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Heritability of individual fiber medullation in Peruvian alpacas

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ARTICLE INFO

Keywords:

Alpaca
Genetic parameters
Medullated fiber
Prickle factor

ABSTRACT

The aim of this research was to estimate for the first time the heritability and genetic relationship between medullation and fiber diameter in each fiber by itself. A total of 21,600 fibers from 36 samples from white fleeces, 600 fibers each sample, from males between 0.4 and 10.4 years old from Pacamarca experimental farm (Inca Group, Puno, Peru) were tested using projection microscope (PM). The individual fiber diameter (FD) and the category of medullation (CM) was recorded in each fiber. CM of each fiber was assigned to one of the five categories established in the literature. The percentage of medullated fiber ranged from 12.33% to 91.67% per sample. The correlation between OFDA 100[®] medullation percentage and PM measurements was 0.79. The statistical model used for estimation of genetic parameters for CM and FD included the age as a linear and quadratic covariate as systematic effect, and the additive genetic and the permanent environmental as random effects. The pedigree that served to predict genetic values was very robust and strong, allowing obtaining reliable and significant parameters. Univariate and bivariate models were used to estimate heritability for CM and DF, as well as its genetic correlation. Different models considering CM as continuous or categorical trait were tested. The highest heritability estimate for CM was 0.36 ± 0.13 obtained using a bivariate continuous model. Using the same model, the heritability estimate for FD was 0.35 ± 0.15 and the genetic correlation between CM and FD was 0.93 ± 0.12 . These results implied that selection against medullated fiber is feasible while at the same time reducing the FD in alpacas. Since measurement of CM per fiber sample was time-consuming, PM measured by OFDA 100[®] would be useful as an indicator to reduce the number of medullated fiber in alpaca fleeces.

1. Introduction

Alpaca fiber quality is worldwide considered among the best for the textile industry. However its price is still far from other fine animal fibers like cashmere. The main argued reason is the prickle factor associated to alpaca fiber. Big efforts have been made in order to remove this particular issue. Thus, prickling has been linked to fiber diameter, particularly to fibers thicker than 30 μm , and consequently comfort factor has been defined as the percentage of fibers lower than that value (McGregor, 1997; Frank et al., 2006), as an interesting trait to work with. In order to remove prickle factor, selection has been carried out based on the reduction of fiber diameter as selection criterion in Pacamarca experimental farm (Gutiérrez et al., 2011), and a fast reduction has been achieved (Gutiérrez et al., 2014), but prickle factor has not completely been removed. The medullated fiber and type of medullation has alternatively been blamed as responsible for prickle factor (Frank et al., 2014; Frank et al., 2017; McGregor, 1997). They called

them objectionable fiber, appearing to have opacity greater than 94% and a diameter greater than 25 μm (IWTO, 1998). If selection objective in fiber has been traditionally the thinness of the fiber and prickle factor still remains, an alternative would be to move the selection criterion from fiber diameter to fiber medullation to reduce prickle factor. A strong genetic relationship between medullation and thickness seems to exist but it would have to be studied individually in each fiber; working with global parameters as mean fiber diameter and medullation percentage might hide information. Before implementing selection based on medullation, that relationship would have to be firstly carefully studied as it would imply important changes, and the first step is to know how heritable individual medullation would be, as well as the genetic relationship between diameter and medullation within each fiber. Such genetic parameters have never been previously estimated in alpacas. Thus, the objective of this study was to estimate genetic parameters of individual fiber medullation in alpacas, as well as to explore its relationship with fineness in each fiber itself, and the

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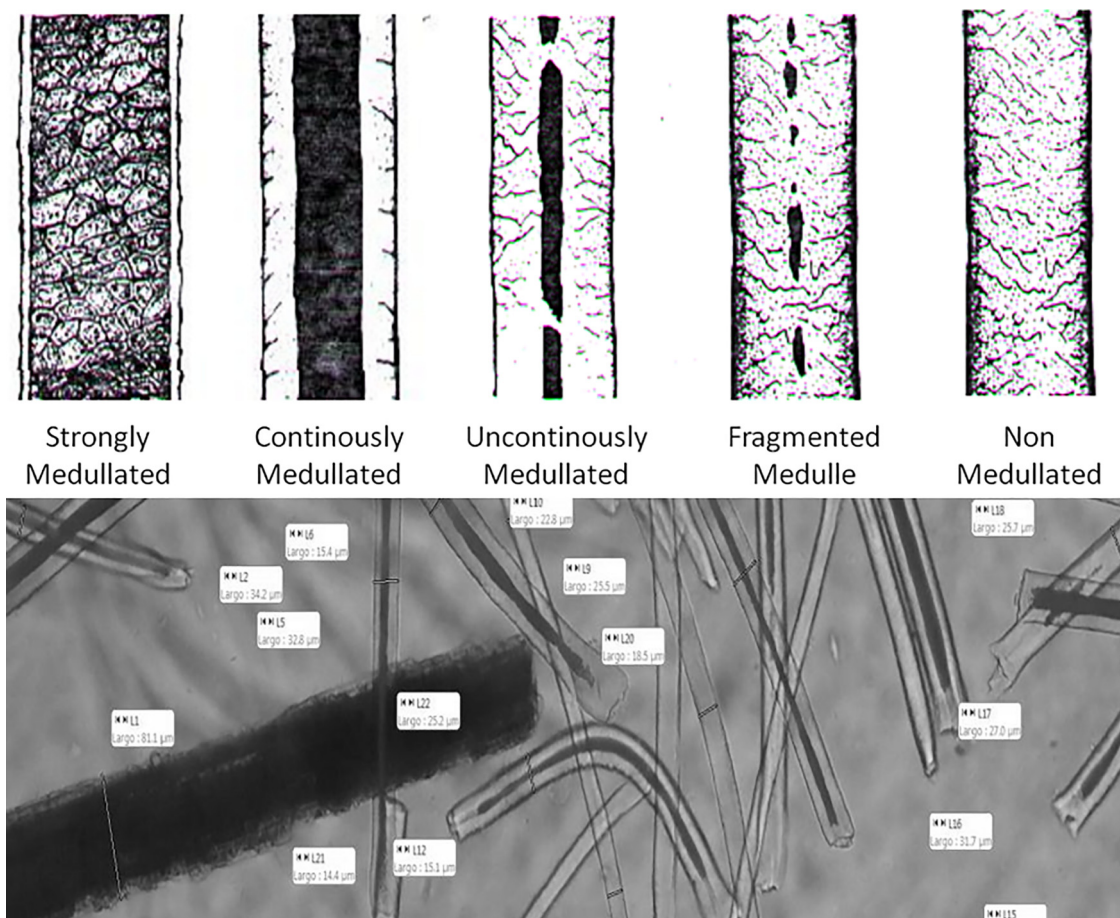


Fig. 1. Categorization of the fibers according to the type of medulla and a picture sample under projection microscope gathering all different categories.

possible ways to model the medullation classification to predict breeding values useful in selection of animals.

2. Material and Methods

A total of 21,600 fibers from 36 samples of white fleeces, 600 fibers each sample, from white Huacaya males between 0.4 and 10.4 years old from Pacamarca experimental farm (Inca Group, Puno, Peru) were analyzed. The fiber samples were prepared and analyzed according to IWTO-8-2011 (IWTO, 2011) procedure at the Universidad Nacional Agraria La Molina (Lima, Perú).

Each individual fiber was considered as one record. Note that this consideration provides 600 records per sample, and the resulting trait differs from the usual trait called fiber medullation which simply addresses, in a unique figure, the percentage of medullation in a sample. Thus, for each of the 36 samples, 600 fibers were randomly chosen and each classified according to their medullation category using microscope projection (Frank et al., 2007; Villarroel, 1963) in to: non medullated, fragmented, uncontinuously medullated, continuously medullated, and strongly medullated (Fig. 1). Fiber diameter was determined for each fiber computing later the mean, the standard deviation and the comfort factor as the percentage of fibers lower than 30 µm. Each sample took about one and a half effective working day to be processed, and the analysis required trained staff.

Pacomarca has simultaneously started to register the percentage of medullation by using an OFDA 100 ° device (Lupton and Pfeiffer, 1998). This device counts total medullated fibers as described in the IWTO-57-98 (IWTO, 1998). The calibration of the OFDA device was certified by the official service called Inter wool labs. The OFDA records were used to correlate with those from PM belonged to the same 36

samples of the analysis, except one that was accidentally lost. On the other hand, as detailed below, in order to correlate breeding values from different models with a reference value, the 1478 samples registered during 2016 in the Pacamarca experimental farm were also used to estimate environmental effects from a fixed model and to deregress those 36 that were finally used as reference. The fiber measurements from PM, with the age of animals and medullation distribution of each of the 36 samples are shown in Table 1, jointly with the percentage of medullation assessed by OFDA 100 ° device. As the influence of animal age on diameter fiber is a well known phenomenon (Gutiérrez et al., 2011) and its influence is also clear on medullation (McGregor, 2006), age of registered animals is also shown in Table 1.

Pedigree of the recorded individuals was tracked back to the founders to complete a pedigree of 121 individuals, with 100% of the parents known as well as 71% of the grandparents, 20% of the great grandparents and less than 1% of the great great grandparents identified. Numerator relationship matrix, computed using Endog v4.8 software (Gutiérrez and Goyache, 2005) showed a strong connectedness between animals as shown in Fig. 3. Despite only the group of males was taken, there was a strong genetic connection among them, justifying their representativeness in the whole population. On the other hand, even when the number of animals is scarce, the high number of records helped to obtain reliable estimates. The final reliability of these analyses can fortunately be known; using the Bayesian approach in the present study helps to properly quantify the levels of uncertainty, once convergence was proofed.

Category and diameter of each fiber were modeled to estimate variance components. Fiber medullation as described here is a categorical trait. Thus, threshold models are indicated to perform the estimation of genetic parameters for this trait (Gianola and Foulley, 1983;

Table 1

Mean fiber diameter, standard deviations, comfort factor and medullation category by the projection microscope device for 600 fibers for sample and percentage of medullation assessed by the OFDA 100[®] belonging to white Huacaya males.

Projection Microscope									OFDA 100 PM (%)
Age (years)	MFD (μm)	SD (μm)	Comfort Factor (%)	N (%)	F (%)	D (%)	C (%)	S (%)	
1.4	16.7	4.3	99.2	87.7	10.0	1.2	1.2	0.0	2.1
5.7	20.7	5.0	96.2	45.2	38.8	10.2	5.7	0.2	8.5
1.6	21.8	5.0	95.2	36.7	48.0	5.3	10.0	0.0	–
2.4	21.1	5.4	94.5	73.3	16.5	3.2	7.0	0.0	4.3
2.6	16.4	4.3	99.2	48.5	34.3	5.8	11.3	0.0	17.3
1.4	21.8	4.7	94.0	50.2	34.2	4.0	11.3	0.3	7.0
1.4	16.8	5.0	98.3	49.2	26.2	12.3	12.3	0.0	5.5
5.5	18.3	4.6	98.7	30.7	51.5	5.2	12.7	0.0	7.3
3.6	16.4	4.8	99.3	46.5	35.0	5.5	13.0	0.0	6.6
2.6	17.4	5.2	97.8	48.5	27.3	10.0	14.2	0.0	7.3
5.5	26.5	5.2	78.2	16.2	21.0	44.5	18.3	0.0	23.8
4.4	20.4	6.2	93.3	48.0	19.0	14.3	18.7	0.0	7.4
2.4	20.9	5.1	94.5	48.0	16.7	16.2	19.2	0.0	15.2
6.4	24.7	6.2	84.2	41.2	15.2	23.7	19.3	0.7	19.0
2.4	20.4	5.4	95.7	33.3	31.2	15.7	19.8	0.0	7.2
1.5	20.8	5.6	93.7	47.3	24.0	8.7	20.0	0.0	10.9
1.4	24.0	5.3	91.0	22.3	49.5	7.7	20.2	0.3	9.2
6.5	26.5	6.4	74.8	12.7	45.7	20.0	21.7	0.0	13.2
2.6	20.2	4.4	98.2	22.5	49.0	6.2	22.3	0.0	28.6
5.5	28.2	6.8	65.7	30.2	28.0	18.5	22.8	0.5	27.6
2.6	22.3	6.9	88.0	42.2	19.5	13.3	24.7	0.3	36.7
9.5	24.1	5.5	87.0	23.8	40.0	10.5	25.7	0.0	13.4
0.5	21.4	5.3	94.5	41.0	22.8	9.5	26.7	0.0	15.2
0.5	21.8	5.1	97.2	33.5	29.8	8.5	27.7	0.5	19.3
7.3	27.6	6.8	73.7	15.8	27.0	27.3	28.0	1.8	32.8
1.5	19.8	5.3	97.2	23.2	37.3	9.5	30.0	0.0	14.1
0.4	22.4	3.9	96.7	15.7	21.7	32.3	30.3	0.0	27.1
7.6	22.7	5.5	92.2	14.3	21.5	31.7	31.3	1.2	17.4
3.6	24.3	6.7	80.5	16.0	27.2	24.0	32.0	0.8	14.3
3.4	25.7	4.7	83.3	16.7	11.5	37.3	33.8	0.7	11.0
1.4	20.7	6.4	93.7	19.8	36.5	7.7	35.7	0.3	23.2
2.4	21.1	5.2	95.2	30.5	17.8	14.7	36.8	0.2	30.1
10.4	26.4	6.3	79.3	8.3	42.8	10.2	38.7	0.0	39.2
9.2	27.5	7.7	67.0	9.5	40.3	9.0	40.8	0.3	24.8
6.8	26.0	6.7	73.8	9.2	25.7	12.8	51.7	0.7	30.3
0.4	23.3	4.9	93.7	14.7	11.8	8.0	65.5	0.0	65.3
Mean	22.1	5.5	89.8	32.6	29.3	14.0	23.9	0.2	18.3

N = not medullated; F = fragmented; D = discontinuous; C = continuous; S = strongly medullated, MFD = mean fiber diameter; SD = standard deviation of fiber diameter, OFDA = optical fiber diameter analyzer, PM = percentage of medullation.

Weller and Gianola, 1989). However linear models have been proven to perform better than threshold models when databases are small (Goyache et al., 2003; Cervantes et al., 2010a, Ibáñez et al., 2014). As it is not initially clear the best way to analyze the medullation trait, in this study, genetic parameters were estimated using both linear and threshold procedures applied to linear mixed models (Altarriba et al., 1998). In addition, sometimes is difficult to define the number of thresholds (Gianola, 1982). Then, also several different ways to consider the categories were studied. According to all this, several possibilities were assessed. Regarding the number of categories:

C5, Five different categories from 1 to 5: 1: non medullated, 2: fragmented, 3: uncontinuously medullated, 4: continuously medullated, and 5: strongly medullated.

C4, Four categories from 1 to 4: 1: non medullated, 2: fragmented, 3: uncontinuously medullated, 4: grouping continuously and strongly medullated.

C2A, Two categories: 1: grouping on one hand, non medullated, fragmented and uncontinuously medullated, 2: grouping on the other hand, continuously and strongly medullated.

C2B, Two categories: 1: non medullated and 2: grouping all the other categories.

The four ways of classifying were analyzed using two different methodologies:

Continuous linear (L) model assuming that the analyzed trait was a continuous variable, and Threshold (T) model, also called probit

(Gianola, 1982; Gianola and Foulley, 1983; Sorensen and Gianola, 2002) that theoretically would better fit the discrete probabilistic nature of the data.

Finally, all combinations were also tested by using a univariate model and a bivariate model combining fiber diameter and medullation. Thus, 16 different estimations of variance components for medullation were carried out.

The linear model equation was:

$$y = Xb + Zu + Wp + e$$

$$\text{with } \text{Var} \begin{bmatrix} u \\ p \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G_0 & 0 & 0 \\ 0 & I_p \otimes P_0 & 0 \\ 0 & 0 & I_e \otimes R_0 \end{bmatrix},$$

where, y is the vector of observations (the individual medullation category or the individual fiber diameter), b is the vector of systematic effects, u is the vector representing the additive genetic effects, p corresponds to the vector of permanent environments of individuals, e is the vector of residuals, X , Z , and P are the incidence matrices for respectively systematic, additive genetic and environmental permanent effects, I_e the identity matrix of order equal to 21,600, the number of records, I_p the identity matrix of order equal to 36, the number of permanent environmental subclasses, A the numerator relationship matrix, R_0 the residual covariance matrix among measurements on the same animal, G_0 the covariance matrix for additive genetic effects, P_0

the covariance matrix for permanent environmental effects and \otimes the Kronecker product. When only medulla score was analyzed under a univariate model, R_0 , G_0 and P_0 became respectively the residual variance σ_e^2 , the additive genetic variance σ_a^2 and the permanent environmental variance σ_{ep}^2 .

Threshold equation model was identical, but in this case y vector represents an underlying variable called liability which explains the corresponding visible category defined by specific values called thresholds (Gianola, 1982). The analysis were carried out with TM software (Legarra et al., 2011). One million of iterations were performed for each model with a burning period of 100000 and with a thin interval of 100. The number of records was big enough, 21600 records, but the number of animals was not, 121. This low number, in addition to the discrete nature of the trait, could lead to difficulties in the estimation process. Thus, convergence was checked to ensure the reliability of the estimates and it was found to be reasonably good for parameters regarding medullation trait. The sound convergence and the relatively not too high standard deviations of the marginal posterior distributions of the parameters allows considering reliable the estimates found, even in this scenario of limited information.

In order to have a reference value to check the breeding values obtained from different models, the 1478 OFDA records belonging to all the recorded animals were used under a fixed model fitted to estimate the age as linear and quadratic covariate, and month, sex and color as systematic effects influencing the percentage of medullation. Note that there were all color and sex classes among all the records taken at the farm, even when only those from 36 animals were involved in the computed correlations. Solutions for this model were used to deregress the percentage of medullation records, and those of the 36 animals involved in this analysis were used as a reference to check the consistency of the breeding values obtained using the 16 essayed models.

Predicted breeding values and heritability estimates were used to discuss the goodness of the models to explain the trait.

3. Results

Variance components estimates for medulla category using several different models combining univariate or bivariate models with fiber diameter, threshold or continuous linear models, and different grouping of medulla categories are shown in Table 2, jointly with the respective standard deviations of their marginal posterior distributions. Heritability estimates for medulla trait ranged from 0.23 to 0.36 in linear models, and from 0.11 to 0.15 in threshold models. All the heritability estimates for medullation can be considered significant according to the magnitude of the standard deviation of their marginal posterior distributions, showing that the amount of information used was sufficient to provide significant estimates. Global average distribution of medullation categories is shown in Fig. 2. There were 21 out of 36 individuals not carrying strongly medullated fibers (coarser category), and those having some, had a maximum of 1.81%. Given the infrequent appearance of strongly medullated fiber, independent classification (C5 models) or inclusion with continuous medullated fiber (C4 models) did not substantially modify the resulting estimates.

Under continuous linear models, the reduction of the number of categories from 4 (or 5) to 2 resulted in a significant increase of the heritability of the medullation trait, going from 0.23 (C4) to 0.35 (C2B) in the univariate model or 0.23-0.36 in the bivariate model, when one of the categories was non-medullated fiber. Also, when all non continuous medullated fiber categories were merged to one group, the heritability estimate was 0.30 (C2A) in both univariate and bivariate models. Heritability for the other studied trait, the individual fiber diameter, was of similar magnitude across models, but less accurate. This trait was only included to try to benefit from adding its information to estimate the parameters of medullation trait, but its heritability can be considered minimally relevant to the focus of this research. Therefore, the joint analysis with fiber diameter did not greatly

Table 2 Variance components estimates \pm standard deviations of their marginal posterior distributions for medulla category using several models: univariate (Uni) or bivariate (Bi) models with individual fiber diameter, under linear (L) or threshold (T) models, considering five categories (C5), four (C4) or two grouping the first categories in the first level (C2A) or all except the first one in the last one (C2B).

Model	Medullation Category					Fiber Diameter					
	σ_a^2	σ_{ep}^2	h^2	c^2	t	r_g	σ_a^2	σ_{ep}^2	h^2	c^2	t
Uni; L; C5	0.41 \pm 0.16	0.14 \pm 0.12	0.24 \pm 0.08	0.08 \pm 0.07	0.32 \pm 0.06	-	-	-	-	-	-
Uni; L; C4	0.25 \pm 0.10	0.09 \pm 0.08	0.23 \pm 0.08	0.08 \pm 0.07	0.31 \pm 0.06	-	-	-	-	-	-
Uni; L; C2A	0.09 \pm 0.04	0.05 \pm 0.04	0.30 \pm 0.12	0.15 \pm 0.11	0.45 \pm 0.06	-	-	-	-	-	-
Uni; L; C2B	0.14 \pm 0.07	0.07 \pm 0.05	0.35 \pm 0.13	0.17 \pm 0.12	0.52 \pm 0.06	-	-	-	-	-	-
Bi; L; C5	0.42 \pm 0.19	0.24 \pm 0.16	0.23 \pm 0.08	0.13 \pm 0.08	0.36 \pm 0.06	0.88 \pm 0.15	20.67 \pm 12.60	20.64 \pm 11.44	0.28 \pm 0.14	0.29 \pm 0.14	0.57 \pm 0.07
Bi; L; C4	0.43 \pm 0.24	0.24 \pm 0.16	0.23 \pm 0.08	0.13 \pm 0.08	0.36 \pm 0.06	0.89 \pm 0.14	21.08 \pm 12.71	20.61 \pm 12.07	0.29 \pm 0.15	0.28 \pm 0.14	0.57 \pm 0.07
Bi; L; C2A	0.10 \pm 0.05	0.07 \pm 0.04	0.30 \pm 0.12	0.20 \pm 0.11	0.50 \pm 0.07	0.91 \pm 0.13	25.58 \pm 14.14	17.07 \pm 11.63	0.34 \pm 0.15	0.23 \pm 0.15	0.58 \pm 0.07
Bi; L; C2B	0.16 \pm 0.08	0.10 \pm 0.06	0.36 \pm 0.13	0.21 \pm 0.12	0.57 \pm 0.07	0.93 \pm 0.12	26.06 \pm 14.09	17.07 \pm 11.88	0.35 \pm 0.15	0.23 \pm 0.14	0.58 \pm 0.07
Uni; T; C5	0.27 \pm 0.12	0.12 \pm 0.10	0.15 \pm 0.06	0.06 \pm 0.05	0.21 \pm 0.05	-	-	-	-	-	-
Uni; T; C4	0.25 \pm 0.12	0.19 \pm 0.10	0.14 \pm 0.05	0.10 \pm 0.05	0.23 \pm 0.05	-	-	-	-	-	-
Uni; T; C2A	0.13 \pm 0.07	0.08 \pm 0.06	0.11 \pm 0.06	0.07 \pm 0.05	0.14 \pm 0.04	-	-	-	-	-	-
Uni; T; C2B	0.19 \pm 0.09	0.09 \pm 0.07	0.15 \pm 0.06	0.07 \pm 0.06	0.22 \pm 0.05	-	-	-	-	-	-
Bi; T; C5	0.28 \pm 0.13	0.18 \pm 0.11	0.14 \pm 0.06	0.09 \pm 0.05	0.23 \pm 0.05	0.60 \pm 0.36	24.58 \pm 14.03	15.01 \pm 11.85	0.34 \pm 0.16	0.21 \pm 0.15	0.55 \pm 0.07
Bi; T; C4	0.30 \pm 0.13	0.16 \pm 0.10	0.15 \pm 0.06	0.08 \pm 0.05	0.23 \pm 0.05	0.68 \pm 0.33	25.12 \pm 13.26	13.94 \pm 10.74	0.36 \pm 0.15	0.20 \pm 0.14	0.56 \pm 0.07
Bi; T; C2A	0.14 \pm 0.08	0.11 \pm 0.06	0.11 \pm 0.05	0.08 \pm 0.05	0.19 \pm 0.05	0.26 \pm 0.51	24.15 \pm 12.76	14.67 \pm 10.60	0.34 \pm 0.15	0.21 \pm 0.14	0.55 \pm 0.07
Bi; T; C2B	0.17 \pm 0.09	0.11 \pm 0.07	0.13 \pm 0.06	0.09 \pm 0.05	0.21 \pm 0.05	0.56 \pm 0.45	24.61 \pm 14.08	15.53 \pm 11.63	0.34 \pm 0.16	0.22 \pm 0.15	0.55 \pm 0.07

σ_a^2 = Additive genetic variance; σ_{ep}^2 = Permanent environmental variance; h^2 = Heritability; c^2 = Permanent environmental ratio over phenotypic variance; t = Repeatability; r_g = Additive genetic correlation.

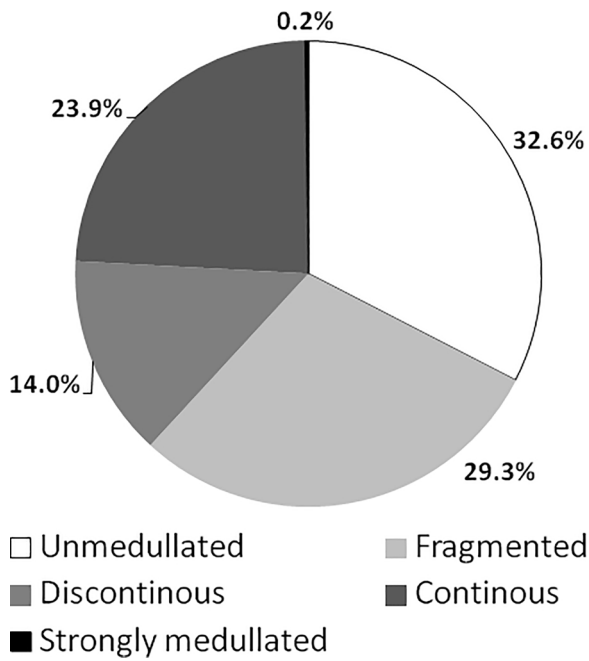


Fig. 2. Medulla categories distribution of samples belonging to 36 white alpaca Huacaya males.

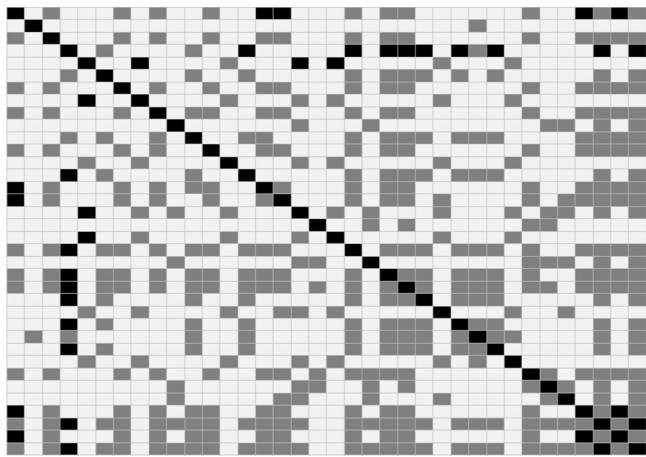


Fig. 3. Representation of relationship between 36 registered white alpaca Huacaya males. Relationship higher than 0.2 in black and higher than 0 in grey colors.

contribute to modify neither the estimates nor the accuracy of the medullation heritability, and it only increased the permanent environmental component in about 0.05 and consequently the repeatability of the medullation traits. Genetic correlation between medullation and fiber diameter was very high in the four continuous linear models, ranging from 0.88 to 0.93.

Heritability estimates from threshold models were lower with a high concordance between univariate and bivariate models. Reducing the number of medullation categories led to decreases in the heritability estimates unlike with continuous linear models. Also, repeatability estimates were much lower, ranging from 0.14 to 0.23, in clear contrast with 0.32–0.57 estimated by continuous linear models. Furthermore, this approach led to much lower estimates of genetic correlations of medullation with fiber diameter, being in addition less accurate as suggested by the standard deviations of their marginal posterior distributions.

Comparing those definitions of only two categories of medullation, the heritability estimates were always higher when non-medullated

Table 3 Correlation among predicted breeding values across models and with the deregressed (DeReg) percentage of medullation. univariate (Uni) or Bivariate (Bi) models with individual fiber diameter, under linear (L) or threshold (T) models, considering five categories (C5), four (C4) or two grouping the first categories in the first level (C2A) or all except the first one in the last one (C2B).

	Uni; L; C4	Uni; L; C5	Bi; L; C4	Bi; L; C5	Uni; T; C2A	Uni; T; C2B	Uni; T; C4	Uni; T; C5	Bi; T; C2A	Bi; T; C2B	Bi; T; C4	Bi; T; C5	DeReg
Uni; L; C5	0.946	0.938	0.979	0.978	0.937	0.948	0.800	0.475	0.726	0.862	0.882	0.862	0.518
Uni; L; C4		0.962	0.904	0.902	0.959	0.910	0.658	0.360	0.504	0.725	0.750	0.506	0.491
Uni; L; C2A			0.886	0.884	0.998	0.965	0.584	0.217	0.465	0.648	0.680	0.381	0.456
Uni; L; C2B			1.000	0.899	0.967	0.998	0.634	0.209	0.582	0.700	0.731	0.385	0.430
Bi; L; C5					0.880	0.893	0.858	0.567	0.781	0.890	0.899	0.694	0.528
Bi; L; C4					0.881	0.895	0.857	0.565	0.779	0.889	0.899	0.692	0.530
Bi; L; C2A						0.969	0.579	0.211	0.467	0.649	0.683	0.378	0.453
Bi; L; C2B							0.628	0.205	0.579	0.700	0.733	0.384	0.428
Uni; T; C5							0.977	0.865	0.958	0.989	0.979	0.934	0.515
Uni; T; C4								0.839	0.934	0.967	0.956	0.906	0.510
Uni; T; C2A									0.787	0.812	0.784	0.978	0.446
Uni; T; C2B										0.941	0.931	0.858	0.452
Bi; T; C5											0.997	0.905	0.526
Bi; T; C4												0.886	0.966
Bi; T; C2A													0.537
Bi; T; C2B													0.504
													0.489

fiber category was an independent group (C2B) than when continuously medullated fiber categories were an independent group (C2A). Therefore, the category (C2B) of medullation, which assumes in the same group all fibers with any degree of medullation, could be more suitable to be used in breeding programs.

To check the consistency of the predictions, the correlation coefficients among predicted breeding values across essayed models was computed, as well as with the deregressed percentage of medullation (Table 3). Consistency was very high within linear continuous models with correlations higher than 0.880 and not so much but also high within threshold models with correlations higher than 0.755. Consistency between models under different approaches was variable from 0.205 to 0.899 depending on how the categorization was defined in crossed comparisons. When comparisons involved bivariate models the correlations were higher. The correlations were low, from 0.205 to 0.694, when they involved grouping independently continuous medullated fibers (C2A). All the sixteen models had very similar correlations with deregressed percentage of medullation, from 0.428 to 0.537. This contrasts with phenotypic correlations. The correlations between percentage of medullation assessed from OFDA 100° and percentage of continuously medullated fibers from PM was 0.79, and the percentage of medullation of OFDA 100° with total medullation of projection microscope was 0.56. OFDA 100° does random punctual reads and does not differentiate the medullation type, but it seems to give figures more related to continuously medullated fibers than the total medullated fibers from the phenotypic point of view. However, from genetic correlations it looks that the different grades of medullation have a common genetic base.

Even though it is clear that a relationship between medullation and diameter exists, it is not so clear how this relationship operates. Fig. 4 shows several distributions of the medulla categorized fibers regarding diameter, explaining the genetic correlation obtained between medullation and thickness, and justifying the selection against fiber diameter in order to reduce the prickling. Fig. 4a shows the distribution of the different categories of medullation within diameter classes, computed from the 36 white Huacaya males of the study. Fig. 4b shows the

distribution of each category of medullation, 4c grouping all non continuous medullated fiber against continuous ones (as considered in C2A grouping), and 4d grouping all somehow medullated fiber against non medullated (as defined in C2B grouping). The threshold of 30 μm is also highlighted in the figure and also the usually defined as comfort and prickling areas are labeled as defined dependant of the 30 μm threshold. Fig. 4b shows the distributions of the different medulla categories regarding fiber diameter, non continuous medullated category appearing as a subset of the continuous medullated category, being fragmented group an intermediate between completely medullated and completely non medullated.

4. Discussion

Over the last years, research on alpaca breeding has been carried out at Pacamarca experimental farm. Some findings have led to some changes in the selection objective (Gutiérrez et al., 2014). Even though initially the textile value was the goal for Pacamarca (Morante et al., 2009), it was shown that the selection response for the goal would be higher if the criterion would focus on the mean fiber diameter of a staple (Gutiérrez et al., 2009). In addition, the selection objective was decided to incorporate traits for decreasing fiber diameter variability and the prickling factor in alpaca fleece, such as standard deviation or coefficient of variation of the fiber diameter. Later these traits were decided to be also combined with subjective morphological traits (Cervantes et al., 2010b). Existence of a major gene for fiber diameter was also reported in the population when searching for a faster response in reducing the diameter and its variability (Pérez-Cabal et al., 2010; Paredes et al., 2014). The Research on the farm evolved to the point of developing selection index to optimally combine several objectives (Gutiérrez et al., 2014), currently thinking about the possibility of adding reproduction (Cruz et al., 2015) and weight traits (Cruz et al., 2017b) to the index. Finally, in order to obtain a higher selection response, last research consisted of improving the accuracy of the estimation of genetic parameters and the prediction of the breeding values by better accounting the pregnant and milking states of the females

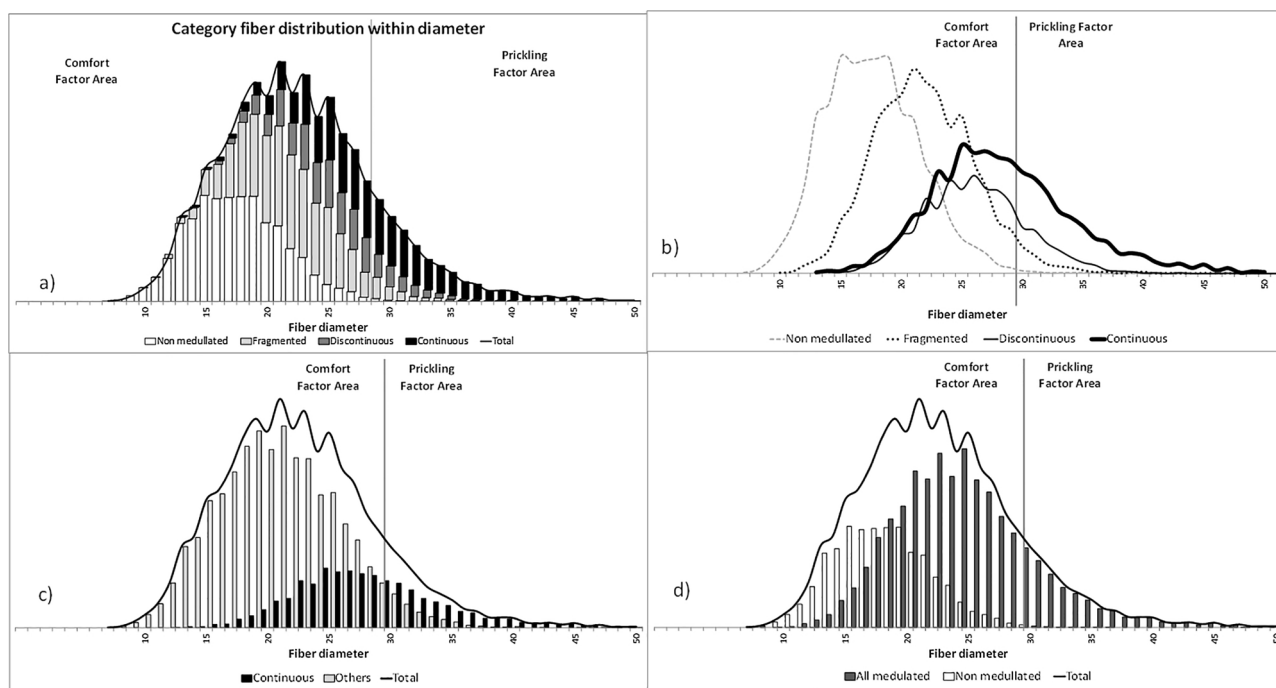


Fig. 4. Category fiber distribution within diameter classes (a), distributions of each category of medullation (b), distribution of non continuous medullated fiber against continuous ones (c) and distribution of non medullated fibers against somehow medullated ones (d), from 36 random white alpaca Huacaya males. Threshold of 30 μm is also highlighted.

(Cruz et al., 2017a).

As a result of these selection approaches, a favorable genetic response for fiber diameter was achieved, but little for prickling factor as correlated genetic response. Currently a big debate exists about the way to remove the prickling factor by selection (Frank et al., 2011; Sánchez et al., 2016), having evidence that fiber medullation (continuously and strongly medullation categories) is in fact, the responsible of this unpleasant issue (McGregor, 1997; Frank et al., 2014). Then, efforts focused on the diameter have become inefficient in the actual objective of removing the prickle factor.

Disentangling if thickness, medullation, or combinations of them are causing the prickling, would be essential. This research does not give a solution to that, but studying the different categories can contribute. Two Gaussian independent overlapped distributions can be identified in Fig. 4c and d, suggesting in both cases that they can be understood as independent traits. It can also be noted that, despite there is a clear relationship between medullation and thickness (Lupton et al., 1991; McGregor, 2006; McGregor et al., 2013), there are still medullated fibers even from 13 μm , and there are also non medullated fibers up to 46 μm . The latest pattern was also observed in Romney sheep (Scobie et al., 1993). Finer medullated fibers and coarse non medullated fibers can be produced by secondary follicles (Antonini et al., 2004).

As fiber diameter has not been shown to be useful regarding prickling, comfort factor, based on fiber diameter, would not then become an indicator of true comfort. Selection objective has been traditionally the thinness of the fiber, but an alternative selection objective would be removing the prickling factor. A selection criterion in this case could be the fiber medullation.

In this work, the heritability of medullation and fiber diameter has been assessed for individual fibers in a sample, unlike the usual way of recording mean values in a staple. A limitation of this research was the limited number of records for medullated fibers by PM. Collecting and using this type of information is cumbersome, which explains why information on these traits is scarce. Additionally, the required time to process each sample is very long; this analysis requires trained staff and takes a qualified technician about one day and a half per animal. Fortunately the strong genetic connectedness between animals has importantly contributed as shown by the relatively low standard deviation of the estimated parameters (Table 2) making these results reliable. On the other hand, OFDA 100° records have been taken as reference because up to date it can be widely recorded in the population.

Likewise, repeatability here has not been a parameter conceived temporarily as usual, but spatially, as it describes how the traits are repeated within the sample. Heritability was found to be medium, allowing being optimistic with respect to the success expected by artificial selection, if medullation would be used as a criterion for artificial selection. Similar heritability estimate was reported in Corriedale sheep, (0.37 ± 0.10) for presence/absence of medullated fiber (Sánchez et al., 2016). Also heritabilities were 0.23 ± 0.02 and 0.32 ± 0.02 for OFDA medullated content and OFDA kemp content, respectively in Angora goats (Allain and Roguet, 2006). Finally, a heritability of 0.29 ± 0.04 for total medullation grades has been reported by Frank et al. (2011) in llama fiber. However, this is the first time that any kind of medullation heritability has been estimated in alpacas, and the first time that individual fiber medullation has been reported in any species to our knowledge.

Comparing models is not straightforward because, primarily, it is unknown what would be the right way to select against prickle factor. Prickling is supposed to be due to the resistance of a fiber to be bended, and both thickness and medullation can contribute to that. In this study, the research focus is on medullation, but determining it, remains an open issue. In order to have a reference, medullation percentages as provided by the OFDA 100° device were used. First, fixed models were used to estimate some environmental effects, such as sex, color, month or age, and then the estimations were used to correct the performances for such environmental influences obtaining deregressed values. The

correlations between the deregressed values and the breeding values predicted under each model were computed to assess the prediction ability of each of them. Medullation percentage expresses an estimation of the percentage of medullated fibers in a staple, but the OFDA 100° automation cannot avoid a fiber being measured several times in different points and cannot distinguish if a punctual positive medullation score corresponds to a continuous, non continuous or fragmented medulla. From a different view, a quick view to Table 1 leads to think that OFDA 100° essentially measures percentage of continuously medullated fibers. For example, the average percentage of this group with projection microscope was 24%, higher than the mean OFDA 100° value, 18% (Table 1). Furthermore, the correlation between these two values computed with the 35 available samples was 0.79, decreasing to 0.56 when all type of medullated fiber were counted. In addition, this device is capable of providing the information relatively fast and it is potentially less expensive (Lupton and Pfeiffer, 1998). Thus, deregressed medullation percentage provided by OFDA 100° can be considered a useful reference.

Regarding heritability estimates, and assuming that higher heritability within linear or threshold approaches, can be understood as the trait having more genetic sense, the best way to codify the medullation was gathering all somehow medullated fibers in the same group (C2B). It was not clear what the best one under threshold models was, but it was always better C2B than C2A. Unfortunately OFDA medullation, a device allowing to record more animals in much less time, seems to be grouping more similar to C2A. As an approximate idea of how these discrepancies can affect the predicted breeding values when selecting via OFDA 100° records, the correlation between OFDA deregressed values and predicted breeding values from all models were computed. Fortunately all the models seemed to similarly perform fairly well (Table 3), but some small differences were found. Thus, correlations trend to be higher than 0.5 when categorization is done in four of five classes, and lower if they are classified in only two. These last were just those models with the highest heritability when linear continuous models were fitted. If only two categories had less genetic sense in linear models fitting individual medullation, then medullation percentage, also with only two categories, would be worse performing this trait. However such conclusions would not be matched under threshold models.

Summarizing, linear continuous models performed better than threshold models in terms of heritability. Among them, that one grouping all fibers with any degree of medullation in a unique class would be the best way to deal with fiber medullation addressed from unique fibers. But differences among all checked linear models essayed were not large and finally it is not still possible to decide what conceptual model would be the most appropriate to be used for genetic evaluation of animals. However, as medullation heritability has been found to have consistent moderate magnitude, if medulla is the true responsible of prickling, selecting to decrease the fiber diameter would not be the best criterion. Instead, linear continuous or threshold models applied on whichever method of scoring medullation, including OFDA 100° scores, seem to be promising in the final goal of reducing the prickling. This will help to increase the alpaca fiber price in the international textile market, which will have repercussions on the incomes of the small Andean producer.

5. Conclusion

The heritability of the individual fiber medullation under a continuous linear model was found to be moderate, suggesting that medullation can be used as a selection criterion to decrease the effect of the prickle factor, as itself or maybe combined with fiber diameter. Among all the possible models and grouping ways essayed, grouping jointly all type of medullated fibers will be the trait to use in breeding programs, but the great cost of work under projection microscope suggests rather using the percentage of medullation obtained from

OFDA device, thus achieving a big amount of records under much lower cost. A limitation of this research was the limited number of animals recorded, but the final estimates seem to be sound. It was probably helped by the strong genetic relationship between the animals in the population and the high number of records per animal. Other important issue, not addressed here, is the effect that different types of medullated fiber on the prickle factor should be explored. Individual medullation appeared also highly correlated with the fiber diameter. Considering that both fiber diameter and medullation contribute to the prickling performance of alpaca clothes another possibility would be combining them under a genetic index to carry out selection.

Conflict of interest

None.

Acknowledgment

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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