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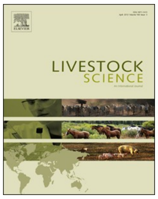

Genetic (co)variance across age of fiber diameter and standard deviation in Huacaya alpacas, estimated by repeatability, multi-trait and random regression models

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ABSTRACT

A total of 14,378 records of fiber diameter (FD) and its standard deviation (SD) from Huacaya alpaca recorded between 2001 and 2017 at Pacomarca genetic center were used in this study. These records were analyzed by a repeatability (RM), multitrait (MT) and random regression (RRM) models. The heritability (h^2) estimates were 0.263 and 0.368 for FD and SD respectively under a RM model; these ranged from 0.653 to 0.742 for FD and 0.627 to 0.764 for SD under MT and from 0.561 to 0.614 for FD and 0.556 to 0.702 for SD under RRM. The MT and RRM show a pattern of increase in variances and heritability as age increases for SD and till 6 years of age for FD, while the genetic correlation (rg) decrease for both traits between 1 and 5 years of ages. The breeding value for the three models show a linear relationship for FD and SD across age at shearing, meaning that any of these models can be used in the selection process. The results of this study shows that during this period of time a highly favorable selection response was obtained for fiber quality in Huacaya alpaca using RM, however the use of the RRM approach can offer more valuable information, particularly in the persistence of the genetic merit of the animals at 5 years respect to 1 years old at shearing. More research is needed on the use and relationship between persistence and others economical traits in alpaca.

1. Introduction

The production of alpaca fiber is one of the main sources of income for the high Andean inhabitants of South America Andes. Its profitability is influenced by the quantity and quality of the fleece that each alpaca produces. The alpaca fleece weight is of about 2.2 kg and usually performing steadily from one year of age up to ten years with a maximum of weight around 2.7 kg in the fourth or five year of age. The quality refers to the diameter of the fiber; those of smaller diameters or called fine fibers offer greater opportunities to produce textiles of greater acceptance in the market, competing commercially with fiber of other species such as goats and rabbits (Allain and Renieri, 2010). Fiber diameter usually ranges from 19 to 36 µm (Cruz et al., 2019), but there exists still finer fiber, like the new commercial category called "alpaca sixteen" referring to mean fiber diameter below 17 µm. In addition, for an optimal quality, the fiber diameter must be accompanied by uniformity, and this is assessed by low values of standard deviation. There are many factors that affect the production and quality of alpaca fiber, some directly linked to the fiber itself, such as follicular density and staple length that depends on the interval between shearing and others linked to the seasonality and the number of shearing of each alpaca concomitant with age (Gutiérrez et al., 2011).

The animal selection can be a very important tool taking into account the important genetic variability in several traits of economic importance in alpaca (Cervantes et al., 2010; Cruz et al., 2015, 2017a, 2019; Gutiérrez et al., 2009, 2011; Pinares et al., 2018); so that one of the basic objectives has so far focused on decreasing fiber diameter, with satisfactory results (Cruz et al., 2017a; Gutiérrez et al., 2014; Morante et al., 2009). These authors have applied a repeatability multitrait model (MT) for predicting of the breeding values and the estimation of (co)variance components, which implies assuming the same form of response to the selection throughout the different

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shearing of the alpaca. However, some evidence indicates that genetic parameters may be different when the number of shearing is treated as independent traits within a multivariate animal model (MT), as indicated by Pun et al. (2011) in alpacas and Wang et al. (2014) in cashmere goats. Comparing among performances of an individual across its productive life allows dealing with properties as plasticity and persistence. Plasticity would be the ability of an animal to change its phenotype when conditions environmental changes, while persistence would refer to the ability of an animal to keep performing across its productive life. A plastic animal would also be more persistent as it would accommodate its performance level across its life.

Many of the traits of economic interest are expressed and recorded repeatedly throughout the life of the animal and are called as Function Value Traits (FVT) cited by de Jong (1990), which can be analyzed by longitudinal models and the study of alpaca fiber diameter can be included as an example of FVT. The practical use of this concept of FVT allows to make more precise descriptions of the trajectory of a trait in terms of the variations of its genetic components throughout the productive age of the animal. Random regression models (RRM) are the statistical procedure that have proven useful for this type of traits (Schaeffer, 2004), in different scenarios of animal production and is currently the method recommended in the analysis and estimation of genetic variance components (Martínez et al., 2011). Under certain conditions the MT and RRM models can produce similar results. However, in practical terms the superiority of RRM in growth traits has been demonstrated (Speidel, 2009) as well as in milk production (Mrode and Coffey, 2008) among others.

The purpose of this paper was to estimate (co)variance components, heritability and genetic correlation of fiber diameter (FD) and its standard deviation (SD) in Alpacas of the Huacaya type estimated by repeatability, multitrait and random regression models along the age at shearing trajectory. The comparison between models would allow making better decisions about the use of these tools during the selection of alpacas.

2. Material and methods

2.1. Data

The data were taken from the Genetic Center of Pacomarca, dedicated to the production of fiber for textile production, located in southern Peru. The fiber samplings were carried out at the time of the shearing of the alpacas, fiber samples of approximately 100 gr were taken mid-side of the animal, which is the most representative area of the fleece and which is best correlated with other body parts (McGregor et al., 2012), these samples were washed and bent in four, sectioning the fiber in snippets of approximately 2 mm. An Optical Fiber Diameter Analyzer – (OFDA) was used to measure FD and SD, 4000 fibers per sample were read (IWTO-47–95, 1995). These data were systematized in PacoPro v.5.9, which is proprietary Pacomarca software that helps manage the information generated by the genetic center.

For this analysis, a total of 14,378 individual records were available with fiber diameter (FD) and the standard deviation (SD) of each observation for the Huacaya Alpacas, maintained under the conditions from the Pacomarca experimental farm, located in Puno, Peru. This database contains the results of shearing conducted between February 2001 and October 2017 with 4552 animals registered from 198 fathers and 1404 mothers of the Huacaya alpacas, the pedigree contains 7468 animals.

The general indicators of the data analyzed are presented in Table 1 showing an adequate structure where most of the parents are presented in the data vector and each ancestor is represented by an adequate number of progenies. This is the most numerous database on Huacaya alpacas from Pacomarca of those studied up to the present.

Table 1
Some indicators of the Huacaya type alpaca database.

Description	Indicator
Numbers of records	14,378
Numbers of animals	4552
Numbers of fathers	198
Numbers of mothers	1404
Numbers of progenies by fathers*	22.9 (72.60)
Numbers of progenies by mothers*	3.24 (10.20)
Numbers of fathers in the data	146
Numbers of mothers in the data	822
Fiber Diameter (mean)	22.05 ± 3.69
Standard Deviation (mean)	5.26 ± 1.03

* Between brackets is the total numbers of records by fathers and mothers.

2.2. Statistical procedure

Several fixed effects models were performed to represent the response curves of FD and SD for the factors included in order to facilitate the genetic analysis.

To estimate the (co)variance components for both variables were analyzed by three different approaches were compared:

- A repeatability model (RM) that assumes that the phenotypic manifestation of FD and SD do not vary more than a systematic age effect along the trajectory of different ages.
- A multitrait (MT) within FD or SD, assuming FD and SD as different traits in each of the first 4 years and a fifth or more shearing.
- A random regression model (RRM of order $r = 1$, 2 and 3) that considers the possible existence of individual variations in the form of response of each trait along the ages scale.

The equation of the three different models was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wp} + \mathbf{e}$$

where

$\mathbf{y}$ is the vector of the dependent variables FD or SD.

$\mathbf{b}$ is a vector of fixed effects defined as: sex (2 levels); fiber color (3 levels); age at shearing in years at the time of recording (10 levels); the combination of year-month of recording (63 levels) were previously edited and those combining in the same level if one of them had less than 9 records, were combined with the previous or next month, at the same time, the interaction sex x color were included. In the MT and RRM models the age effect were modeled by a Legendre polynomial of order 3.

$\mathbf{a}$; $\mathbf{p}$ and $\mathbf{e}$ are vectors of random effects due to animal genetic effects; permanent environmental effects ($\mathbf{p}$) and the residual error ($\mathbf{e}$) respectively. In RRM models, it was also considered a heterogeneity residual variance with 5 levels (1 to 5 or more years old).

$\mathbf{Wp}$ was not fitted in MT model.

The matrices $\mathbf{X}$; $\mathbf{Z}$ and $\mathbf{W}$ are incidence matrices that connect the fixed and random effects with the dependent variable. In these models the expected (co)variances components were assumed as:

$$\mathbf{var}\begin{bmatrix}\mathbf{a}\\ \mathbf{w}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\otimes\mathbf{G} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I_p}\otimes\mathbf{W} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I_n}\otimes\mathbf{R}\end{bmatrix}$$

in which $\mathbf{G}$ is an additive genetic (co)variance matrix among all animals; $\mathbf{W}$ and $\mathbf{R}$ are respective (co) variance matrices among permanent environments and residuals, $\mathbf{A}$ is the relationship matrix between all animals in the pedigree; $\mathbf{I_p}$ and $\mathbf{I_n}$ are identity matrices of respective order number of animals with own record (p) and number of records (n), and $\otimes$is the Kronecker product.

Even when dealing with the same traits, the variance distribution of the data presents some differences according to the model applied.

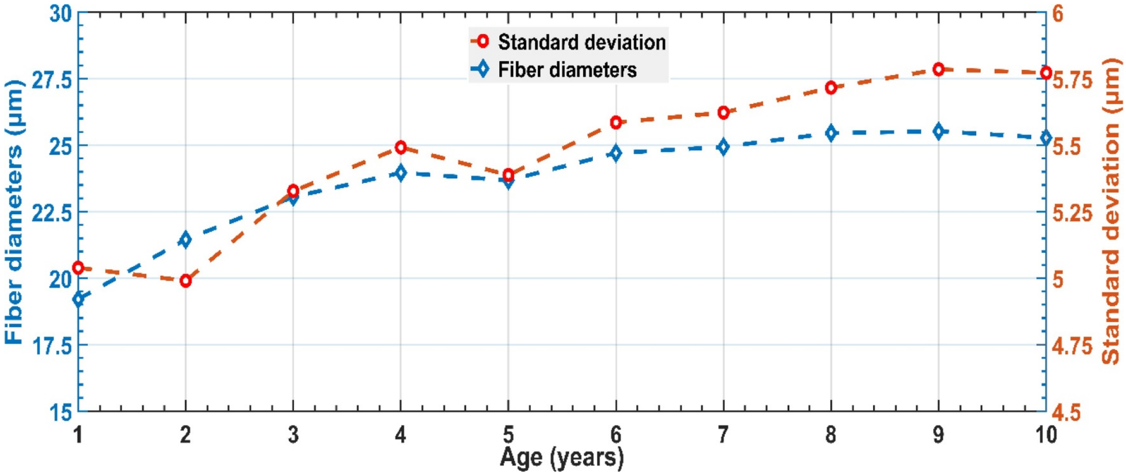

Fig. 1. Effect of age on fiber diameter and standard deviations in Huacaya type alpaca.

Under the RM model, $\mathbf{Var}(\mathbf{y}) = \mathbf{ZAZ}'\sigma_{\mathbf{a}}^2 + \mathbf{WW}'\sigma_{\mathbf{p}}^2 + \mathbf{I_n}\boldsymbol{\sigma}_{\mathbf{e}}^2$, where $\boldsymbol{\sigma}_{\mathbf{a}}^2$, $\boldsymbol{\sigma}_{\mathbf{p}}^2$ and $\boldsymbol{\sigma}_{\mathbf{e}}^2$ are the additive genetic, permanent and residual environment variances respectively. In this model, the genetic parameters of heritability (h^2) and repeatability (R) were estimated using classical formulas (Falconer and MacKay, 1996).

Under MT model, (co)variances were defined as:

$$\mathbf{Var}(\mathbf{a}) = \begin{bmatrix} \boldsymbol{\sigma}_{\mathbf{a_1}}^2 & \boldsymbol{\sigma}_{\mathbf{a_1a_2}} & \boldsymbol{\sigma}_{\mathbf{a_1a_3}} & \boldsymbol{\sigma}_{\mathbf{a_1a_4}} & \boldsymbol{\sigma}_{\mathbf{a_1a_5}} \\ \boldsymbol{\sigma}_{\mathbf{a_1a_2}} & \boldsymbol{\sigma}_{\mathbf{a_2}}^2 & \boldsymbol{\sigma}_{\mathbf{a_2a_3}} & \boldsymbol{\sigma}_{\mathbf{a_2a_4}} & \boldsymbol{\sigma}_{\mathbf{a_2a_5}} \\ \boldsymbol{\sigma}_{\mathbf{a_1a_3}} & \boldsymbol{\sigma}_{\mathbf{a_2a_3}} & \boldsymbol{\sigma}_{\mathbf{a_3}}^2 & \boldsymbol{\sigma}_{\mathbf{a_3a_4}} & \boldsymbol{\sigma}_{\mathbf{a_3a_5}} \\ \boldsymbol{\sigma}_{\mathbf{a_1a_4}} & \boldsymbol{\sigma}_{\mathbf{a_2a_4}} & \boldsymbol{\sigma}_{\mathbf{a_3a_4}} & \boldsymbol{\sigma}_{\mathbf{a_4}}^2 & \boldsymbol{\sigma}_{\mathbf{a_4a_5}} \\ \boldsymbol{\sigma}_{\mathbf{a_1a_5}} & \boldsymbol{\sigma}_{\mathbf{a_2a_5}} & \boldsymbol{\sigma}_{\mathbf{a_3a_5}} & \boldsymbol{\sigma}_{\mathbf{a_4a_5}} & \boldsymbol{\sigma}_{\mathbf{a_5}}^2 \end{bmatrix} \otimes \ \mathbf{A}\,\text{and}\,\mathbf{Var}\begin{bmatrix} \mathbf{e_{i_1}} \\ \mathbf{e_{i_2}} \\ \mathbf{e_{i_3}} \\ \mathbf{e_{i_4}} \\ \mathbf{e_{i_5}} \end{bmatrix}$$

$$= \begin{bmatrix} \boldsymbol{\sigma}_{\mathbf{e_1}}^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{\sigma}_{\mathbf{e_2}}^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \boldsymbol{\sigma}_{\mathbf{e_3}}^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \boldsymbol{\sigma}_{\mathbf{e_4}}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \boldsymbol{\sigma}_{\mathbf{e_5}}^2 \end{bmatrix}$$

being $\boldsymbol{\sigma}_{\mathbf{a_j}}^2$ the additive genetic variance associated to the j^{th} age at shearing, $\boldsymbol{\sigma}_{\mathbf{a_ja_k}}$ the additive genetic covariance between the j^{th} and k^{th} age at shearings, and $\mathbf{e_{i_j}}$ the residual associated to the j^{th} age at shearing of the i^{th} animal. All covariances between any additive genetic value and any residual were assumed null.

Under RRM model, (co)variances were defined as:

$$\mathbf{Var}(\mathbf{a}) = \Phi\mathbf{K_G}\boldsymbol{\Phi}' \otimes \ \mathbf{A}$$

being $\mathbf{K_G} = \begin{bmatrix} \boldsymbol{\sigma}_{\mathbf{a_o}}^2 & \boldsymbol{\sigma}_{\mathbf{a_{os}}} & \boldsymbol{\sigma}_{\mathbf{a_{oq}}} & \boldsymbol{\sigma}_{\mathbf{a_{oc}}} \\ \boldsymbol{\sigma}_{\mathbf{a_{os}}} & \boldsymbol{\sigma}_{\mathbf{a_s}}^2 & \boldsymbol{\sigma}_{\mathbf{a_{sq}}} & \boldsymbol{\sigma}_{\mathbf{a_{sc}}} \\ \boldsymbol{\sigma}_{\mathbf{a_{oq}}} & \boldsymbol{\sigma}_{\mathbf{a_{sq}}} & \boldsymbol{\sigma}_{\mathbf{a_q}}^2 & \boldsymbol{\sigma}_{\mathbf{a_{qc}}} \\ \boldsymbol{\sigma}_{\mathbf{a_{oc}}} & \boldsymbol{\sigma}_{\mathbf{a_{sc}}} & \boldsymbol{\sigma}_{\mathbf{a_{qc}}} & \boldsymbol{\sigma}_{\mathbf{a_c}}^2 \end{bmatrix}$ corresponding with the (co)variances associated to the coefficients of the Legendre polynomial of order 3, where $\boldsymbol{\sigma}_{\mathbf{a_o}}^2, \sigma_{\mathbf{a_s}}^2, \sigma_{\mathbf{a_q}}^2\,\mathbf{and}\boldsymbol{\sigma}_{\mathbf{ac}}^2$ represent the additive genetic variances for the intercept (*o*); slopes (*s*); quadratic terms (*q*) and cubic terms (*c*) respectively, while the covariances between all these components are identified on both sides of the diagonal with the subscripts *o, s, q* and *c* respectively, and $\boldsymbol{\Phi}$ is a *t* by *k* matrix with orthogonal polynomials, being *t* the number if shearings and *k* the order of the Legendre polynomial plus one. (Co)variances for the permanent environmental effect were defined as $\mathbf{Var}(\mathbf{p}) = \Phi\mathbf{K_P}\boldsymbol{\Phi}' \otimes \ \mathbf{I}$ having similar definitions to that of additive genetic variances, but $\mathbf{K_p}$ being of order one with $\boldsymbol{\sigma}_{\mathbf{w_o}}^2, \sigma_{\mathbf{w_s}}^2, \mathbf{and}\boldsymbol{\sigma}_{\mathbf{w_{os}}}$ the permanent variances for *o, s* and its covariance respectively. Residual variances were as in MT model. The (co)variance components and genetic parameters were estimated by a procedure proposed by Jamrozik and Schaeffer (1997) shown in supplementary material S1.

In RRM models, the solution corresponding to each $\mathbf{x^{th}}$ animal were expressed in terms of a genetic function: $\mathbf{f_x}=[\mathbf{a_{x_o}}\mathbf{a_{x_s}}\mathbf{a_{x_q}}\mathbf{a_{x_c}}]$ with as many elements as the adjustment order of the applied polynomial. These coefficients are a unique value that represents the genetic merit of each animal or its capacity for reaction to manifest changes in its estimated breeding values (EBV) along the trajectory of the $\mathbf{z^{th}}$ ages. The differences in those functions at 4 years respect to 1 year at shearing were used as an indicator of plasticity and persistence of the performance of the animals.

All the genetic parameters were estimated following the procedure proposed by Jamrozik and Schaeffer (1997). Supplementary material S1 show all details respect to the persistence estimates, the expected breeding values of the animals, the (co)variance components and the genetic parameters.

The matrices **G** and $\mathbf{K_G}$ according to the MT and RRM models were subjected to a principal component analysis (Matlab, 2018) in order to generalize about the forms of response of FD and SD as a function of age. In this study, a complex statistical procedure has been applied, nevertheless a very useful additional information can be obtained that may represent important benefits for the breeding improvement for the fiber quality of the in the Huacaya alpaca.

Finally, the EBV of each animal estimated by the different models, were combined with their respective years of birth, in order to represent the evolution of the genetic merit achieved in the time period represented in this database. All the genetic (co)variance components were estimated with ASReml software (Gilmour et al., 2009).

3. Results

The results of the first fixed effects model showed highly significant differences for the age effects, the least square means evolution of FD and SD is shown in Fig. 1. This representation can be interpreted as the maturity pattern for FD and SD which apparently show the same form, but with some differences. For FD, a first stage was manifested with a sustained increase until 5 years of age (23.96 µm) with increases of 19.61% per year with regard to the mean at first shearing (19.20 µm), after which the rate of increase was less intensive, the order of 3.60% per year (25.27 µm at 10 years old). On the contrary, for SD the response curve presented a more homogeneous pattern with increases of 11.82% per year between 1 (5.03 µm) and 5 (5.38 µm) years and of 8.78% per year in the rest of the years of shearing (5.77 µm at 10 years old). During the time period represented in this study, the least square

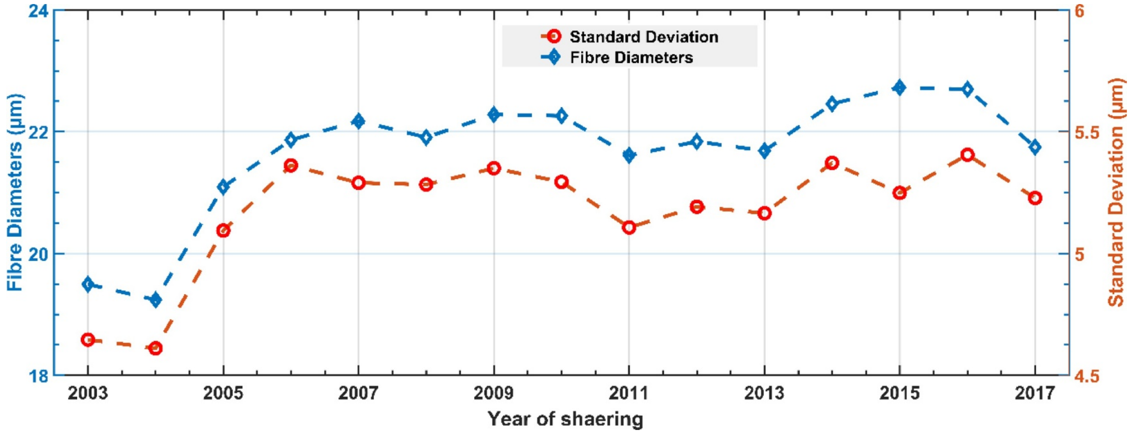

Fig. 2. General raw mean for fiber diameter and standard deviations during 2003 to 2017 for Huacaya type alpaca.

means presents a positive response for both variables (Fig. 2). Respect the mean in 2003, these increases were 11.8% and 12.5% for FD and SD respectively in 2017.

3.1. *Repeatability model*

The variance components estimates and the corresponding genetic parameters results of the RM model are presented in the Table 2. The genetic variances components and genetic parameters were moderate, 0.263 and 0.368 for the heritabilities of FD and SD respectively, while the repeatabilities were higher, 0.408 and 0.516 for FD and SD respectively.

3.2. *Multitrait model*

Additive genetic variances and corresponding heritabilities for the five different shearings considered are shown in Table 3. The genetic variances of both traits were increasing with the age at shearing from 2.331 to 9.953 and from 0.380 to 1.001 for FD and SD respectively. Estimated heritabilities were high, between 0.627 and 0.745 for both traits, showing high variability trend respect to shearing age. The genetic correlations (rg) for each trait (Table 4) between the ages considered show a same pattern for FD and SD and in both cases, being high between 0.605 and 0.974 with a significant decrease between the expression of the trait is recorded at 1 year and 5 years or more age.

3.3. *Random regression model*

The different RRM models used contain the same fixed effects and the differences are due to the order of adjustment of the polynomial used (r), therefore, they can be compared using informative criteria following the proposal of Foulley and Robert-Granie (2002) and this model comparison results are presented in Table 5.

The general rules are higher value of logL and lower for AIC and BIC and accordingly the model of order *r* = 3 and heterogeneous residual variance (H) with 18 total parameters was the best fit to the data. This trend was similar for FD and SD although with different values. The genetic parameters according to this model is presented in the Table 6 for both dependent variables, showing a pattern of increases in variances and corresponding heritability as age increases, from 0.556 to 0.702 for 1 to 10 years of age for SD, and till 6 years of age (from 0.561 to 0.609 for FD) and then showed a variable trend. Genetic correlations

Table 2
Components of (co) variance and genetic parameters for fiber diameter (FD) and standard deviation (SD) in Huacaya type alpaca estimated with repeatability model (standard error in brackets).

Description	FD	SD
Genetic variance	1.889 (0.002)	0.298 (0.001)
Perm environmental variance	1.046 (0.001)	0.120 (0.001)
Residual variance	4.252 (0.030)	0.392 (0.001)
Heritability	0.263 (0.010)	0.368 (0.020)
Repeatability	0.408 (0.010)	0.516 (0.010)

Table 3
Components of (co) variance (*) and genetic parameters for fiber diameter (FD) and standard deviation (SD) throughout the age (years) to shearing estimated with Multitrait model. .

Parameters	Age	FD	SD
Genetic variance	1	2.331 (1.188)	0.380 (0.225)
	2	6.072 (2.112)	0.678 (0.232)
	3	8.444 (4.135)	0.831 (0.318)
	4	9.277 (4.925)	1.027 (0.316)
	5^+	9.535 (5.024)	1.001 (0.402)
Heritability	1	0.662 ± 0.023	0.627 ± 0.022
	2	0.742 ± 0.027	0.745 ± 0.023
	3	0.671 ± 0.024	0.723 ± 0.022
	4	0.653 ± 0.021	0.764 ± 0.026
	5^+	0.655 ± 0.010	0.713 ± 0.010

[*] Between brackets is the ratio between the components and their standard error.

Table 4
Genetic correlations (rg) between fiber diameter (on diagonal) and standard deviation (below diagonal) for 1 to 5 o more years at shearing estimated with Multitrait model in Huacaya type alpaca.

Age (years)	1	2	3	4	5 or more
1		0.828	0.702	0.642	0.605
2	0.864		0.924	0.904	0.786
3	0.789	0.913		0.965	0.877
4	0.701	0.816	0.974		0.931
5 or more	0.654	0.757	0.904	0.959	

Table 5
Comparison of random regression models of different adjustment order for fiber diameter and standard deviations in Huacaya type alpacas .

Model	P	Infomartive critrium		
		logL	AIC	BIC
Order 1	5	−9124	18,258	18,295
Order 2	8	−8935	17,886	17,946
Order 2 H	12	−8368	16,760	16,850
Order 3 H	18	−8318	16,666	16,779

Table 6
Components of variance and heritability for fiber diameter (FD) and standard deviations (SD) throughout the ages at each shearing, estimated with random regression models.

Age at Shearing (years)	Genetic Parameters for FD			Genetic Parameters for SD		
	Var Genetic	Var Phenot	h^2	Var Genetic	Var Phenot	h^2
1	1.886	3.364	0.561	0.326	0.586	0.556
2	4.216	7.251	0.581	0.498	0.855	0.582
3	6.830	11.725	0.582	0.694	1.071	0.649
4	8.483	13.984	0.607	0.823	1.223	0.673
5	9.032	14.702	0.614	0.888	1.328	0.669
6	8.835	14.505	0.609	0.922	1.362	0.677
7	8.347	14.018	0.595	0.951	1.391	0.684
8	7.918	13.588	0.583	0.978	1.418	0.690
9	7.782	13.452	0.578	0.997	1.437	0.694
10	8.255	13.925	0.593	1.034	1.474	0.702

for FD and SD were very variable throughout the age at shearing (from 0.421 to 1.000), but higher in the last years. These results are presented in the Table 7.

The comparative analysis of the rg of the MT models (Table 4) and RRM (Table 7) show the same pattern with decrease in rg between the records of both variables between 1 and 5 years of ages, but the estimates are much higher at adjacent ages. From this type of response, the existence of redundant information can be inferred, which can be examined through a principal component analysis (PCA) of the $\mathbf{G}$ and $\mathbf{K_G}$ matrices and the results are shown in the Tables 8 and 9 for the MT and RRM models respectively.

Even though the PCA results of both models are somewhat different in numerical terms, but the response pattern is very similar, in which the two first eigenvectors account for most of the total genetic variance between 96 and 99%. The results of the MT model are related to the manifestation of both traits in terms of the EBV, evidencing that if the selection favors the coefficients of the first eigenvector, there will be increases in all the first 5 or more years of age, that is why it is called *size vector* and explains most of the variance. The second eigenvector is known as a *shape vector* since the coefficients will favor increases in FD and SD in the first two years and a posteriori decrease**,** although the variances explained by this eigenvector will be small.

In the RRM model, the PCA results are related to the genetic variances whose direction can be represented by calculating the eigenfunction of the $\mathbf{K_G}$ matrix and the applied polynomial coefficients and these results are shown in Fig. 3. The first eigenfunction explains most of the genetic variance for both traits and shows a positive coefficient throughout the ages trajectory, therefore its use will increase the genetic variance across the whole ages scale, while the second eigenfunction although it represents very little magnitude of the genetic variances and their coefficients express the ability of the animal to react differentially by modifying the genetic variance of both traits in terms of age at the time of shearing.

Generalizing the results of MT and RRM models, the same answers will be reached, both in the estimates of heritabilities (Table 3 and 6) and in the rg of both traits between different ages (Tables 4 and 7). According to these results, changes in the order of merit between the EBV from MT and RRM models should not to be expected, however, as the breeding program established in Pacomarca is based on an RM model, a comparison between the EBVs estimated will be adequate which is shown in Fig. 4. The QQplot, or quantile-quantile plot, showed in Fig. 4 is a graphical tool to help us assess if there is some change in order of merit between the EBV estimated by the two models. In that sense, the results indicate that the relationships are linear, therefore any of these models can be used in the Pacomarca selection breeding program, although with some exceptions with the results at 1 year of age, which is expected in view of the rg estimated (Tables 4 and 7). However, the RRM model provides additional information with the same data available that can provide some margin for a collateral benefit. For this purpose, Fig. 5 presents the frequency distribution of the EBV´s of all the animals for both traits estimated by the RM and the evolution of the EBV of a group from the best 300 (40 to 45 animals in each) throughout ages according to the RRM model.

The left part of the Fig. 5 shows the existent variability in EBV for both traits estimated by the classic RM model whose amplitude represents around 30 to 40% of the average values for these traits presented in Table 1. Note in the right side of the Fig. 5 the evolution of the EBV for a group of these 300 elite animals along the age trajectory, where there are animals expressing their own capacity to modify their potential, manifesting a decrease (beneficial effect in these trait) throughout the age, but more pronounced in the first 4 or 5 years, while others remain stable or decrease in their EBV between 6 and 10 years old. It should be emphasized that such differences need to be considered in the breeding objective of Huacaya type alpaca in Pacomarca breeding program.

During the time period represented in this database an important response to selection was shown, which is presented in Figs. 6 and 7 and 8 for FD and SD respectively (only the results are shown in the first 5 years of age for a better model's comparison). The evolution of EBV presented the same negative trend (favorable effect) for those estimated by RM**,** MT and RRM models although the annual magnitudes present some differences except for the results of the classic RM model showing a parallelism between results for EBV at 1 year of age respect to MT and RRM models. The main effects of the selection process applied in the Alpaca herd of Pacomarca was materialized between 2003 and 2011 and without major changes until the animals born in 2017.

4. Discussion

Improving the fiber textile qualities in both fineness and uniformity is the objective in alpaca production. It has been possible to select very fine animals, but age is crucial in increasing the thickness of the fiber and it would be interesting to look for the animals that maintain the

Table 7
Genetic correlations between fiber diameter (on diagonal) and standard deviation (below diagonal) throughout the ages (years) at each shearing, estimated with random regression models.

	1	2	3	4	5	6	7	8	9	10
1		0.845	0.719	0.639	0.575	0.518	0.467	0.430	0.421	0.451
2	0.882		0.978	0.947	0.911	0.870	0.826	0.790	0.782	0.817
3	0.759	0.974		0.992	0.974	0.946	0.912	0.883	0.877	0.908
4	0.676	0.931	0.988		0.994	0.978	0.953	0.930	0.926	0.953
5	0.614	0.879	0.955	0.989		0.995	0.980	0.964	0.961	0.982
6	0.563	0.818	0.905	0.957	0.989		0.995	0.986	0.985	1.000
7	0.525	0.758	0.850	0.913	0.962	0.992		0.998	0.998	1.000
8	0.513	0.722	0.811	0.879	0.937	0.977	0.996		1.000	1.000
9	0.539	0.733	0.814	0.879	0.934	0.974	0.994	0.999		0.999
10	0.608	0.805	0.873	0.922	0.961	0.984	0.990	0.988	0.992	

Table 8
Results of the principal components analysis (PCA) for fiber diameter (FD) and standard deviations (SD), estimated with multitrait model for the eigenvectors in the different shearings.

	PCA for FD					PCA for SD				
	EV1	EV2	EV3	EV4	EV5	EV1	EV2	EV3	EV4	EV5
1	0.1972	0.5393	−0.6562	−0.2805	0.4012	0.2643	0.5615	−0.7051	0.3425	0.0182
2	0.4067	0.5421	0.0397	0.5652	0.4687	0.3981	0.5807	0.3398	−0.5729	0.2463
3	0.5014	0.1346	0.4256	−0.7062	0.2249	0.4817	0.0753	0.3848	0.3347	−0.7087
4	0.5304	−0.1523	0.3242	0.3206	−0.6983	0.5311	−0.3086	0.1813	0.4357	0.6324
5	0.5128	−0.6115	−0.5306	0.0185	0.2850	0.5074	−0.4966	−0.4543	−0.5027	−0.1920
VAR%	90.1	6.1	2.7	0.80	0.30	89.4	7.5	1.8	1.1	0.023
Cummulative Var%		96.2	98.9	99.7	100		96.9	98.7	99.8	100

Table 9
Results of the principal components analysis (PCA) for fiber diameter (FD) and standard deviations (SD), estimated with random regression models.

	PCA for FD				PCA for SD			
	EV1	EV2	EV3	EV4	EV1	EV2	EV3	EV4
1	0.9812	0.1276	0.1438	0.0146	0.9835	0.1468	0.0985	−0.0386
2	0.1218	−0.9675	0.0043	0.2217	0.1519	−0.9455	0.0048	0.2881
3	−0.1332	0.1399	0.7170	0.6698	−0.0902	0.1220	0.8883	0.4334
4	0.0676	0.1678	−0.6821	0.7085	0.0390	0.2639	−0.4485	0.8531
VAR%	95.10	4.50	0.30	0.10	92.60	6.20	1.10	0.10
Cummulative Var%		99.6	99.9	100		98.8	99.9	100

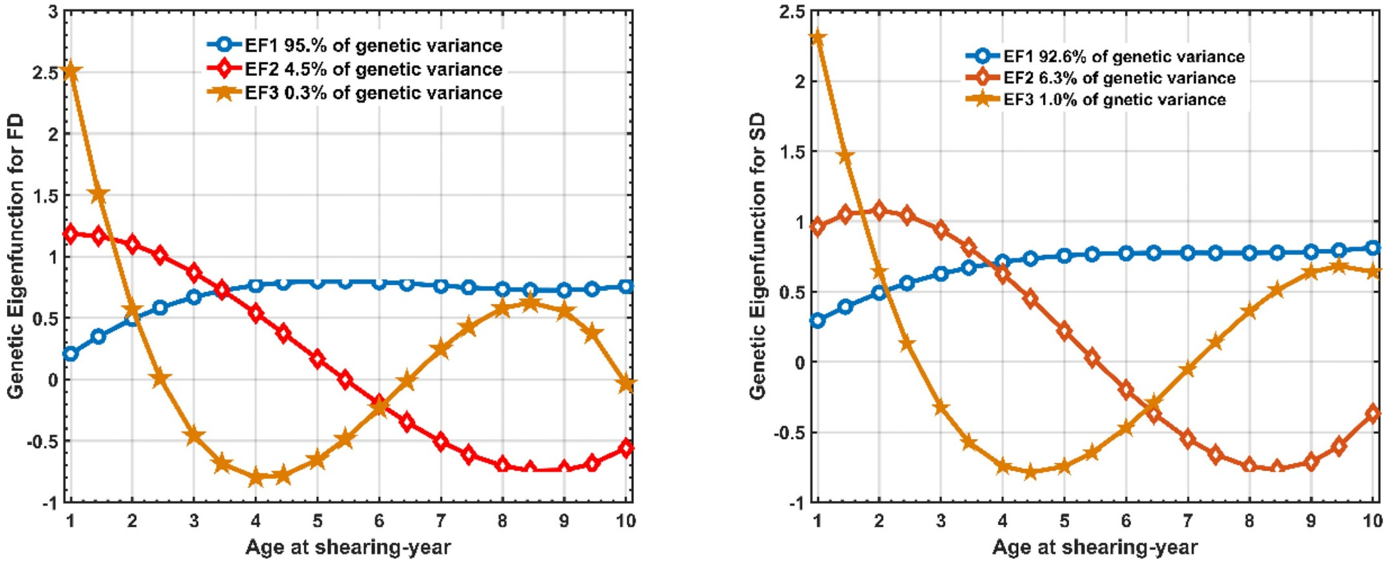

Fig. 3. Evolution of the direction of the eigenfunction for fiber diameter - FD (left) and standard deviation - SD (right), estimated with a random regression model.

fineness throughout the different shearing, the effects of age show a pattern of increase in FD and SD up to 4 years of age, increasing from 19.20 to 23.96 µm in only four years. This increase of 4.76 µm represents a 78.42% of the total increase in the first half of the productive life, which still increases up to an average of 25.27 at 10 years of shearing. This increase becomes an important disadvantage for the alpaca fiber which competes in the textile industry with other animals producing fiber, for which fineness still holds from the fifth shearing. This result is consistent with those published by Cruz et al. (2017)a, 2019), Gutiérrez et al. (2011), 2014) and Morante et al. (2009) in Pacomarca's own herd as well as in other regions of Peru (Roque and Ormachea, 2018) and in Australia (McGregor and Butler, 2004). The similar results of the Pacomarca program had already been indicated by Cervantes et al. (2010), Cruz et al. (2017a, 2019), Gutiérrez et al. (2009), 2011), Morante et al. (2009) and Pinares et al. (2018) and the current study with the largest number of observations corroborates the same type of favorable response for the quality of the Huacaya alpaca fiber in the period between 2003 and 2017.

In terms of genetic parameters, the estimates of heritability between 0.263 and 0.368 for FD and SD respectively according to the RM model (Table 2), were within the range of publications available that has been compiled in Table 10 with heritabilities between 0.24 and 0.73. In all these cases, a transversal approach were applied in which it is considered that there are no variations in the form of response, nor in (co) variance genetic components in FD and SD throughout the age, in other words, it is assumed that it is the same trait across of years of shearing. However, the results of this study demonstrate the existence of different expression in the age scale, in correspondence with the characteristics of both traits that are expressed and recorded repeatedly along the

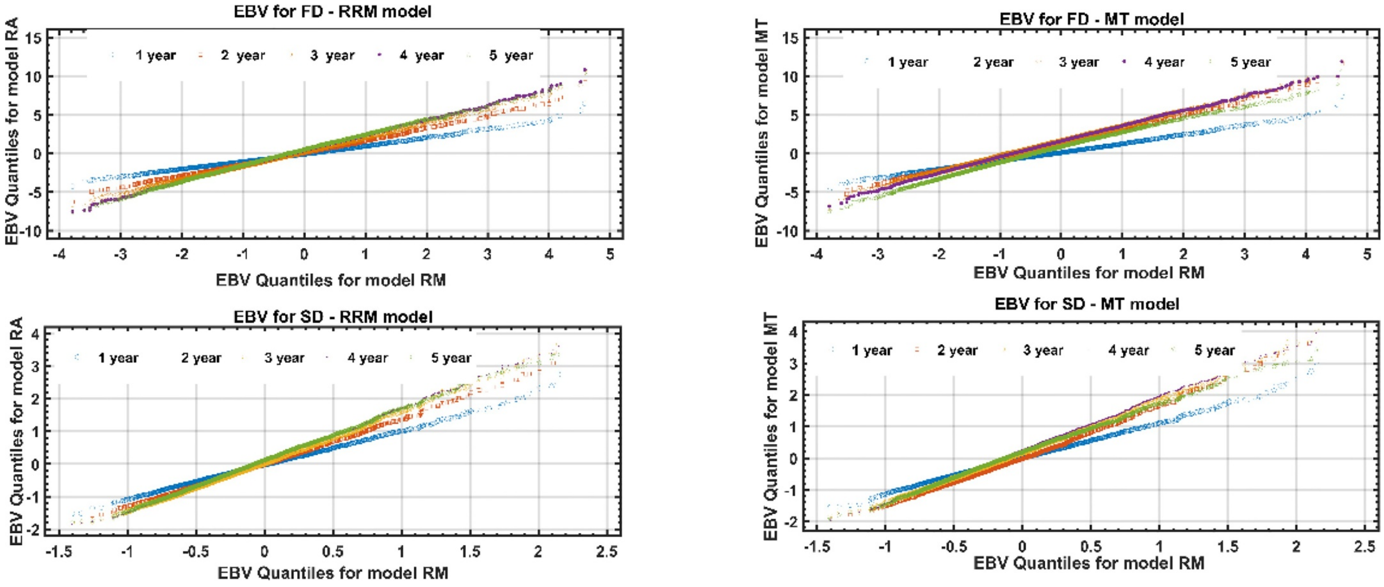

Fig. 4. QQplot of the estimated breeding values (EBV) estimated for each trait, according to multitrait (MT) and random regression (RRM) models during the first 5 years of age with respect to the results of the repeatability model (RM).

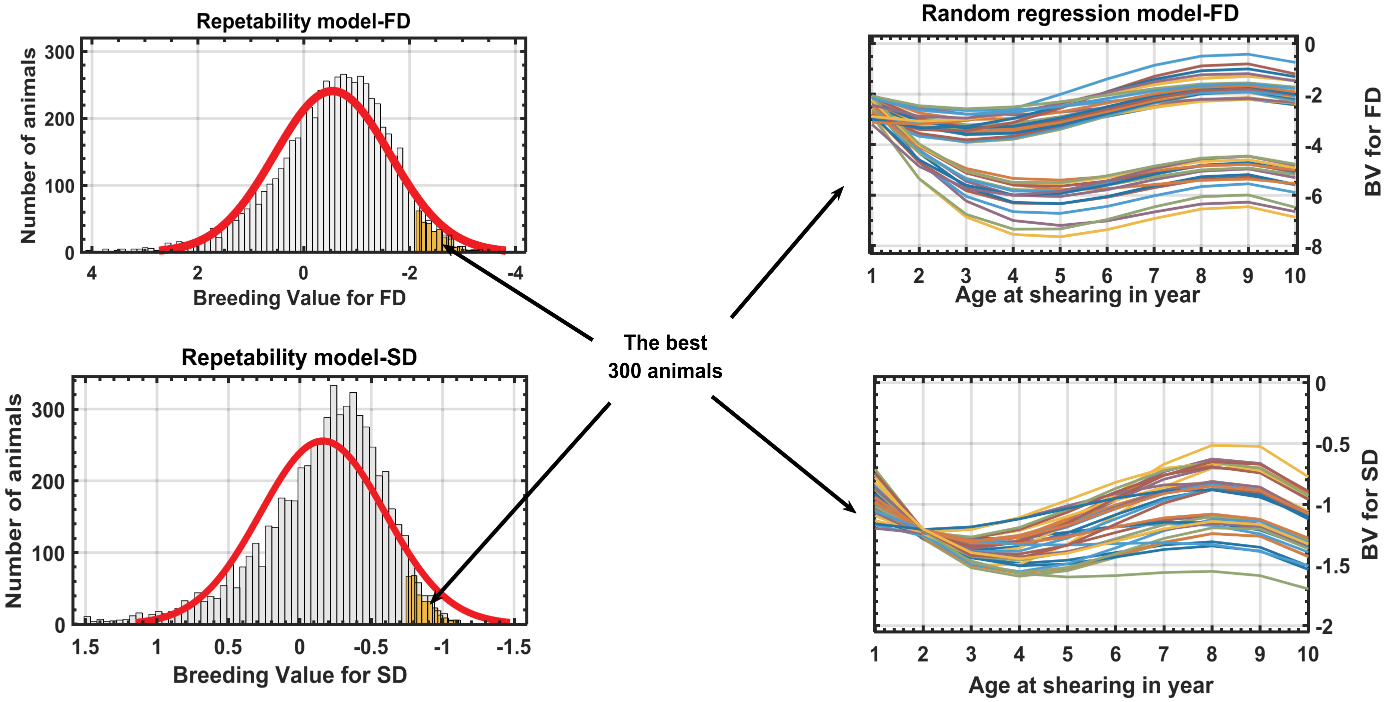

Fig. 5. Frequency distribution of estimated breeding values (EBV) for fiber diameter (FD) and standard deviation (SD) of all the animals and of the best 300 animals according to results of the classic repeatability model (RM) and evolution of the EBV of the same animals throughout the age at shearing, estimated by random regression model (RRM).

productive life of the Alpaca, that is, it is a trait of the type FVT already indicated in the introduction.

The heritabilities for FD and SD estimated by MT (0.627 to 0.764) and RRM (0.556 to 0.702) shown in Tables 3 and 6, as well as the rg between the same trait at different ages (0.642 to 0.974 and 0.421 to 1.00) shown in Tables 4 and 7, show a positive pattern higher between records at adjacent ages, although it decreases between the results at 1 year and the rest of the ages at shearing. The heritabilities values for both traits according to these models are much higher than the classic RM used to the present. This same trend was presented by Pun et al. (2011) with a sample of these same population and applying a model of MT type estimating values of heritabilities between 0.56 to 0.70 for FD. while Wuliji et al. (2000) reports a value of 0.73 very similar to those found in this study. This superiority of the longitudinal models had previously been indicated in Merino sheep wool in the United States (Okut et al., 1999) as well as in alpacas (McGregor and Butler, 2004); in cashmere goats (Wang et al., 2014) and have already been successfully applied to growth traits (Speidel, 2009), as well as milk production (Schaeffer and Jamrozik, 2008). The coherence of results between MT and RRM of this study is the expected response when the type of distribution of the covariate used has the same continuity scale, expressed both in discrete terms (MT model) and continuous variable (RRM model). Therefore, both models can produce similar and interchangeable results (de Jong, 1990; Via et al., 1995).

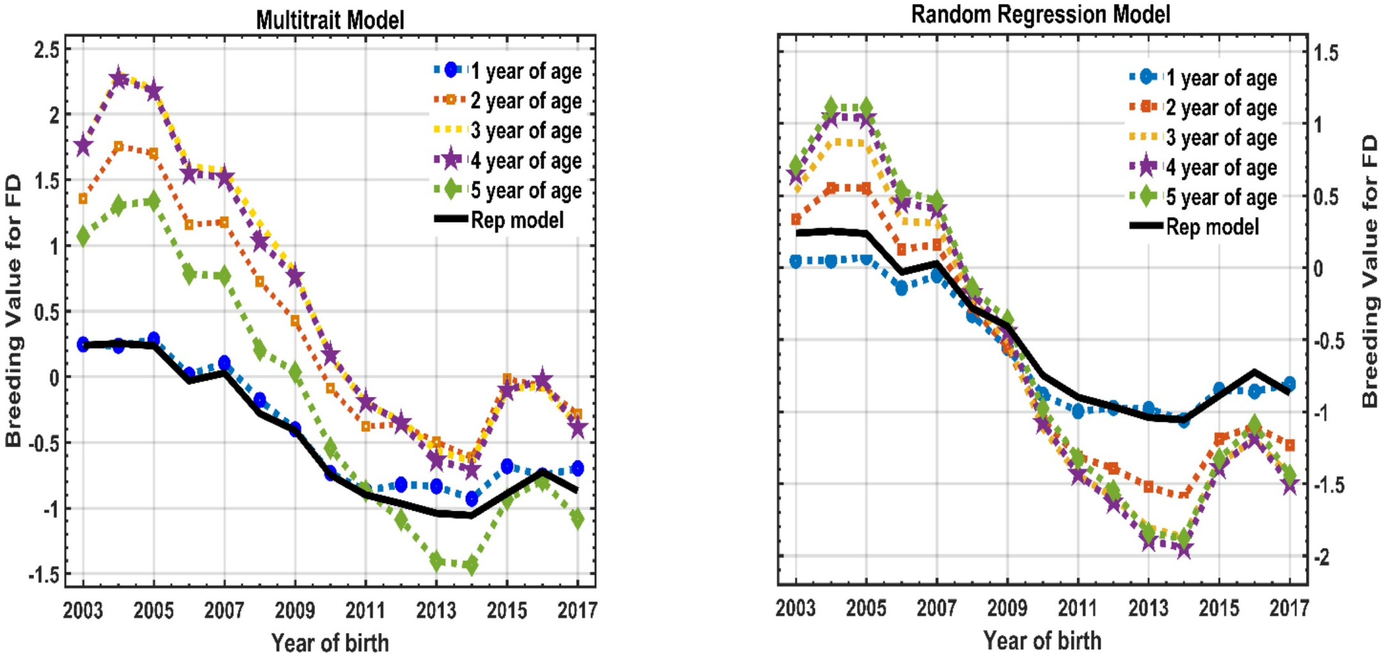

Fig. 6. Evolution of the estimated breeding values (EBV) for fiber diameter (FD) in based on the first 5 years of birth estimated by repeatability model (RM), multitrait model (MT) and random regression model (RRM).

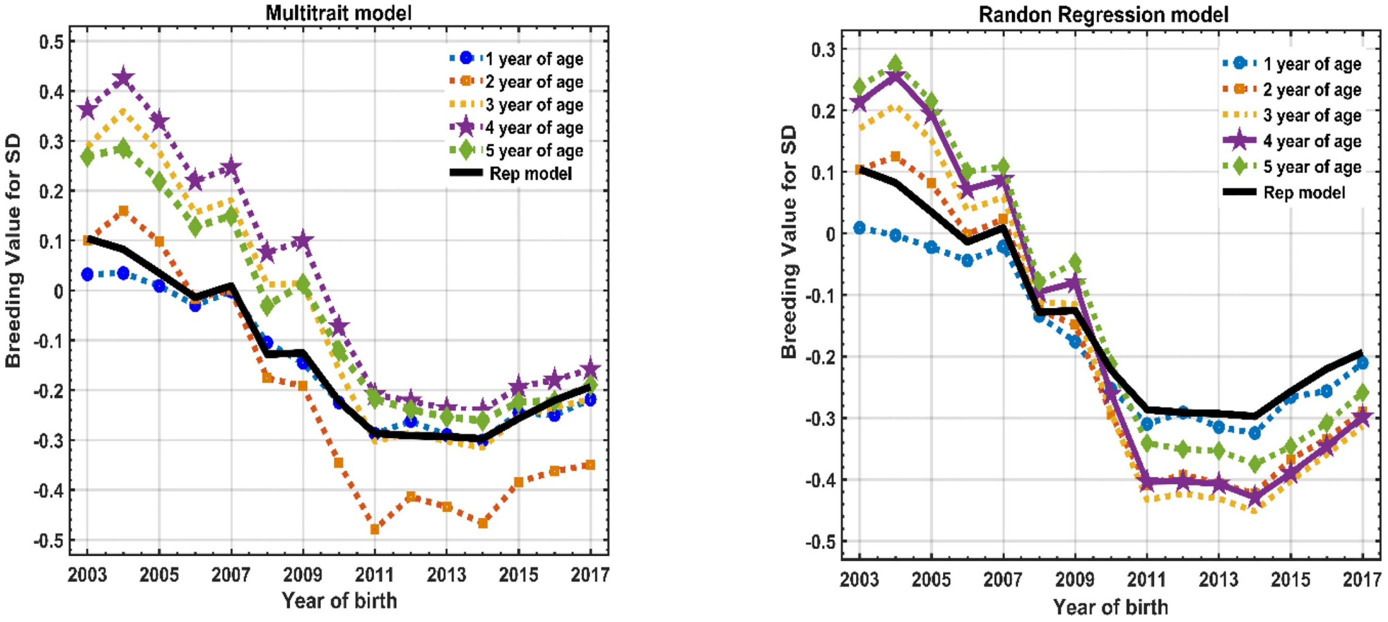

Fig. 7. Evolution of the estimated breeding values (EBV) for standard deviations (SD) in based on the first 5 years of birth estimated by repeatability model (RM), multitrait model (MT) and random regression model (RRM).

The principal components analysis performed on the $\mathbf{K_G}$ matrix of the RRM model allowed us to make a representation of the corresponding eigenfunction (Fig. 3) showing that early selection allows to identify possible changes in the form of response of genetic origin, as well as the possible direction of the genetic variances of both traits throughout the age scale. The first eigenfunction explained 95.1% and 92.6% of the total variability for FD and SD respectively, indicating that most of the response will be manifested in the first 4 or 5 years, keeping a stable pattern afterwards. The second eigenfunction, explaining 4.5% and 6.2% of the variability respectively for FD and SD, and the third eigenfunction, explaining only 0.3% and 1.1% of the variability, only exercised modifications in the form of response determined basically by the first one (Tables 8 and 9). The results of this work demonstrate the existence of a linear evolution (Fig. 4) of the EBV estimated by RRM with respect to the RM model, which is consistent with the conclusions of Gutiérrez et al. (2011)), so not important changes in merit order across ages will be expected, therefore the classic model used of the RM type will provide positive selection results.

The above is related to the high correlations between the EBV estimated by the different models, however, the RRM model provides additional information with the same data available that can provide some margin of collateral benefits which is rarely presented. Fig. 5 shows that from the 300 best animals selected by the RM model for FD and SD among which there are no changes in the order of merit. However, the detailed analysis of their manifestations along the trajectory of age, they show the existence of diverse forms of response in

Tabla 10
Revision of the heritabilities (h^2) for fiber diameter (FD) and standard deviations (SD) in alpacas estimated with MT and RM models.

Author	Type	Country	h^2 of FD	h^2 of SD
Ponzoni et al., 1999	Both	Australia	0.67	
Wuliji et al., 2000	Huacaya	New Zeland	0.73	
Morante et al., 2009	Both	Perú	0.43	0.46
Gutiérrez et al., 2009	Both	Perú	0.41	
Cervantes et al., 2010	Huacaya	Perú	0.37	0.42
	Suri	Perú	0.70	0.68
Pérez-Cabal et al., 2010	Huacaya	Perú	0.24	0.21
	Suri	Perú	0.28	0.30
Gutiérrez et al., 2014	Huacaya	Perú	0.34	0.39
	Suri	Perú	0.49	0.46
Cruz et al., 2015	Huacaya	Perú	0.32	0.40
	Suri	Perú	0.50	0.50
Pinares et al., 2018	Huacaya	Perú	0.34	
Cruz et al., 2019	Huacaya	Perú	0.35	0.39
	Suri	Perú	0.44	0.44

this group of elite animals, which requires some additional comments given their potential for the Pacomarca breeding program.

In general, a total decrease of mean EBV for fiber diameter was reached from −0.855 to −2.149 from 1 to 4 years of shearing when estimated by RRM, while a mean of −1.108 µm was obtained for the unique EBV estimated by RM. For SD the corresponding values were −0.219 and −0.512 for the EBV under RRM and −0.297 under RM. Even though these results are very positive, they represent between 3.9% and 9.5% of improvement for respectively FD and SD in these 15 years of improvement. The use of longitudinal approach allowed to identify an important source of variability related to the persistence of the EBV estimated as the difference between the EBV at 4 year of age respect to 1 year. The estimated persistence showed a favorable decrease of −1.292 µm for FD and of −0.292 for SD.

The analysis procedure of these FVT allows to identify those animals that show changes in their genetic expressions according to their ability to adapt to the trajectory of the environmental circumstances that surround them. This is called Plasticity or Reaction Norm, a concept that has regained its importance in various scenarios of animal breeding (de Jong and Bijma, 2002). The published results using this approach, either in wild animals (Brommer et al., 2008); genotype environment interaction (Calus and Verkamp, 2003); tolerance to thermal stress (Carabaño et al., 2019) or shape of the lactation curve (Cobuci et al., 2007) have demonstrated the validity and possible impact of the procedure. In the context of this study, the term persistence is highly related to plasticity. It could be possible also to deal with a complementary parameter related to maintaining the same performance level in various stages of its productive life or at different reproductive states that can influence the variables (Cruz et al., 2017b); in this study throughout the ages to shearing. Fig. 8 presents a QQplot of the estimates of persistence according to MT and RRM with respect to the results of the classic RM model, the results indicate clearly that precisely the persistence increases in those animals considered as the best or worst depending on the model of the RM model. It should be considered that in this study the best animals are on the negative scale, that is, those producing finest fibers pattern.

Only the comparative results for FD are shown since SD showed the same answers. According to the properties of QQplot, it should be expected that the EBV distribution are distributed according to a straight line, similar to that presented in Fig. 4, however, this is not particularly true in the group of animals classified as elites with very obvious deviations. The results according to MT and RRM models show the same response forms, this group of animals must be the parents of the next generation, so that the current practice of applying selection according to a transversal model (RM model) can have an undesirable effect in terms of persistence of FD production. It should be pointing out that only 146 of the 300 animals selected according to the classic RM model were still the best in persistence. Nevertheless further studies are required.

5. Conclusion

In conclusion, the use of a transversal RM model used till present time of selection process in Pacomarca herd have provided important results of genetic progress. The MT and RRM models showed the same

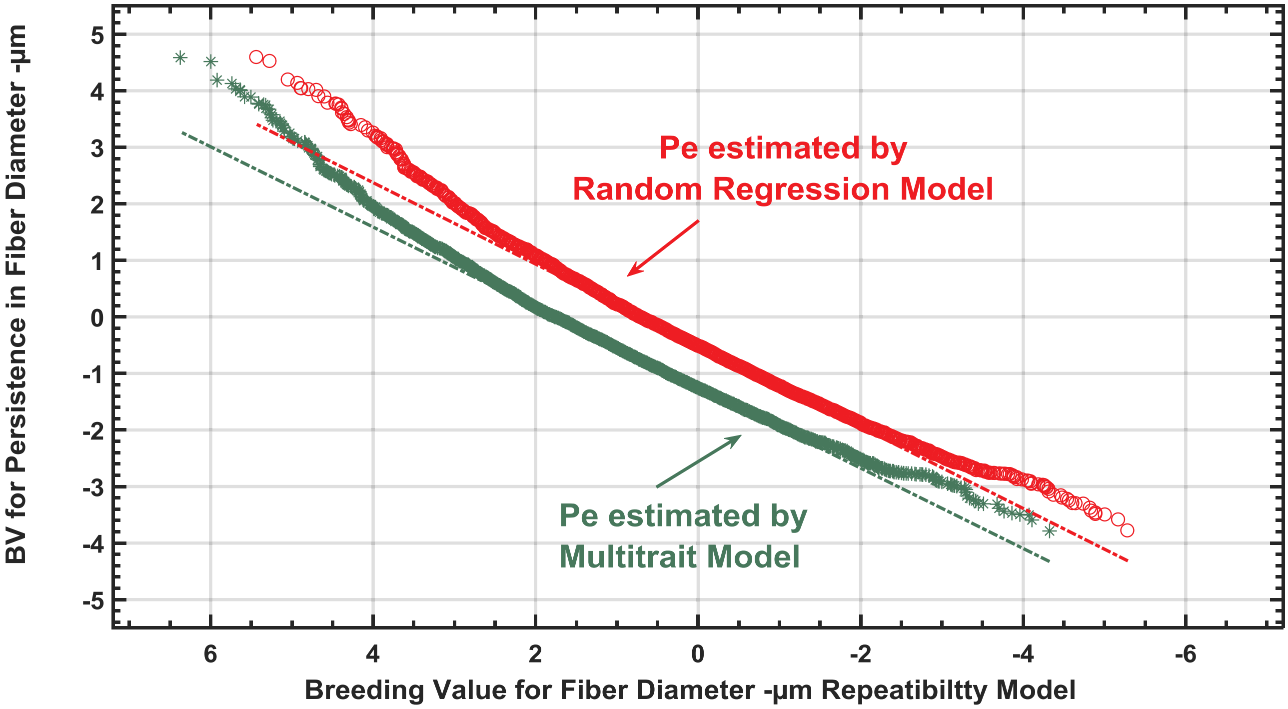

Fig. 8. QQplot for the persistence of estimated breeding values for fiber diameter (FD) estimated by multitrait model (MT) and random regression model, with respect to the repeatability model (RM).

expected response for both traits. Nevertheless, the RRM provided additional information that might be used to deal with persistence. The breeding program in Pacomarca could use a screening process based in the persistence results for the selection of the parents of the next generation. More research is needed to estimate the relationship between persistence and others economical important traits in alpacas.

Declaration of Competing Interest

There is no conflict of interest for this paper.

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Author Declaration

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.livsci.2019.103863.

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