Small Ruminant Research 250 (2025) 107558

Contents lists available at ScienceDirect

Small Ruminant Research

journal homepage: www.elsevier.com/locate/smallrumres

Colour phenotypes, genotypes and colorimetry of unprocessed North American Huacaya alpaca fibre, and comparisons with some other common natural fibres

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ARTICLE INFO

Keywords:
Colorimetry
Wool
Alpaca
Eco-friendly
Whiteness
Brightness

ABSTRACT

Standardised fibre colorimetry has been used on midside samples, taken over three seasons, of fleeces from 1192 individual North American Huacaya alpacas. The results have been compared with the *Alpaca Owners Association* colour phenotype coding, and with Mc1R and ASIP genotype data. The analyses show that standardised colorimetry provides accurate phenotyping on average, but measurement imprecision and probable uncertainties associated with subjective colour coding prevents the prediction of such codes from individual measurements, except for the extremes of white and black. The measurements do, however, confirm good correlation between genotypes and colorimetry, thus supporting their use as an inexpensive additional tool for breeders. When compared with published data on other natural fibres - fine and coarse wool, mohair, cashmere, and cotton - the white and beige alpaca fibres show up favourably for whiteness and brightness. Additionally, unlike the other animal fibres, they do not appear to show a significant yellowness versus brightness relationship, which should be environmentally-beneficial from a textile processing perspective. In common with the other animal fibres, they do show a relationship between yellowness and mean fibre diameter, which is probably a physical light-scattering phenomenon, with the finer samples giving whiter results.

1. Introduction

Raw natural fibres used in textiles range widely in colour from black through various shades of brown, yellow and white. White fibre commands the highest price in the commercial textile market because it can be more readily dyed in the wide range of colours desired by consumers (Marler and Samuelsdorff, 1987; Frank et al., 2006). However, the historical demand for undyed textiles in darker natural colours has nonetheless been sufficient to help sustain populations of animals producing darker fleeces, including heritage sheep breeds, angora goats, and alpacas, amongst others, e.g. (Oria et al., 2009; Marin et al., 2018; Dimov and Vuchkov, 2021; Anon, 2025a, 2025b; Islam et al., 2025).

Although objective measures for describing the colour of raw and scoured wool are available and used to help establish the market value of white sheep's wool lots (Cottle and Baxter, 2015), the colour phenotypes in camelids have traditionally been described subjectively and according to standards which vary by industry and region (e.g. Frank et al., 2006; AAA, 2012; AOA, 2024). This makes it more difficult for processors to produce naturally coloured textiles in lots that are colour-consistent over time. It also limits the ability of livestock growers to breed to produce stock that meets processors' objective colour requirements. By contrast, colorimetry relies on objective measurement.

This work describes the application of wool fibre metrology, and specifically CIE-traceable colorimetry, to the objective measurement of alpaca fibre colour. Whilst there has been some previous attempts to apply colorimetry to alpaca fibres (Lupton et al., 2006; Guridi et al., 2011; Cruz et al., 2021; Pinares et al., 2021; Gray et al., 2023), the application of these methods is not yet widespread, and much of the scientific literature has only used subjectively-assessed colour as a factor whilst investigating other fibre characteristics such as diameter, medullation and length: e.g. (Oria et al., 2009; Pinares et al., 2023; Czyż et al., 2024).

Alpacas have not been selected as intensively for white colour since their domestication (Marin et al., 2018) as have some other fibre-producing species, in particular sheep (Millington, 2013). In addition to the commercially-favoured white animals there remain

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https://doi.org/10.1016/j.smallrumres.2025.107558
Received 5 February 2025; Received in revised form 7 June 2025; Accepted 12 June 2025
Available online 18 June 2025

substantial populations of animals producing fibre in various shades of brown and black, as well as mixed colours (Frank et al., 2006). To explore the range of colours that alpaca fibre could exhibit we analysed 2088 samples of fibre taken from 1192 animals located at a large alpaca breeding operation in the United States. Because many of the animals from which the samples were taken had genotyping results for two key genes known to influence base coat colour, the agouti signalling protein gene (ASIP) and the melanocortin-1 receptor gene (Mc1R), we also evaluated the correspondence between our objective colour measurements and the animals' ASIP and Mc1R genotypes. Finally, to place the results for white alpaca in a broader market context we compared the yellowness and brightness of white fibre produced at the U.S. alpaca farm to previously published results for the wool of merino and New Zealand crossbred sheep as well as to samples of white cashmere and cotton.

2. Methods

The midside samples used in this work were taken from fleeces during annual shearing of '*Snowmass*' and '*Accoyo America*' Huacaya stock located at two properties in central New York State, USA, over a period of 3 years. The two properties are approximately 400 km apart but are under common management and have similar, although not identical seasonal weather, and differing stocking rates - with one property having richer pasture conditions. Animals may sometimes be moved between locations. The samples were supplied with additional data such as Alpaca Registry ID, date of birth, date of shearing, fleece weight, gender, location, and colour code. The colour codes for each animal had been assigned using the *Alpaca Owners Association (AOA) Color Chart* (AOA, 2024).

The 2088 samples analysed represented 1192 individual animals, and of these, 70 % (832) also had Mc1R and ASIP colour genotype data, produced by Neogen Corporation. In the data analyses below, in order to maintain comparable levels of precision, only colour measurements undertaken on the first set of samples taken were used in the case where an individual had fleeces measured in more than one season.

The samples were scoured, dried, conditioned and measured for mean fibre diameter and diameter distribution, staple length, medullation, and tristimulus colour at the SGS New Zealand Pty Ltd. fleece testing laboratory. This facility operates under the accreditation requirements of an ISO-17025 quality system (ISO, 2017), and uses standardised procedures based on IWTO test methods: IWTO-47 (IWTO, 2013) for diameter, IWTO-30 (IWTO, 2007) for staple length, IWTO-57 for medullation (IWTO, 2000), and IWTO-56 (IWTO, 2020) for colour.

Reproducible measurements of natural fibre clean colour require strict adherence to very detailed procedures within a standard such as IWTO-56. In brief, the measurement of clean colour for certification requires removal of grease and dirt (and vegetable matter) from the fibre by standardised aqueous scouring; drying of the samples under controlled conditions below 65°C (to avoid yellowing); homogenising and randomising the clean fibres; compression of a standard conditioned mass of clean fibre to a standard density behind optical-quality glass; and replicate measurements of the CIE tristimulus values of X, Y and Z (CIE, 2019a) under illuminant D65 (i.e. daylight) at 10° observing angle, using a 45°/0° illuminant/observer geometry on two separate colorimeters. The instruments and specimen cell windows are calibrated using CIE-traceable certified ceramic tiles. The tristimulus values X, Y and Z numerically represent the human visual brightness perception in the red, green and blue parts of the spectrum (with wavelength distributions in the approximate ranges of 540–670, 490–630 and 410–510 nanometres respectively). It has been found that wool colour can most easily be discriminated on the basis of just the Y value and the Y-Z difference, two parameters that are generally held to characterise lightness (or brightness) and yellowness (as compared with 'whiteness') respectively (Pattinson and Whiteley, 1984).

The CIE tristimulus colour space was initially standardised in 1931. It is based on human visual perception, and serves as the basis for a number of other colour measurement scales. Cruz et al. (2021) showed that using the alternative CIE L*, a* and b* colour space (CIE, 2019b) plus some other derivative parameters, values of L* and b* (which are themselves derivatives of the tristimulus values Y and Y-Z) are "*important traits that can be used as selection criteria*", and are sufficient to cover the colour space for alpacas. Measurement standard IWTO-56 has been chosen for this investigation because of its widespread use in raw wool and other animal fibre trading and its highly-standardised procedures – in particular, the measurement of loose fibre requires specific preparation procedures before confinement behind glass with calibrated spectral performance. It specifies a level of care and attention to detail, without which, lightness or brightness in particular is difficult to measure reproducibly between different laboratories. It should be noted that as an accredited laboratory, SGS Wool Testing Services is required to participate in routine interlaboratory trials that monitor and verify the precision and accuracy of their results. Whilst colour measurement of fleece samples is not specifically covered in their accreditation schedule, the measurement systems and instruments were the same as are used for certification services.

The aim of this work is to explore the range of colours that alpaca fibre could exhibit. From this perspective, the measurements on each sample have been treated as an individual observations, even though up to 3 measurements may have been made on successive fleeces from the same animal at different shearings. The measurements thus include variance from a number of sources – not just between animals, but between samples and between growth seasons.

In the analyses that follow, averages, and where there were sufficient sample numbers in each group, standard deviations, have been calculated for the colorimetry results within specific groupings – whether by AOA colour categories, or in the case of the genetic data, by ASIP and Mc1R alleles and their interactions. In determining whether the means for individual groups are statistically similar to those of other groups, the 95 % confidence limits for each group mean have been calculated – thus, group means for which the confidence limits overlap were considered not significantly different at the 0.05 (p-value) level. Chi-squared testing on the cross-tabulation shown in Table 3 was undertaken using Unistat v10 (Unistat, 2022)

3. Results

3.1. Colour group summaries

Bearing in mind the points covered in the introduction, the results are shown in terms of yellowness (Y-Z) versus brightness (Y), and in this way they can also be compared with measurements on other fibres. Table 1 summarises the group means for MFD, coefficient of variation of diameter (CVD), staple length (SL), mean fibre curvature (Curve), medullation (Med) on the lighter tints, and Y-Z and Y values for each colour group.

Fig. 1 shows the yellowness versus brightness relationship for the full range of measurements across the 14 subjective colour codes represented in this set of 2088 samples.

Table 1 shows that the group averages were comparable for the physical characteristics of diameter, diameter distribution, staple length and mean fibre curvature. Table 1 and Fig. 1 illustrate a very wide range of individual yellowness and brightness values and considerable overlap between similar colour codes. The curvilinear relationship between Y-Z and Y is not unexpected because whichever colour scale is chosen, human colour perception is fundamentally non-linear, and consequently there are non-linear relationships between the coordinates. (Judd and Wyszecki, 1975). It would at first appear that there is so much overlap between the subjective colour codes that objective measurements simply could not replicate these. However, if we look at the centroids of the Y-Z versus Y plots for each subjective code, some order does become apparent. This is shown in Fig. 2.

Table 1
Means of MFD, CVD, SL, mean curvature, Y and Y-Z values (with standard deviations - SD) in each colour code. Medullation averages are shown only for colour groups where at least 90 % of the samples were measured and which complied with the colour restrictions in IWTO-57.

Code	AOA colour	samples	Proportion	MFD µm	CVD %	SL mm	Curve °/mm	Med %	Y avg.	SD (Y)	Y-Z avg.	SD (Y-Z)
100	White	1141	55 %	19.7	21.1	115	51	7.5	74.6	4.1	7.3	1.1
201	Beige	213	10 %	19.7	21.1	118	50	7.9	72.4	5.7	7.4	1.3
202	Light Fawn	56	3 %	19.7	21.4	112	51	8.8	53.3	19.8	7.8	1.2
204	Medium Fawn	130	6 %	19.7	22.2	113	51	-	16.9	6.8	6.3	1.4
205	Dark Fawn	124	6 %	19.7	22.6	109	51	-	11.2	5.0	4.8	1.6
209	Light Brown	130	6 %	20.4	22.4	114	50	-	7.6	3.8	3.5	1.5
301	Medium Brown	167	8 %	20.3	22.7	112	50	-	3.9	3.0	1.8	1.4
410	Dark Brown	60	3 %	20.7	22.6	108	49	-	1.7	2.0	0.5	1.2
360	Bay Black	12	0.6 %	20.8	22.8	111	47	-	0.0	0.6	−0.7	0.5
500	True Black	29	1.4 %	20.2	22.3	119	47	-	−0.7	0.3	−1.3	0.1
408	Light Rose Grey	4	0.2 %	20.2	23.4	120	50	-	21.4	4.4	7.1	1.5
211	Medium Rose Grey	8	0.4 %	19.3	22.1	114	52	-	10.1	10.4	2.5	2.3
306	Dark Rose Grey	6	0.3 %	20.8	22.7	94	52	-	2.2	2.2	−0.2	1.3
404	Dark Silver Grey	8	0.4 %	22.7	21.8	103	49	-	0.4	0.9	−1.0	0.3

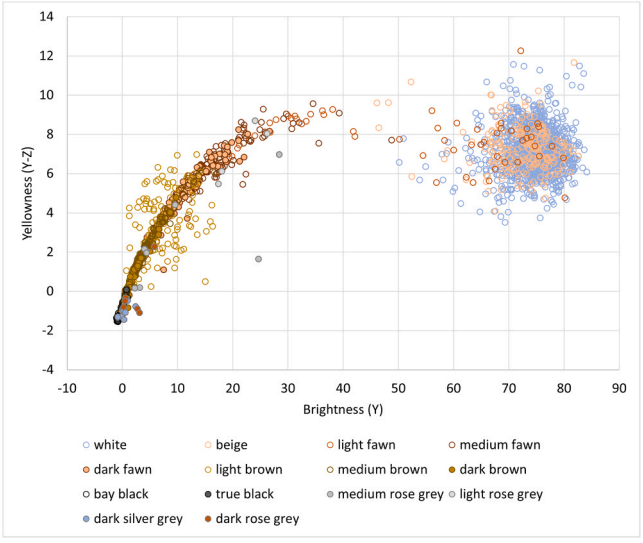

Fig. 1. Yellowness plotted against brightness (D65/10) for all colour codes.

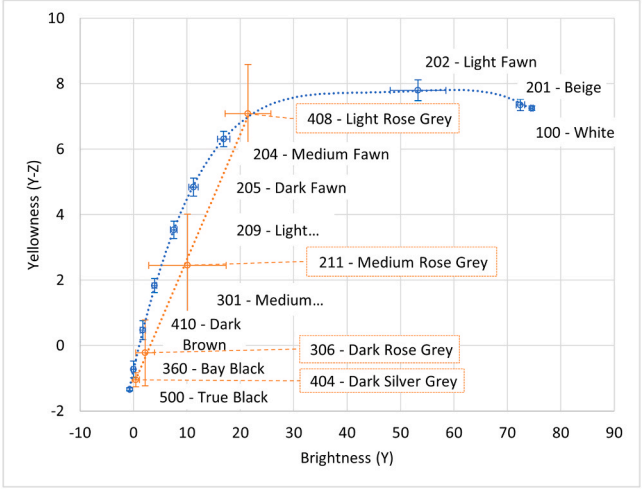

Fig. 2. Centroids of yellowness versus brightness for each of the 14 individual subjective colour codes in the data. The bars represent the 95 % confidence limits on the mean of each group, and the dotted lines show two regression curves: a linear regression for the "greys" and a 4th power quadratic for the remaining 10 codes.

Fig. 2 shows that the subjective colour codes do follow logical objectively-measurable progression from light to dark shades. Because not all colour codes are equally-represented in this dataset, the uncertainties on the centroid locations vary in magnitude, with the greys having the largest uncertainties simply because there were only small numbers of samples in these groups. Apart from the greys, few of the confidence limits around the centroids for each colour code overlap to any great extent.

3.2. *Measured colour versus genotypes*

Natural colour in animal fibres that are used for textiles occurs because of variations in melanin content. There are two types of melanin involved: eumelanin (EM) which is largely responsible for degrees of blackness, and pheomelanin (PM) which produces colours in the yellow to red part of the spectrum. In alpacas, phenotypic base coat colour appears to be primarily the result of the interaction between two genes, the melanoncortin-1 receptor gene (Mc1R), loss of function mutations in which result in predominantly pheomelanin production, and the agouti signaling protein gene (ASIP), loss of function mutations in which result increased production of eumelanin. Various combinations of ASIP and Mc1R genotypes result in a range of base coat colour phenotypes (Gray et al., 2023). In alpacas, much of the variation in base coat colour observed is due to varying amounts of EM, and the levels of PM are generally very low (Fan et al., 2010).

The alleles with which we are primarily concerned are:Mc1R: The 'EE' genotype allows for the expression of the ASIP genotype, while the "Ee" and "ee" genotypes result in reduced EM production and lighter coat colours than would otherwise be dictated by the ASIP genotype. ASIP: The "Aa" and "aa" genotypes result in greater production of EM than is produced by the "AA" genotype, holding the Mc1R genotype constant. There are three different "a" alleles: 'a1' results in the greatest increase in EM production, 'a2' the second largest increase, and 'a3' the lowest increase of the three gene variants.

The average brightness and yellowness for the animals with each combination of the Mc1R and ASIP genotypes, for the 832 animals for which data were available, are shown in Table 2, together with the number of animals in each combination. Fig. 3 summarises the yellowness versus brightness relationship for the major combinations that contain sufficient numbers of results for the averages to be meaningful.

For completeness, Table 3 shows the number of animals within each genotype for each of the AOA phenotypes. Because this is an observational study of a commercial herd at the times of sampling, the distribution within the phenoptype/genotype matrix is not well-balanced statistically, and the selection of animals was certainly not random, which imposes some limitations on the interpretation of statistical testing. Nevertheless, the Pearson Chi-Squared test shows a right tail

Table 2
Averages of Brightness Y and Yellowness Y-Z with standard deviations in parentheses (except when only one observation) for each combination of alleles of Mc1R and ASIP genes. Superscripts of the same letter show Y averages that are not significantly different from each other at the 0.05 significance level.

ASIP	Mc1R:	EE (n = 95)		Ee (n = 226)		ee (n = 511)	
	(n)	Y (sd)	Y-Z (sd)	Y (sd)	Y-Z (sd)	Y (sd)	Y-Z (sd)
AA		4.4 (3.2)[d]	2.1 (1.6)	14.1 (7.0)[b]	5.5 (1.9)	74.6 (5.5)[a]	7.0 (1.3)
	460	(n = 35)		(n = 85)		(n = 340)	
Aa		2.4	1.1				
	1	(n = 1)					
Aa1		2.6 (2.5)[d]	1.1 (1.6)	7.9 (4.7)[c]	3.5 (1.8)	73.3 (5.3)[a]	7.0 (1.5)
	80	(n = 3)		(n = 25)		(n = 52)	
Aa2		2.4 (2.2)[d]	0.8 (1.1)	9.6 (5.6)[c]	4.1 (2.0)	73.3 (5.5)[a]	7.2 (1.2)
	85	(n = 7)		(n = 28)		(n = 50)	
Aa3		3.1 (2.5)	1.3 (1.4)	9.0 (4.4)[c]	4.0 (1.6)	72.8 (6.0)[a]	6.8 (1.3)
	129	(n = 28)		(n = 44)		(n = 57)	
Total (Aa)		*2.9 (2.4)[d]*	*1.2 (1.3)*	*8.9 (4.8)[c]*	*3.9 (1.7)*	*73.8 (5.7)[a]*	*7.0 (1.3)*
	295	*(n = 39)*		*(n = 97)*		*(n = 159)*	
a1a1		−0.9	−1.4	−0.8 (0.4)	−1.3 (0.1)	54.5	6.9
	4	(n = 1)		(n = 2)		(n = 1)	
a1a2		−0.3 (0.4)[e]	−1.2 (0.1)	0.4 (1.6)[e]	−0.5 (1.1)	18.6 (9.6)	6.8 (1.5)
	11	(n = 3)		(n = 6)		(n = 2)	
a1a3		0.3 (0.8)[e]	−0.6 (0.5)	1.8 (3.8)[e]	0.2 (2.1)	44.6 (21.6)[f]	7.7 (1.4)
	18	(n = 4)		(n = 9)		(n = 5)	
a2a2		−0.8 (0.1)[e]	−1.5 (0.1)				
	2	(n = 2)					
a2a3		1.4 (1.7)[e]	0.1 (1.5)	1.8 (3.0)[e]	0.3 (1.7)	39.2 (9.1)[f]	9.2 (0.4)
	18	(n = 2)		(n = 13)		(n = 3)	
a3a3		0.9 (1.3)[e]	−0.6 (0.8)	3.2 (7.2)[e]	0.0 (0.9)	57.1	8.3
	19	(n = 8)		(n = 10)		(n = 1)	
aa		−0.5	−1.5	5.8 (5.9)[e]	2.2 (2.8)		
	5	(n = 1)		(n = 4)			
Total (aa)		*0.4 (1.2)[e]*	*−0.7 (0.8)*	*1.8 (4.5)[e]*	*0.0 (1.5)*	*40.8 (18.2)[f]*	*7.9 (1.3)*
	77	*(n = 21)*		*(n = 44)*		*(n = 12)*	

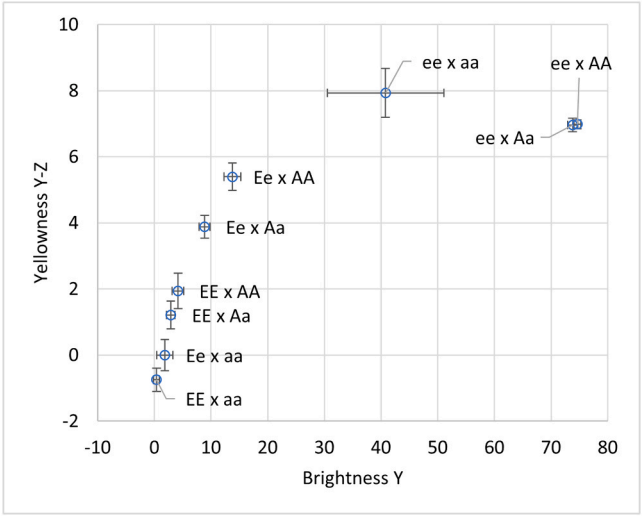

Fig. 3. Group means of Yellowness (Y-Z) versus Brightness (Y), with 95 % confidence limits on the means shown as error bars, for the major Mc1R and ASIP allele groups. Error bars that overlap indicate group means that are not significantly different from each other at the 0.05 level.

probability of <<0.001, indicating some degree of association between the phenotype categories and the genotypes, with a Spearman Rank Correlation of 0.22 (confidence interval 0.14–0.31).

3.3. Comparison of white/beige with other natural fibres

Because of the relatively poor standardisation of colour measurement for raw natural fibres other than wool, it has not been possible to provide "all colours" comparisons for other materials. However, we focus on the commercially more important white and beige alpaca colour codes. In the current work there was considerable overlap and no statistically significant difference between the Y-Z versus Y relationship for these two groups, which is consistent with the hypothesis that most whites are extremely dilute fawns (Munyard, 2011). In an analysis of variance and covariance, from all the variables known or measured, only MFD and sex showed a statistically-significant effect on Y-Z for the white+beige group. It has been possible to extract data from SGS Wool Testing Services archives, and some of the published literature on colour measurements for notionally-white fibres, that were sufficiently detailed to allow conversion of the results to the CIE D65/10, 45/0 measurement regime. These were: fine and coarse wools (Baxter and Wear, 2021); and some limited numbers of samples of cashmere (Baxter, 1998; McGregor and Tucker, 2010); mohair (McGregor, 2012; McGregor and Stapleton, 2016); and cotton (Jahagirdar et al., 2002; Khan, 2017).

Data for fine and coarse wools was originally reported in the C/2w coordinates that are used in the New Zealand wool industry, but the original measurements were made in D65/10 and there are appropriate formulae within IWTO-56 to allow conversion. The critical aspects of instrumentation and other measurement characteristics remained the same so the comparisons are directly valid, although it should be noted that the results shown are for sale lots, not individual animal fleece samples. In the case of the cashmere measurements, which were carried out over 2 decades ago, even though the instrumentation was of an earlier generation, the reporting coordinates were still C/2w and the IWTO-56 conversions could be used – it should be noted that these measurements were made "as-is", i.e. without re-scouring, so there is a possibility that the reported Y values could be slightly lower in comparison with the other animal fibre results. However, these data are consistent with results reported by McGregor and Tucker (2010) (after digitizing Fig. 1 in their paper and using 'clean cashmere weight' as the linking variable, and converting from presumed C/2 to D65/10 co-ordinates); and also the averages and ranges shown in Table 1 of McGregor (2015).

In the case of the mohair measurements, whilst they were reported (perhaps incorrectly) as being measured against IWTO E-14, which was

Table 3
Distribution of the number of animals across the principal genotypes for each AOA phenotype.

Code	AOA colour	EE AA	EE Aa	EE aa	Ee AA	Ee Aa	Ee aa	ee AA	ee Aa	ee aa
100	White							283	131	
201	Beige							51	28	3
202	Light Fawn				4	1		6		5
204	Medium Fawn	2	2		30	12				3
205	Dark Fawn	3	2		23	34	1			1
209	Light Brown	8	7		17	21	3			
301	Medium Brown	20	15	2	10	22	8			
410	Dark Brown	3	9	6	1	4	6			
360	Bay Black		2	1			5			
500	True Black	1		7	1		8			
408	Light Rose Grey				2					
211	Med. Rose Grey				1	3	2			
306	Dark Rose Grey		1	2			4			
404	Dark Silver Grey			2			3			

an earlier draft version of IWTO-56, review of the reported information and data indicates that in all probability they were measured in compliance with IWTO-56, and reported in D65/10 coordinates. Two sets of data for this comparison were extracted by digitizing plots of Y versus MFD and Y-Z versus MFD in Figs. 2 and 4 of McGregor and Stapleton (2016) and Fig. 1 of McGregor (2012), and then matching the Y and Y-Z results using MFD as the independent linking variable in each case. These data were for main lines and sale lots containing low medullation, and for selected white fleece samples respectively.

Whilst there are a number of publications covering the measurement of colour on cotton, they generally reference the proprietary measurement units of Reflectance (Rd) and Yellowness (+b) reported by the High Volume Instrument (HVI) commonly used for objective classing (Matusiak and Walawska, 2010). Because of the way the samples are measured by this instrument (Rodgers et al., 2008), and the limited amount of published data, we have found difficulty in translating the few published measurements into an equivalent coordinate space to that used in IWTO-56. Nevertheless, we have been able to extract data from two papers in which modern spectrophotometers and CIE coordinates were used (Duckett et al., 1999; Khan, 2017), and these are shown in Fig. 9 below. Since the test procedures used would almost certainly not have complied with IWTO-56, these results are for information only, and the results will be discussed below.

Apart from the results on cotton, mean fibre diameter measurements (MFD) were also available on the comparison samples, and since there seemed to be a weak but statistically-significant correlation between Y-Z and MFD on the white+beige sub-set of the alpaca samples, this relationship was also able to be explored for the other animal fibres. The relationships are shown in Figs. 4 through 8, where the same scales have been used to allow easy comparison. Fig. 9

4. Discussion

To our knowledge there has only been one previously-published detailed quantification of colorimetry for a full range of Huacaya alpaca colours, and it is therefore instructive to compare our results with those of Cruz et al. (2021). [Whilst Lupton et al. (2006) provided averages on 5 colour groups for US alpacas, it is unclear which calibration was used, and they mixed coordinate systems, which makes comparison difficult. Bartolomé et al. (2009) focussed on predicting subjectively-assessed colours from objectively-measured colour, but did not provide any measurement data.] There are clear similarities between our Fig. 1 and Fig. 1 from the Cruz et al. paper – there is a wide range of results with a significant amount of scatter, the general trend is curvilinear, and there is much overlap even though they only used 9 colour codes. The results shown in their paper are reported in CIE L*a*b*, and although their Fig. 1 is actually a plot of two principal components, these were fundamentally driven by brightness and yellowness. Using Table 2 of their paper, and converting to the D65/10 coordinate system, we can replot their data in the same format as our Fig. 2, as shown following in Fig. 10.

Comparing Figs. 2 and 10, it can be seen that in both cases the relationships between the objectively-measured and subjectively-assessed colour groups are logical and progressive. Comparing the two regression relationships is instructive:

Cruz et al.: Y-Z = -0.000002 Y^4 + 0.0003 Y^3 – 0.025 Y^2 + 0.84 Y – 2.02 R^2 = 0.9998

This paper: Y-Z = -0.000002 Y^4 + 0.0003 Y^3 – 0.023 Y^2 + 0.72 Y – 0.73 R^2 = 0.9998

Both fits are remarkable in terms of amount of variance explained, as indicated by R^2, and the first 3 regression coefficients are almost identical, with only the constant and slope coefficients being slightly different. This suggests that fundamentally the relatively minor

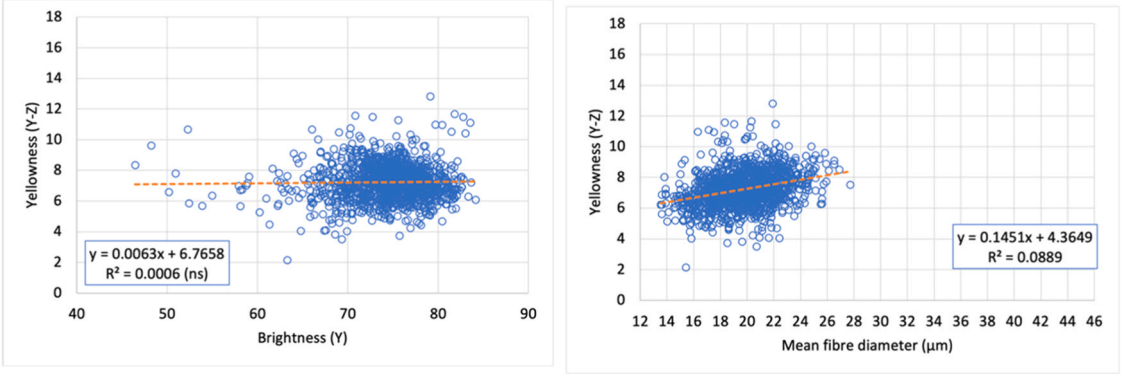

Fig. 4. a) Yellowness versus brightness and b) Yellowness versus MFD for white and beige alpaca samples.

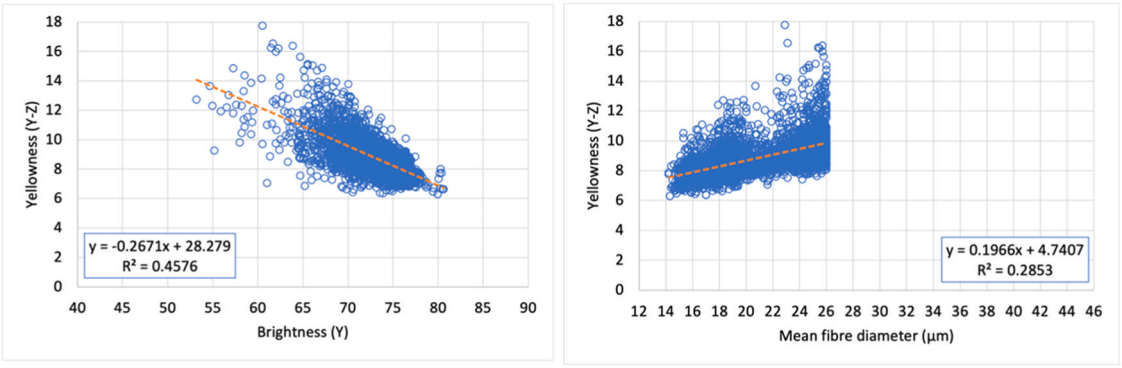

Fig. 5. a) Yellowness versus brightness and b) Yellowness versus MFD for New Zealand fine wool (mainly merino) samples (SGS archives – the sharp cutoff at 26 microns was used to separate fine from crossbred wools).

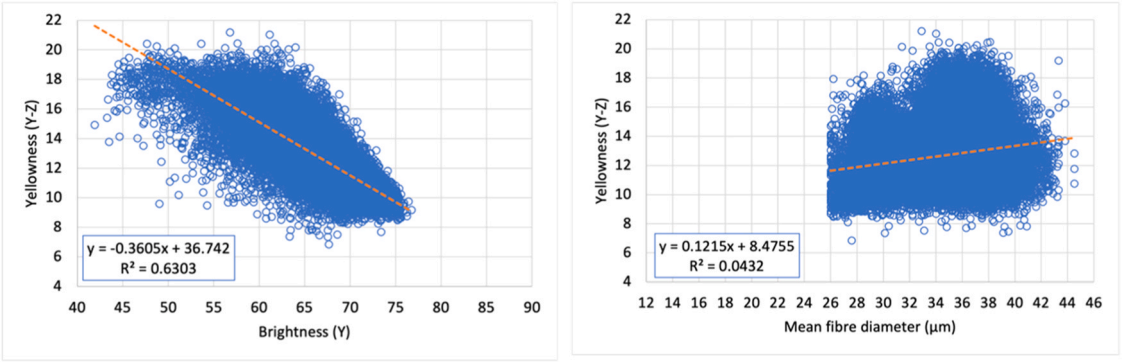

Fig. 6. a) Yellowness versus brightness and b) Yellowness versus MFD for New Zealand crossbred wool samples (data extracted from Baxter and Wear (2021) dataset and converted to D65/10 – the sharp cutoff at 26 microns was used to separate crossbred from fine wool samples). (Note that the Y-Z scale has been shifted compared with Figs. 4, 5 and 7 - 9.).

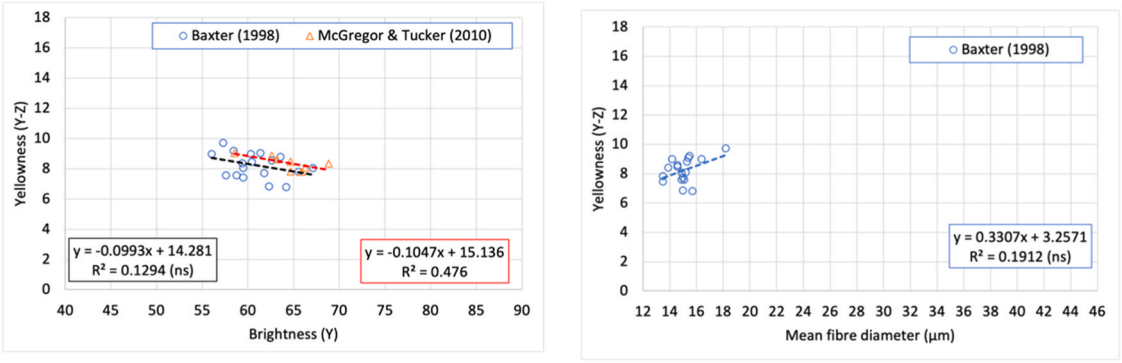

Fig. 7. a) Yellowness versus brightness and b) Yellowness versus MFD for a range of natural cashmere samples (data extracted from Baxter (1998) and McGregor and Tucker (2010), converted to D65/10).

differences between the plots are probably due to measurement procedures or calibration (or both). The most significant difference is in the placing of the centroid of the white group, for which the Cruz et al. results show this group be apparently less yellow than the results in this paper. As noted below, our results are, however, more consistent with third-party data on other natural fibres.

The second issue of interest in this consideration of the full range of colours is the observation by Cruz et al. that their 'grey' group did not fit the pattern of the other colours, which they surmised as being possibly due to a different genetic control mechanism, as suggested by Jones et al. (2019). Munyard (2011) suggested that grey is actually a pattern, not a colour, perhaps controlled by a single incompletely dominant gene. Our results show that the 4 grey groups fit a completely different colorimetric relationship to the other groups, lending further credence to this hypothesis. The "greys" for which we have colour test results are all considered roans (Voss et al., 2022), with coats that are a mix of either black and white fibers (the "silver" roans) or some shade of brown and white (the "rose" roans). In 2023 AOA stopped referring to these animals as 'grey' and now uses the term 'roan' in a way that is consistent with its use in other species.

Fig. 1 clearly confirms the conclusions of Cruz et al. (2021) and Bartolomé et al. (2009) that predicting subjective colour codes from objective measurements may not be reliable except, perhaps, for white/beige and black – there is too much overlap between similar codes. Both of these authors recommended use of a smaller number of subjective colours than currently listed by AOA. We cannot comment on

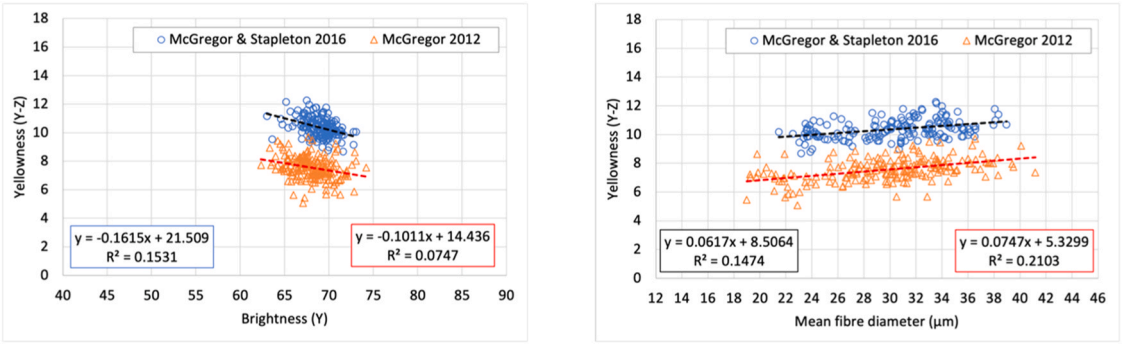

Fig. 8. a) Yellowness versus brightness and b) Yellowness versus MFD for a range of Australian white mohair samples – upper plots: sale lot data extracted from McGregor and Stapleton (2016), lower plots: fleece sample data extracted from McGregor (2012).

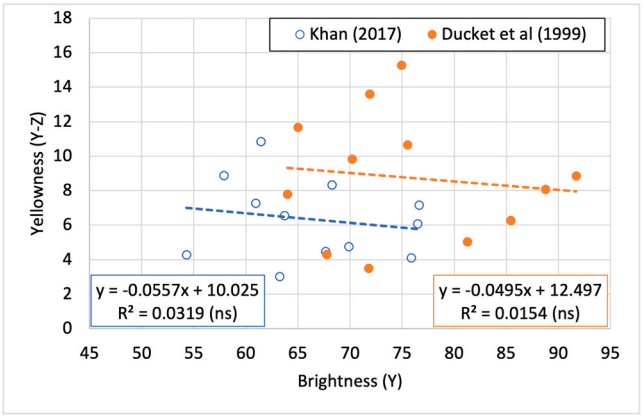

Fig. 9. Yellowness versus brightness for standard cotton samples. Data were extracted from Table 1 of Duckett et al. (1999), converted to D65/10; and Table 4 of Khan (2017). (Note that the brightness scales have been right-shifted compared with Figs. 4 to 8).

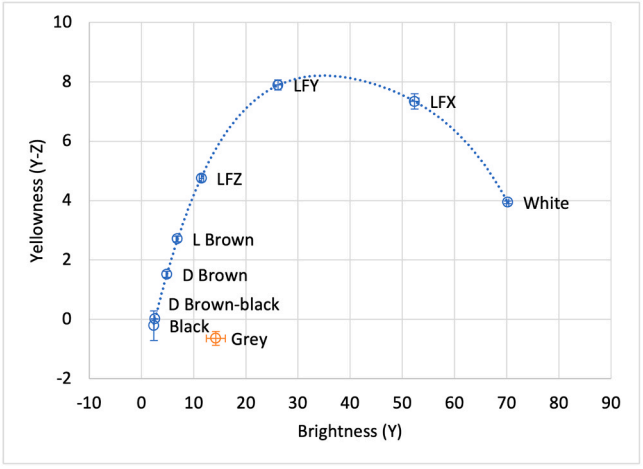

Fig. 10. Centroids of yellowness versus brightness for each of the 9 individual subjective colour codes in the Cruz et al. (2021) data on Peruvian Huacaya alpacas, after conversion from L*a*b* to D65/10 coordinates. The bars represent estimates of the 95 % confidence limits on the mean of each group, and the dotted lines shows a 4th power quadratic for the remaining 8 codes after excluding "grey".

whether the problem is primarily due to the difficulties of assigning colours subjectively, a factor clearly identified in the wool industry (Thompson and Whiteley, 1986; Thompson, 1987), the cotton industry (Duckett et al., 1999; Matusiak and Walawska, 2010; Khan et al., 2016), and in alpaca breeding (Feeley et al., 2011), or whether there is some other aspect of alpaca fibre colour that cannot easily be measured objectively (Fan et al., 2010; Feeley et al., 2011; Munyard, 2011; Gray et al., 2023). It is noted, however, that alpaca colour codes are usually assigned at birth, and may sometimes subsequently be considered erroneous, but are seldom changed. In this project, a handful of animals have been re-assigned (to adjacent codes) after careful consideration of the colorimetry data and examination of later-age photographs of the animals and their fleeces.

4.1. Colour genotypes

It should be noted that because the US has a closed alpaca registry, it is considered important to minimise the loss of genetic diversity, which is done by targeting a coefficient of inbreeding (CoI) of between 3 % and 3.5 % in the annual cria groups in this herd. The stud produces approximately 2/3 white crias, the remaining 1/3 are coloured (see Table 1 for the proportions applicable during this investigation), and tries to produce animals that are homozygous in parts of the genotype that influence key fibre traits. These factors clearly act as constraints on some of the conclusions that can be drawn from an observational study of this type.

However, Tables 2 and 3 probably summarise the largest colour Mc1R and ASIP genotype database for North American Huacaya alpacas published to date. Statistics that can be easily summarised are: all animals that were subjectively categorised as White - 100 were genotyped as 'AA ee' (68 %) or 'Aa ee' (32 %). Beige - 201 comprised 62 % 'AA ee', 34 % 'Aa ee' and 4 % 'aa ee'. At the other extreme, True Black – 500 comprised only 17 animals that were genotyped as 53 % 'aa Ee' and 47 % 'aa EE'. For this herd, white and beige phenotypes were largely (96 %) genotyped as 'AA ee' or 'Aa ee'. The 3 variants of the 'a' allele do not seem to have any obvious effect on the brightness and whiteness of this combined phenotype. However, if we break the data down to the colour groups with adequate numbers of members for statistically-significant comparison, there are some subtle differences at the 0.05 level of significance, as can be seen in Fig. 11.

Fig. 11 shows that there was no significant difference in the average yellowness values between the 4 white and 1 beige groups shown. However, there were some statistically different mean brightness values between 'ee AA' and 'ee Aa1' white on the one hand, and the almost identical 'ee Aa3' white and 'ee AA' beige colorimetric centroids on the other, with the averages of the latter two groups being over 2 tristimulus units less bright than the former. Whilst the 'ee Aa2' white brightness confidence limits overlapped the 'ee AA', 'ee Aa1' and 'ee Aa3' white means, there was an apparent sequence of diminishing brightness from the 'AA' and 'Aa1' group, to the 'Aa2' group and then to the 'Aa3' group. However, it should be stressed that this apparent trend was not significant at the 0.05 level.

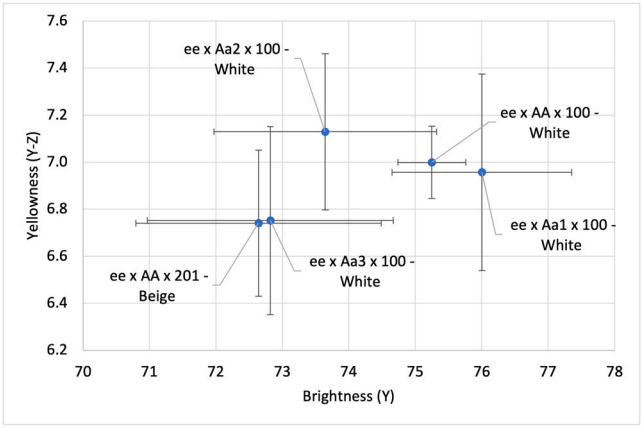

Fig. 11. Group means of Yellowness (Y-Z) versus Brightness (Y), with 95 % confidence limits on the means shown as error bars, for the major (n > 43) Mc1R and ASIP allele groups for White-100 and Beige-201 AOA colour groups. Error bars that overlap indicate group means that are not significantly different from each other at the 0.05 significance level.

We are reminded that the 'a2' and 'a3' alleles both represent change to a single nucleotide, and of those two the 'a2' mutation increases eumelanin production more than does the 'a3', which is the "least black" of the three black mutations (Feeley et al., 2011). If any black allele was going to show up as making the whites and beiges look less bright, logically it should be the 'a1' allele since that should have the greatest impact on pigment production. However, the 'a' alleles are not randomly distributed through the population. The animals that carry each black allele type are on average more closely related to others that carry that allele type than they are to the rest of the group. Thus, we cannot assume that all other factors are constant in these animal genotypes in this herd, and the group of animals carrying 'a1' alleles will have different ancestry concentrations in their pedigrees than the groups carrying 'a2' and 'a3' alleles. Other genetic differences affecting phenotypic brightness and yellowness may be travelling with these alleles and obscuring the expected trend.

The lower half of Table 3 shows a similar lack of differentiation by subjective colour group as was seen in Table 1 and Fig. 1. The limited number of results available for the darker fleeces did not appear to be inconsistent with the results of Pallotti et al. (2020) with respect to black and brown coat colours in Peruvian alpacas, although in this work, perhaps due to the larger sample size (83 "brown" compared with 17), or diverging genetics, it was observed that approximately 40 % of the medium and dark brown phenotypes were heterozygous compared with 100 % reported in that paper.

There is commercial interest in breeding for alpacas that produce black fibre that does not require dying. However, this has been difficult to date, in part because breeders have historically lacked a way to describe the depth of black colour, and have not been rewarded for achieving it. Because there were only 17 animals from a single breeding operation with the True Black phenotype in this dataset, it was not feasible to draw any definative conclusions with respect to the depth of black colour that is either typical of, or possible to achieve, in alpaca fleece. This work suggests that a combination of colorimetry and genotyping data across larger sample groups of black alpacas should provide useful guidance.

When we are dealing with small numbers of measurements in any one group, it should be noted that one limiting factor with colorimetry is the precision of measurement. Whilst this has been well documented for the use of test method IWTO-56 on core samples taken from sale lots of wool, there is no published information on the measurement on small fleece samples – in this respect there are several extra sources of variance at play – within-fleece sample, between-fleece samples, between animals, plus the within- and between-laboratory components of variance, and these are expected to increase the total uncertainty on an individual test result. As an example, IWTO-56 indicates 95 % confidence limits of ± 3.1 units for Y and ± 0.9 units for Y-Z, but this is for cored samples from sale lots of several bales of wool, and was determined on samples with Y values over 40 and Y-Z values perhaps up to 14. We have been able to review repeat measurements on individual alpacas taken over 3 seasons, and find that the residual variance changes in a heteroscedastic manner across the range of colours. Our approximate estimates of 95 % confidence limits range from ± 1–4 units in Y (from black to white) and ± 0.3–1.2 units in Y-Z (over the range from 0 to 9 units). These estimates, however, include year to year variances, and are therefore on the high side. From this preliminary data we can nevertheless estimate that we'd need to average results from up to 25 samples in order to be able to distinguish between group means of 0.3–1.1 units apart in Y, and 0.1–0.3 units difference in Y-Z (over the full range of alpaca colours). Nevertheless, it should be clear from the data presented above that colorimetry is a useful and relatively inexpensive tool to assist in breeding decisions.

4.2. *Comparisons with other fibres*

The two most obvious observations from Figs. 4 to 9 are that yellowness (in the D65/10 space) appears to vary with brightness in fine and crossbred wool, and in cashmere and mohair, but not in alpaca. With the limited amount of data available for cotton, no conclusions can be drawn in this respect. The data also shows that yellowness appears to increase with mean fibre diameter for alpaca and fine and crossbred wool, and less so for mohair. Even though a similar trend is shown for cashmere, probably because of the paucity of data, the regression slope was not significantly different to zero at the 0.05 level.

Focussing on the white/beige colour group and comparisons with other fibres, it is notable that amongst the animal fibres compared here, only the alpaca samples appeared to show no relationship between yellowness and brightness. Whilst the regression for one set of data on cashmere is statistically not significant at the 0.05 level, it does, nevertheless, follow a similar trend to the other set, and the trends seen in the relationships for fine and coarse wool and for mohair, all of which show yellowness decreasing with brightness to a greater or lesser extent, with crossbred wool showing the largest slope. There is not enough data to confirm whether there is any level-dependent effect for cotton, but the two sets of data shown here in Fig. 9 suggest not, or, if there is any effect, the slope is very small.

Why should alpacas be apparently different to sheep and goats in terms of the relationship between yellowness and brightness? Most authors agree that alpacas with homozygous dilution alleles 'e' in Mc1R will most probably be phenotypically white or beige (Feeley and Munyard, 2009; Munyard, 2011; Chandramohan et al., 2015; Gray et al., 2023), which implies that the level of EM will be low and the colour will be determined by the level of PM. Interestingly, and perhaps similarly, a complete loss of function of the Mc1R gene has been associated with the 901 T allele (associated with 'e') in Arabian dromedaries (Almathen et al., 2018). However, importantly, Fan et al. (2010) showed that in alpacas the levels of PM remained very low irrespective of the phenotypic colour, which was primarily influenced by the levels of EM.

This appears to be different to what has been observed in sheep, where although the same two genes are active, the implementation is different - Aliev et al. (1990) found that for Asiatic sheep, whilst EM rose significantly in level from white through to black, and PM was also seen to rise in white through brown phenotypes. Sponenberg et al. (1988) had earlier indicated that whilst mohair goats had higher levels of EM and PM than white sheep, they expected sheep and goats to have similar mechanisms controlling colour phenotypes. Hoekstra (2006) suggested that, apart from Mc1R and ASIP, several other genes could play a part in controlling the density and distribution of melanosomes, even within species and in selective environments. Våge et al. (2003) highlight that the Mc1R gene has 3 alleles in sheep: E^{+}, E^{D}, and e. Several authors

highlight the fact that the full white phenotype is dominant over brown or black in merino sheep, that the Agouti locus is responsible for the PM levels in modern sheep breeds (with A^{wt} being a dominant allele), and importantly, there is a 190 kb tandem duplication in the ASIP gene in some breeds (Norris and Whan, 2008; Renieri et al., 2008; Fontanesi et al., 2010; Hepp et al., 2016; Kalds et al., 2022). Henkel et al. (2019) indicated that A^{wt} is also responsible for white in goats, and in some breeds the ASIP gene is triplicated. Zhang et al. (2023) and Gratten et al. (2007), Rochus et al. (2014), amongst others, confirmed that in some sheep breeds, especially those that have been less domesticated (Gratten et al., 2010; Cavalcanti et al., 2017; Stamatis et al., 2017), several other genes may be involved. They also noted that environment and diet also affect the coat colour – a fact well known by sheep breeders, e.g. Neimaur et al., 2022. Azam et al. (2024), referring to cashmere goats, found the highest nucleotide diversity was found in white phenotypes, and commented that genetic diversity measures are breed- or population-specific and can differ significantly from population to population, even within the same breed, due to selection practices and breeding methods. Ganbold et al. (2019) indicated that in Mongolian cashmere goats, whilst mutations in Mc1R may play a crucial role in regulating EM and PM phenotypes, the mechanisms are far from clear.

In summary, there is ample evidence to suggest that the genetics of colour for sheep and goats may be more complicated than for alpacas (and perhaps other camelids), and, critically, the levels of PM appear to be higher in these species and under more variable control. This hypothesis may at least partially account for the differences observed in the yellowness/brightness relationships.

In terms of whiteness (i.e. the lack of yellowness), the data presented here suggests that for these samples, raw alpaca fibre may be on par with cotton, close to results for the finest mohair, and only the very brightest (and finest) of the fine wools. The Y-Z values for crossbred wools, and on the limited number of cashmere samples, were higher on average than for alpaca. The lack of level-dependency with brightness for the alpaca samples should provide an advantage compared with the other samples of animal fibres shown here. The paucity of comparable data on cotton requires further work. The two sets of data on mohair are approximately 2 units different on Y-Z – this might be due to the fact that one set of measurements came from sale lots, which would be blends of fleeces from several animals (as with the results for wool shown here, but with the difference that wool sale lots have the advantage of being selected from much higher volumes of much more similar fleeces, and thus are likely more uniform than most mohair sale lots). The other mohair data set was from selected midside samples from individual white fleeces – which would be comparable to the type of sampling carried out on the alpacas.

In terms of brightness, the range of alpaca Y values appears similar to that of fine wools, with the results on some samples exceeding the highest fine wool Y values. Given the uncertainty about the method equivalence for the cotton measurements, it's not possible to draw any definitive conclusions, but in general terms the brightest alpaca sample Y values seem similar to the brightest cotton values based on the limited number of cotton results. The results on crossbred wool, and the small numbers of results on cashmere and those on mohair show lower brightness values.

It is important to recognise that the relatively low yellowness (or high whiteness) of the alpaca samples, across a wide range of brightness values, provides a potential commercial benefit, since it allows the production of white or pale-dyed fabrics requiring less chemical processing than for other animal fibres. With the generally low grease levels found in the raw fibre (Hunter, 2012), white/beige and true black colours would not only require less chemical inputs in scouring, but should require less or no bleaching and cleaner or no dying, and could thus be considered relatively eco-friendly.

4.3. Colour and diameter

The other important parameter to take into account is MFD. Figs. 4–8 show that the results on alpaca, fine and crossbred wool, and mohair, each show a diameter-dependent effect on Y-Z. Although the linear regression for the small number of cashmere samples is not significant at the 0.05 level, it is probable, because of the physics (see below), that this fibre also has some MFD level-dependency. An interesting observation is that the slope of the linear regression appears different for each fibre. The regression for Y-Z versus MFD for NZ fine wools (which are mainly merinos) is very similar to that obtained by Wang and Mahar (2008) for Australian merinos averaged over 6 different periods (Y-Z = 4.2 + 0.21 MFD, R^2 = 0.23, compared with Y-Z = 4.7 + 0.20 MFD, R^2 = 0.29 shown in Fig. 5). Their regression for Australian crossbred wools also showed a lower slope than for merino, although the equation was not as similar (Y-Z = 5.4 + 0.15 MFD, R^2 = 0.12, compared with Y-Z = 8.5 + 0.12 MFD, R^2 = 0.04 shown in Fig. 6) – this is probably due to the fact that Australian crossbreds cover a much narrower range of diameters (and breeds) than NZ crossbreds. They noted that the diameter effect varied from season to season.

The physics of colour dependency of fibres on MFD was examined by Wang et al. (2011). Nominally white (unmedullated) animal fibres, when seen under a microscope, are essentially transparent. The appearance of white is due to the multiple scattering taking place when the fibres are assembled en mass – this is somewhat similar to the bright white appearance of transparent glass when it is broken into small fragments. In their paper they used unpigmented polypropylene (PP) to show that the spectral intensity of the reflectance varied significantly and in a linear manner with the diameter of the PP fibres, and this diameter-dependent aspect could be used to correct for MFD, so that the different diameters then gave virtually the same (fairly uniform) spectral intensity curve. A similar technique was then applied to merino wool samples, such that the diameter-dependence could also be removed, and it became clear that the largest differences were at the shorter wavelengths (mainly in the blue region, which determines the Z values) – and hence the primary effect is observed on Y-Z. The authors hypothesized that: "*It may be the existence of scales on the surface of the wool fibres which is fundamentally responsible for the different reflectance of wool fibres in this region of the spectrum. The frequency and morphological structure of the scales may change light scattering behaviour preferentially across the wavelength range, with more effect in the lower wavelength area.*" They did not, however, discuss the possibility of the chromophore concentration being regulated by changing fibre growth rates (which would presumably show effects for both MFD as well as fibre length (Edens, 2017)).

If their hypothesis were correct, then it would make sense for different animal fibres to show different diameter-dependence of Y-Z, given that they each have slightly different scale topologies. However, the literature does not evidence consistent coverage of scale morphologies or topologies. There seems to be reasonable agreement on scale thicknesses: approximately 0.3–0.4 microns for alpaca, mohair and cashmere (Phan et al., 1987; Wortmann and Wortman, 1991; Liu et al., 2004; Valbonesi et al., 2010; McGregor and Quispe Peña, 2017), and approximately 0.8 microns for wool. For context, the wavelength of yellow light (approximately corresponding to tristimulus Y-Z) is approximately 0.57–0.6 microns. By comparison, reported results for scale frequency vary widely, from 5 to 8 per 100 microns for wool (Langley and Kennedy, 1981; Liu et al., 2004; Pikhtirova and Ivchenco, 2018), approximately 7 per 100 microns for cashmere and mohair, and 9–10 per 100 microns for alpaca (Langley and Kennedy, 1981; Phan et al., 1987; Liu et al., 2004; Valbonesi et al., 2010; McGregor and Quispe Peña, 2017). It is also worth noting that McGregor and Liu (2017) found that for cashmere goats, scale frequency varied significantly with both MFD and nutrition, and whilst there is plenty of evidence linking nutrition to fibre growth rate for other ruminants (Reis and Sahlu, 1994), the effects on scale frequency do not yet seem to have been explored. Although incidental to the purpose of his study, Sumner

(2009) demonstrated good correlation between staple growth rate and scale length and scale height (r = 0.76 and 0.65 respectively) over 6 different wool breeds, but the correlations could have been due to factors other than nutrition. It seems clear that there is potentially significant variability in the statistics of scale morphologies, and much more work would be needed before this hypothesis could be advanced.

For the available data on cotton, there was no correlation between Y-Z and the micronaire values for the samples detailed in the references. No published data was found to otherwise assess whether there would be a fineness-dependent effect with cotton, but this fibre in its mature form firstly has no scales, and secondly has a ribbon-like rather than a cylindrical morphology, and MFD may not be an appropriate indicator for fibre thickness, which in cotton is normally measured in terms of fineness and maturity ratio (Ramey, 1982). The light-scattering from cotton fibres would thus not necessarily follow the relationship described above for cylindrical artificial or animal fibres.

The principal point from these data is that, similar to other animal fibres, the lower Y-Z values (or better whiteness) are exhibited by the samples with the lower MFD values.

5. Conclusions

This work has demonstrated that subjective colour assessments of Huacaya alpacas bred in the USA follow a logical progression in yellowness and brightness when measured objectively. Relatively inexpensive colorimetry, carried out to published standards, has been shown to be reliable and could be of assistance not only in making breeding decisions, where it is more likely to provide unambiguous phenotype to genotype mapping, but also to processors in assembling consistent batches of fibre of similar colour.

We confirmed that virtually all white and beige phenotypes in this herd have homozygous Mc1R 'ee' genotypes with either 'AA' (68 %) or 'Aa' (32 %) ASIP genotypes. At the other end of the colour scale, the True Black phenotype was found in animals with homozygous 'aa' ASIP genotypes with either 'EE' or 'Ee' Mc1R genotypes in approximately even proportions, although not all animals with those genotypes had true black base coats.

In common with other animal fibres, the measurements showed a positive correlation between yellowness and mean fibre diameter. However, compared with some other natural fibres, white alpaca showed no level-dependency of whiteness with brightness. It is suggested that this may be the result of the different genetics of sheep and goats on the one hand, and alpacas on the other.

CRediT authorship contribution statement

B. Peter Baxter: Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lynn Edens:** Writing – review & editing, Resources, Data curation, Conceptualization. **Jeremy L. Wear:** Writing – review & editing, Resources, Methodology, Data curation, Conceptualization.

Declaration of Competing Interest

BPB & JLW are consultant and employee respectively of SGS New Zealand Ltd, and LE is a partner in Snowmass Alpacas LLC, but the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgements

Thanks to Allan deBoos, Vicky Fish & David Crowe for supplying copies of some of the references. Ioasa Kosena was responsible for optimising the laboratory processes for colour measurement on small fleece samples. We are also grateful for helpful comments of two anonymous reviewers.

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