of 8600, green line a k value of 15600.

We need to take a closer look at how one parameterizes hyperbolic data. There is a way of transforming data to hyperbolic coordinates. For a point (x,y) in one quadrant with Cartesian coordinates (ie as in the plot of N against A), the corresponding hyperbolic coordinates plotted on a Cartesian quadrant are defined as

$$\begin{aligned} u &= \ln \sqrt{\frac{x}{y}} \\ v &= \sqrt{xy} \end{aligned}$$

The inverse mapping is

$$\begin{aligned} x &= v \exp u \\ y &= v \exp -u \end{aligned}$$

So v is \sqrt{xy} , which is just the geometric mean of x and y , but u is something

new. u is called the hyperbolic angle to (x, y) , and it is a measure of how far along the curves of equal k the point (x, y) is located.

Figure 24 plots u against v for the Carter(1968) data.

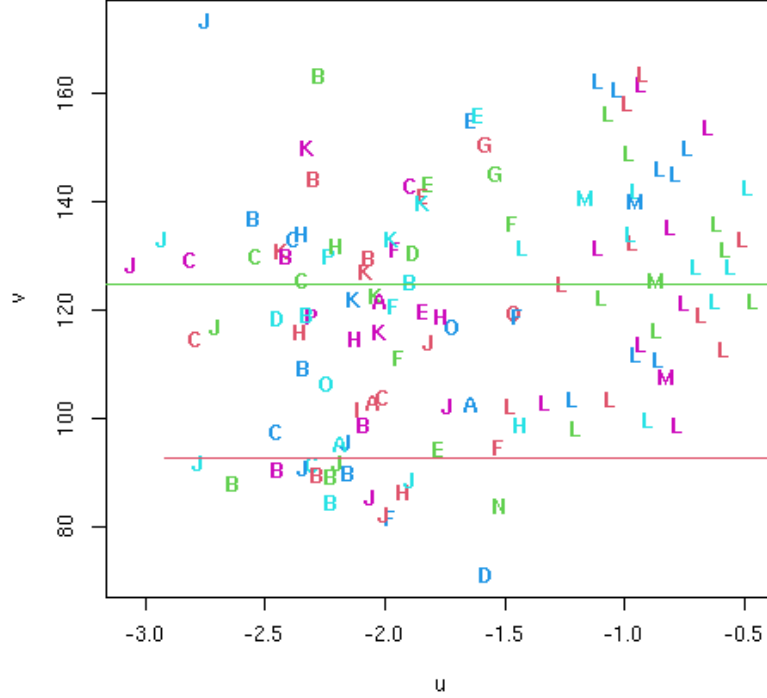


Figure 24: Plot of breed means for hyperbolic coordinates u and v for data from Carter(1968) [6]. Red line shows points with a k value of 8600, green line a k value of 15600.

We see that u puts Merino sheep (coded L) to the far right side of the graph, ie to high values of u , and puts Indian breeds (hair sheep coded J) to the far left. So the positioning along the hyperbola has been transformed to the u coordinate, ie to a linear scale. The red and green lines for $k = 8600$ and $k = 15600$ are seen to correspond to v . It would seem that u and v are independent. A and N are certainly not independent.

Can we arrive at a biological interpretation of u , and is it useful? Yes u is $\ln \sqrt{\frac{N}{A}}$. So u is the variable that describes the process in the Moore dermal papilla cell model whereby a small number of dermal papilla cells per initiating follicle leads to both a larger number of initiating follicles (N) and to smaller fibres (A). This is expressed by $\frac{N}{A}$. The rest (ie the square root and log) are

just scaling.

If $k = v^2$ is all effects on A except density, and u is the Moore model effect of A on density, there remains the issue of 'can we get at A_B (the maximum value of A determined by dermal papilla cell number? The answer is that A_B is the value of A at $N = 1$ (ie where there are no other fibres). Given $k = NA$, if we substitute $N = 1$ we get $A_B = k$. So k is both 'non-density effects on A ' and A_B . How can it be both? Well, 2 things can be numerically equal without being the same, but that begs the question. We need to investigate the following

- is the (N,A) relationship really an hyperbola, and is it centred on (0,0)? The (1/N,A) plots being linear supports it being an hyperbola.
- an alternative is a negative exponential curve. Exponential decay curves intersect the Y axis but are asymptotic to the X axis. In this case A_B would be the point of intersection with the Y axis. So is the check process like radioactive decay?
- can we gain any understanding from other physical 'laws' which are hyperbolic - eg Ohms law, Boyles law. Anywhere 2 variates are multiplied leads to an hyperbolic 'law'.
- our graphs of the (N,A) function look regular - but that is because we have scaled the axes. If we plotted with equal units for N and A the hyperbolic curve would not have its axis at 45 degrees but the origin would still be (0,0) so long as we plotted $NA = k$. If we plotted $(N - h)(A - j) = k$ the origin would be at (h,j). Not sure if we could determine whether a particular set of points had origin (0,0), but the regressions of A on $1/N$ being thru the origin suggest that the origin is indeed (0,0).

4 Discussion

..... this came from poisson.tex ignore it Our thesis is that most of the variation in diameter between fibres within a sheep is controlled by a random sampling of dermal papilla cell numbers forming aggregates. That is , it is not controlled at all, it is chance variation. We emulate this with sampling from a Poisson distribution.

However there is a small amount of fibre diameter variation that is due to systematic differences in dermal papilla cell number between follicle types (Pc, Pl, So, Sd) within a sheep. This variation is under genetic control, and is what is responsible for skewed within sheep fibre diameter distributions. We have been able to show that one can simulate fibre diameter distributions with skewness or bimodality, simply by allocating more dermal papilla cells to the earlier forming follicle types (Pc, Pl, So).

It may be that instead of making follicle types, the most realistic strategy may be to allocate dermal papilla cell numbers to follicles according to their time of initiation. The effect on diameter distribution would be similar. We have not tried this approach, but it may be more biologically meaningful.

..... This bit might stay

While we are sure that dermal papilla cell number controls maximum or potential or base diameter (actually cross sectional area) , all observed data are of *checked* diameter, ie what the follicles grow when they have to share a limited nutrient supply among all the follicles in a trio group.

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A Appendix

The raw data are listed here for completeness