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Genetic parameters for fleece uniformity in alpacas

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Abstract

Fiber diameter is the main selection objective and criterion in alpaca breeding programs, but it can vary across anatomic regions of the animal. As fiber diameter is usually registered from a unique sample from the mid side of the body, fiber diameter variability within fleece is never addressed and phenotypic and genetic differences may exist for fleece uniformity in alpaca populations. The objective of this work was to estimate the genetic parameters of fleece uniformity in an alpaca population. Fiber diameters measured in three different locations were used as repeated records of the same animal and studied for fitting a model that considers heterogeneous the residual variance of the model. Also, the logarithm of the standard deviation of the three measures was used as a measure of the fleece variability. Estimate of the additive genetic variance of the environmental variability was 0.43 ± 0.14, enough high to suggest the existence of wide room to select for fleece uniformity. Genetic correlation of the trait with its environmental variability was 0.76 ± 0.13 showing that fleece uniformity will be indirectly selected when aiming to reduce the fiber diameter. In the light of these parameters, and due to the cost of registering and the cost of opportunity, it looks no worthy to include uniformity as a selection criterion in alpaca breeding programs.

Lay Summary

The quality of alpaca fiber is mainly assessed by a low fiber diameter. However, the fiber diameter can greatly vary along the different body locations of the animal, the industry demands not only the fineness of the fiber but also the fleece uniformity. This work studied the genetic parameters related to fleece uniformity by analyzing the diameter of three samples from different body locations (mid side, shoulder, and thigh) under two different models of analysis. The results showed variability between sampling locations and the existence of important genetic variability susceptible to being used in alpaca selection. Nevertheless, selection based on a single measurement could be used as the high correlations between locations and between the trait and its variability, saving the cost of sample analyses, being the fleece uniformity indirectly selected.

Key words: alpaca, fiber diameter, fleece uniformity, heterogeneity

Abbreviations: CV, coefficient of variation; DIC, deviance information criterion;FD, fiber diameter; GCV, genetic coefficient of variation; HE, heterogeneity model; HO, homogeneity model; M, mid side; S, shoulder; SD, standard deviation; SDF, standard deviation across fleece; T, thigh

Introduction

The differences in price of the different categories of animal fiber are defined mainly by their diameter; the textile industry must deal with the problem of the fiber variability. In addition to the great differences between animals, the fiber diameter variability within the fleece also produces different fiber qualities, and this is transferred into economic losses that are finally derived by the fiber stakeholders, the breeders among them. The fleece uniformity has been of concern in animal breeding programs of fiber animals such as goats (Taddeo et al., 2000; McGregor and Butler, 2008), sheep (Scobie et al., 2015; Tao et al., 2017), and also alpacas (Aylan-Parker and McGregor, 2002; McGregor et al., 2012). Several studies have been carried out to evaluate this variability in alpacas, mainly analyzing the fiber diameter to choose the best sampling area (Aylan-Parker and McGregor, 2002; McGregor et al., 2012), or to predict the performance of the whole fleece from a sample (Aylan-Parker and McGregor, 2002).

Fleece uniformity has not been implemented in alpaca breeding programs. Instead, fiber diameter is the main selection objective and criterion (Gutiérrez et al., 2009). However, fiber diameter can vary along the different anatomical regions of the animal (Cruz, 2017). As this trait is usually registered in a sample from the mid side of the body, fiber diameter variability within fleece is never addressed, but genetic differences may exist for fleece uniformity in alpaca populations.

The cost of registering and analyzing fiber samples is important, particularly for the Altiplano farmers. In addition, the availability of sound datasets of alpaca breeding programs is still very scarce. Thus, no genetic analyses exist on fleece uniformity in alpacas. Fortunately, the dataset management software of the alpaca breeding population of Pacomarca

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Research Station has been shown to be very useful to estimate the genetic parameters of several traits (Gutiérrez et al., 2009; Cervantes et al., 2010; Cruz et al., 2015, 2017, 2019), and some information exists to deal with this issue.

On the other hand, models analyzing performance variability exist (SanCristobal-Gaudy et al., 1998) and have been proven to be useful to select a target of homogeneity (Formoso-Rafferty et al., 2016b, 2020). An alternative would be the use of homogeneous classical models to analyze the standard deviation of fiber diameter measured at different locations of an animal as a direct measure of variability.

The objective of this work was to estimate genetic parameters of fleece uniformity in the Pacomarca alpaca breeding population using heterogeneous and homogeneous models.

Material and Methods

The information proceeded from the daily routine registration of the Pacomarca Scientific Station (Pinares et al., 2018; Cruz et al., 2019) which complies with international legislation on animal ethics. Samples from 547 alpacas were taken from three different locations of the body, mid side (M), shoulder (S), and thigh (T) at two campaigns, at Pacomarca Research Station, counting 1,641 total records of white females of Huacaya ecotype. Records were taken in August 2003 (120), September 2003 (645), October 2002 (192), and December 2002 (684). There was only one shearing considered for each animal. Fiber analyses were done on washed samples after minicored and 2 mm snippets using an Optical Fibre Diameter Analyser (IWTO-47-95). Fiber diameter (FD) and standard deviation (SD) were measured in each location being considered as repetitions of the same FD and SD traits, but also, they were analyzed as independent traits (FDM, FDS, FDT, SDM, SDS, and SDT). Finally, standard deviation of the three FD measures within fleece (FDM, FDS, and FDT) was computed and understood as a measure of diameter variability across the fleece. Due to the right skewed distribution of the standard deviation of these three measures of FD within animal, natural logarithm of this standard deviation was taken to convert it to a Gaussian distribution, and this was taken as the trait measuring variability across fleece (SDF). Distribution of both the standard deviation of the FD and SDF is shown in Figure 1. Age of the animals ranged from 512 to 3,402 d and distributed among 25, 90, 111, 178, 88, 37, 14, and 4 animals from 1 to 8 years old respectively.

There were 1,085 animals in the pedigree file, with 77 different dams and 16 different sires. Of the 547 females with their own record, 125 had offspring in the data.

Mean ± standard deviation of FDM, FDS, FDT, SDM, SDS, SDT, and SDF traits resulted in 21.78 ± 2.76, 21.96 ± 2.87, 22.21 ± 2.85, 5.08 ± 0.98 5.36 ± 2.07, 5.44 ± 1.39, and −0.17 ± 0.32 (Table 1). Coefficient of variation (CV) of FD was very uniform across locations while SD was not, being SDM with the lowest CV.

Models assuming heterogeneity (HE) in the residuals were fitted besides classical homogeneity models (HO) to analyze FD. Under HE model, FD is considered as a unique trait, with different locations assumed as repetitions of the same trait, fitting the model with a genetic breeding value for the FD trait and another one for the environmental variability of FD trait. HE model definition was:

$$y_i = \mathbf{x_i b} + \mathbf{z_i a} + \mathbf{w_i c} + \mathrm{e}^{1/2(\mathbf{x_i b*} + \mathbf{z_i a*} + \mathbf{w_i c*})}\varepsilon_i$$

and

$$\begin{pmatrix} \mathbf{a} \\ \mathbf{a*} \\ \mathbf{c} \\ \mathbf{c*} \end{pmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{A}\rho\sigma_a\sigma_{a*} & 0 & 0 \\ \mathbf{A}\rho\sigma_a\sigma_{a*} & \mathbf{A}\sigma_{a*}^2 & 0 & 0 \\ 0 & 0 & \mathbf{I_c}\sigma_c^2 & 0 \\ 0 & 0 & & \mathbf{I_c}\sigma_{c*}^2 \end{bmatrix} \right)$$

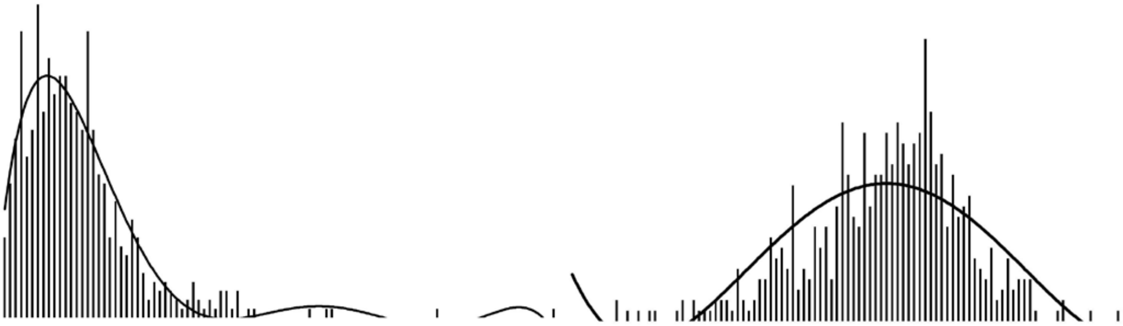

Figure 1. Distribution and fitted trends of standard deviation of fiber diameter in three body locations (left) and of its natural logarithm (right).

Table 1. Statistic description of fiber traits in three body locations in alpacas

	FDM	FDS	FDT	SDM	SDS	SDT	SDF
Mean	21.78	21.96	22.22	5.08	5.36	5.44	−0.17
SD	2.76	2.87	2.85	0.98	2.07	1.39	0.32
CV	0.13	0.13	0.13	0.19	0.39	0.26	−1.84
Minimum	16.00	14.69	15.71	2.25	3.02	3.32	−1.45
Maximum	34.74	35.95	36.87	11.67	46.20	21.70	0.77

FD, fiber diameter of mid side (M), shoulder (S), and thigh (T); SD, standard deviation of mid side (M), shoulder (S), thigh (T), and along of the fleece (F); CV, coefficient of variation.

where y_i is the ith FD, $\mathbf{b}$ and $\mathbf{b}^*$ are the vectors for systematic effects, $\mathbf{a}$ and $\mathbf{a}^*$ are the vectors of the 1,085 additive genetic effects, $\mathbf{c}$ and $\mathbf{c}^*$ are the vectors of the 547 permanent effects, * means the effect affecting the environmental variability, $\mathbf{x}_i$, $\mathbf{z}_i$, and $\mathbf{w}_i$ are the incidence vectors for systematic, animal, and permanent effects, respectively, $\mathbf{I}_c$ is the identity matrix of equal order to the number of animals recorded (547), $\mathbf{A}$ is the numerator relationship matrix, σ_a^2 and σ_{a*}^2 are the additive genetic variances affecting the trait and its environmental variability, σ_c^2 and σ_{c*}^2 are the permanent environmental variances affecting the trait and its environmental variability, and ρ is the genetic correlation between the trait and the variability. ε_i is an unscaled residual: $\varepsilon_i \sim N(0,1)$. Note that under this model, the scale of the residual is explained by an exponential function that depends on systematic and random effects including an additive genetic effect (a^*) and a permanent effect (c^*) among them that can be solved via Bayesian methodology (Gutierrez et al., 2006).

Month*year of shearing (4 levels) and body location (3 levels) were fitted as systematic class effects and age at shearing as a linear covariate.

In order to keep the estimability of the corresponding linear combination, solutions for all the levels of each of the other systematic effects were averaged within the effect and added to the solution for a particular desired level of the systematic effect (Formoso-Rafferty et al., 2017). Therefore, the estimated mean value of FD for a particular level l of a systematic effect s was:

$$\hat{\mu}_{sl} = \sum_{i=1,\text{systematic}}^{i\neq s} \left(\sum_{j=1,n_s} \frac{\hat{b}_{ij}}{n_s} \right) + \hat{b}_{sl}$$

Similarly, the overall mean of the FD in a hypothetic average scenario of levels defined by the systematic effects conditions, was estimated as

$$\hat{\mu} = \sum_{i=1,\text{systematic}} \left(\sum_{j=1,n_s} \frac{\hat{b}_{ij}}{n_s} \right)$$

Conversely, and in order to provide estimates of some genetic parameters, a residual variance in an average scenario was estimated as

$$\hat{\sigma}_e^2 = \exp\left(\sum_{i=1,\text{systematic}} \left(\sum_{j=1,n_s} \frac{\hat{b}_{ij}^*}{n_s} \right) + \frac{\sigma_{a*}^2}{2} + \frac{\sigma_{c*}^2}{2} \right)$$

It allowed to obtain a global heritability value ($\hat{h}^2 = \hat{\sigma}_a^2/(\hat{\sigma}_a^2 + \hat{\sigma}_c^2 + \hat{\sigma}_e^2)$) as well as a ratio of the permanent environmental variance over the phenotypic variance ($\hat{c}^2 = \hat{\sigma}_c^2/(\hat{\sigma}_a^2 + \hat{\sigma}_c^2 + \hat{\sigma}_e^2)$). Similarly, residual variances in the specific levels l of the systematic effect s, were computed as

$$\hat{\sigma}_{e_{sl}}^2 = \exp\left(\sum_{i=1,\text{systematic}}^{i\neq s} \left(\sum_{j=1,n_s} \frac{\hat{b}_{ij}^*}{n_s} \right) + \hat{b}_{sl}^* + \frac{\sigma_{a*}^2}{2} + \frac{\sigma_{c*}^2}{2} \right).$$

These expressions are extensions of the methodology by Formoso-Rafferty et al. (2017) to estimate heritabilities at particular levels of systematic effects.

Equation of the HO model was

$$y_i = \mathbf{x}_i\mathbf{b} + \mathbf{z}_i\mathbf{a} + \mathbf{w}_i\mathbf{c} + e_i$$

and,

$$\begin{pmatrix} \mathbf{a} \\ \mathbf{c} \\ \mathbf{e} \end{pmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 & 0 \\ 0 & \mathbf{I}_c\sigma_c^2 & 0 \\ 0 & 0 & \mathbf{I}_e\sigma_e^2 \end{bmatrix} \right)$$

where all is as in the HE model, being $\mathbf{e}$ the vector of residuals, $\mathbf{I}_e$ the identity matrix of equal order to the number of records (1,641), and σ_e^2 the residual variance. HE and HO models were solved using the GSEVM program (Ibañez-Escriche et al., 2010), in order to count with a deviance information criterion (DIC) value for both models (Spiegelhalter et al., 2002) to decide which model had a better fit. Prediction criterion was not used to compare models as HO model does not provide breeding values for variability. Given the Bayesian procedure used by this software, estimates across the text will be provided as the means and the standard deviations of the marginal posterior distributions of each parameter. Significance of estimated parameters was assumed when the interval including the mean plus 1.98 times this standard deviation did not include the zero.

A variance component estimation by Restricted Maximum Likelihood model under a multivariate analysis was also carried out fitting an HO model as above involving FDM, FDS, FDT, SDM, SDS, SDT, and SDF traits, but in which permanent environmental effect was not fitted. VCE program (Neumaier and Groeneveld, 1998) was used to perform the multivariate analysis.

Results

Estimates of the genetic parameters of FD both under HO and HE models are shown in Table 2. Heritability and c^2 ratios ± standard deviations were, respectively, 0.65 ± 0.17 and 0.21 ± 0.17 under the HE model, and 0.83 ± 0.03 and 0.04 ± 0.03 under the HO model. Sample size was large enough to provide significant parameters for heritabilities and genetic correlations. DIC value was clearly lower (better) under the HE model suggesting a much better fit of the trait under the HE model. For this reason, only results from HE model will be commented below. $\hat{\sigma}_{a*}^2$ was 0.43 ± 0.14 showing there is a considerable room for improvement of the fleece uniformity by artificial selection. The estimated genetic correlation between the FD and its environmental variability was very high (0.76 ± 0.13), suggesting that fleece uniformity would be indirectly selected when selecting for fineness.

Systematic effects influenced the fiber diameter as shown in Figure 2. The month*year of shearing was the effect most affecting FD, ranging from 21.2 µm (August 2003) to 22.6 µm (December 2002). FD was finer in the usual body place where the samples are usually taken for performance recording, the mid side of the animal (21.6 µm), and slightly thicker in the shoulder (21.7 µm) and thigh (21.9 µm).

Residual variance ranged across levels of systematic effects leading to differences among them in fiber diameter heritability (Figure 3), from shoulder location (0.62 ± 0.16) to mid side location (0.67 ± 0.17). Age affected the residual variance leading to a range of heritability from 0.63 ± 0.16 to 0.68 ± 0.18.

Table 2. Means and standard deviations of the marginal posterior distributions of the additive genetic variance for the trait $(\hat{\sigma}_a^2)$ and the environmental variability $(\hat{\sigma}_{a*}^2)$, of the corresponding permanent environmental variances ($\hat{\sigma}_c^2$ and $\hat{\sigma}_{c*}^2$), of the residual variance $(\hat{\sigma}_e^2)$, the heritability $(\hat{h}^2)$ and permanent environmental variance $(\hat{c}^2)$ ratios, and the DIC value under both the heterogeneous and homogeneous models

	Heterogeneous model	Homogeneous model
$\hat{\sigma}_a^2$	4.74 ± 1.26	6.36 ± 0.50
$\hat{\sigma}_{a*}^2$	0.43 ± 0.14	-
$\hat{\rho}$	0.76 ± 0.13	-
$\hat{\sigma}_c^2$	1.53 ± 1.22	0.30 ± 0.25
$\hat{\sigma}_{c*}^2$	0.23 ± 0.12	-
$\hat{\sigma}_e^2$	1.00 ± 0.09	1.02 ± 0.04
$\hat{h}^2$	0.65 ± 0.17	0.83 ± 0.03
$\hat{c}^2$	0.21 ± 0.17	0.04 ± 0.03
DIC	1,815.44	2,212.19

DIC, deviance information criterion.

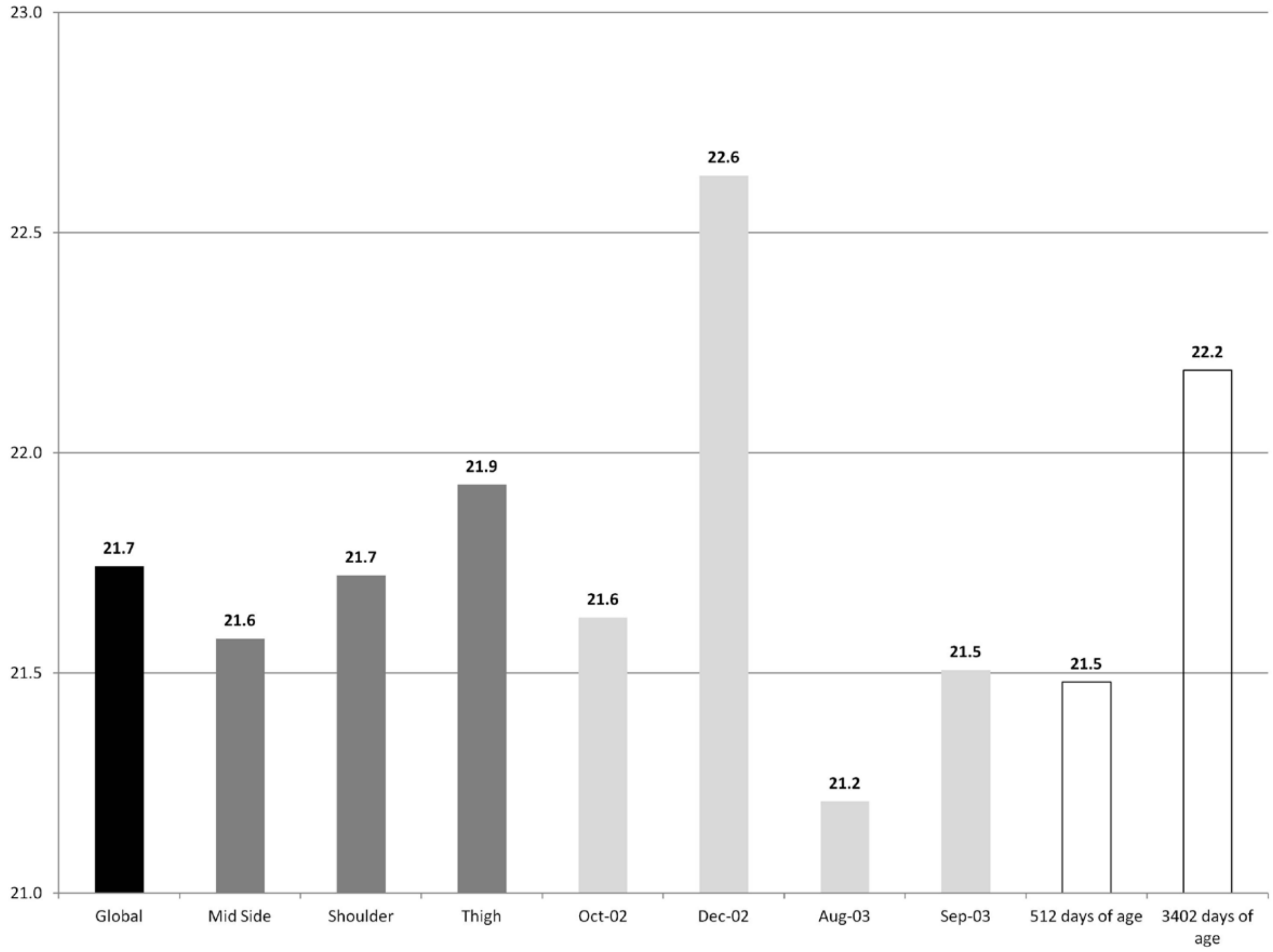

Figure 2. Estimates of the global fiber diameter and by levels of systematic effects in an average scenario of the conditions defined by the systematic effects estimated under a heteroscedastic model.

Estimates of the heritability and genetic and phenotypic correlations of SDF, FDM, FDS, FDT, SDM, SDS, and SDT obtained from a homogeneous multivariate model are shown in Table 3. Heritabilities for all traits were higher than 0.50 ranging from 0.50 for SDS to 0.61 for SDF. Phenotypic correlations were consistent with the genetic correlations and generally some lower in absolute value. All the genetic correlations were mostly significant and positive ranging from 0.11 between SDF and SDS, to 0.88 between FDM and FDS. Genetic correlations among diameter traits were between 0.86 and 0.88, and in a lower range between 0.33 and 0.68 among standard deviation within location traits. Genetic

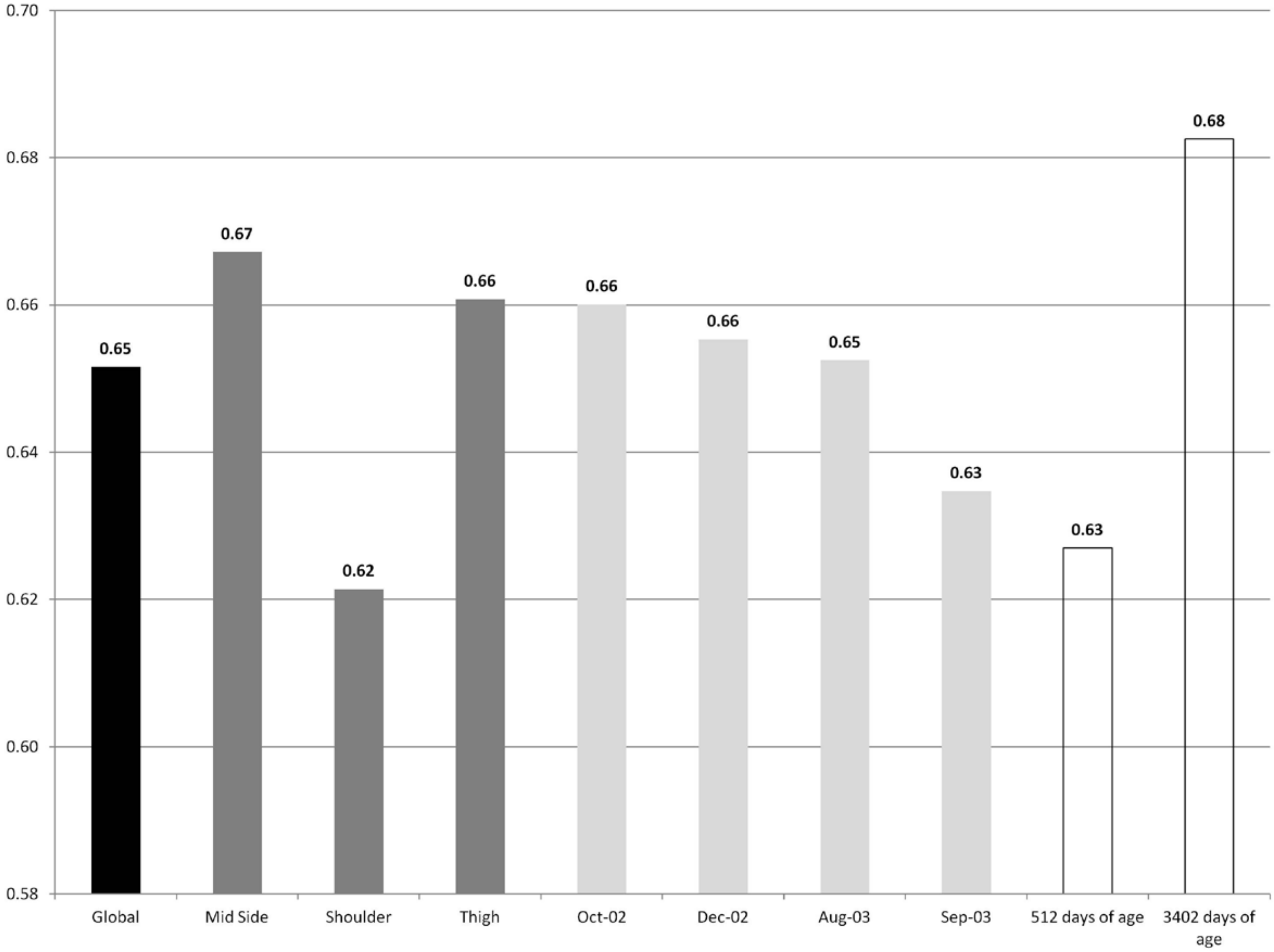

Figure 3. Estimates of the global heritability of the fiber diameter and by levels of systematic effects in an average scenario of the conditions defined by the systematic effects estimated under a heteroscedastic model.

Table 3. Estimates of the heritability (diagonal) and genetic correlations (above diagonal) ± standard error, and phenotypic correlations (below diagonal) of the logarithm of the standard deviation of fiber diameter across body locations (SDF), fiber diameter at mid side (FDM), shoulder (FDS), and thigh (FDT), and the corresponding standard deviations (SDM, SDS, and SDT) obtained from a homogeneous multivariate model

	SDF	FDM	FDS	FDT	SDM	SDS	SDT
SDF	0.61 ± 0.05	0.35 ± 0.06	0.41 ± 0.06	0.51 ± 0.05	0.32 ± 0.07	0.11 ± 0.07	0.35 ± 0.06
FDM	0.17	0.53 ± 0.04	0.88 ± 0.02	0.88 ± 0.02	0.63 ± 0.04	0.29 ± 0.06	0.42 ± 0.05
FDS	0.22	0.88	0.55 ± 0.04	0.86 ± 0.02	0.59 ± 0.04	0.34 ± 0.05	0.44 ± 0.05
FDT	0.29	0.88	0.85	0.58 ± 0.04	0.60 ± 0.04	0.30 ± 0.06	0.55 ± 0.05
SDM	0.19	0.60	0.56	0.57	0.53 ± 0.04	0.43 ± 0.05	0.68 ± 0.04
SDS	0.06	0.28	0.33	0.29	0.44	0.50 ± 0.04	0.33 ± 0.06
SDT	0.21	0.37	0.39	0.21	0.67	0.33	0.53 ± 0.04

correlations between SDF and diameter traits ranged from 0.35 (with FDM) to 0.51 (with FDT), while those between SDF and within sample standard deviation traits were some lower, from 0.11 (with SDS) to 0.35 (with SDT).

Discussion

Fleece uniformity, understood as a low fiber diameter variability across the alpaca fleece, has been of long concern in alpaca fiber production, both from the farm and the textile industry sides (Quispe et al., 2013; Cruz, 2017). McGregor et al. (2012) also reported phenotypic differences in fiber diameter depending on sampling locations. The fiber diameter genetic variability has been traditionally studied within body location registering the SD or CV of the fiber diameter in a unique place, usually from a mid side sample of the animal body (Gutiérrez et al., 2009; Cervantes et al., 2010), or accounting for the variability across the age of the animals (Gutierrez et al., 2011; Cruz et al., 2020b). Sometimes genetic parameters obtained from such analyses have been understood to establish that there was a relationship between the diameter uniformity within sample and fleece uniformity (Aguilar et al., 2019). In this work, the fleece uniformity, and rather the opposite, the fleece variability, has been studied by analyzing samples taken from the same fleece in different locations.

The treatment of repeated information with the search of the homogeneity of several traits by artificial selection has been of research concern for long (Scheiner and Lyman, 1991; Gutierrez et al., 2006). Models involving this aim have been developed, and the one used here (SanCristobal-Gaudy et al., 1998) has been previously shown to be very useful in different species to estimate genetic parameters (Tatliyer et al., 2019), and specifically in alpacas (Gutierrez et al., 2011; Cruz et al., 2020a), obtaining additional benefits in robustness and welfare (Formoso-Rafferty et al., 2022) when analyzed. The use of the predicted breeding values provided by this model to select animals has also been successful in experimental populations such as rabbits and mice (Formoso-Rafferty et al., 2016b, 2017; Blasco et al., 2017) to modify the traits variability. Then this model has been applied in this case. On the other hand, to compare with a more intuitive approach under a less complex model directly dealing with a measure of variability such as the standard deviation, the natural logarithm of this parameter has been analyzed here as a trait (SDF) under a classical HO model.

Results obtained under the HE model suggested that the selection for uniformity would be successful. The additive genetic variance for the environmental variability is a parameter that does not depend on the scale of the trait, and its square root value roughly represents the genetic coefficient of variation (GCV) of the variability (Hill and Mulder, 2010). Tatliyer et al. (2019) reported that the GCV values in the literature never surpassed 0.69, and the square root of the variance estimated here was 0.64 ± 0.11, showing that the possibilities of selection for fleece uniformity using predicted breeding values from this model would be highly promising. The other parameter of interest estimated under the HE model is the genetic correlation between the trait and the variability. Formoso-Rafferty et al. (2016a) in a divergent selection experiment for birth weight environmental variability in mice reported a strongly correlated selection response in birth weight itself having estimated a genetic correlation of 0.32 (Tatliyer et al., 2019). The genetic correlation obtained here was more than double, so a double response would be expected in this case. Conversely, it would also be expected an important improvement in the fleece uniformity if selected for fiber diameter.

Similar statements were concluded from the genetic parameters obtained from the multivariate HO model. All the heritabilities were overestimated if compared with the same parameter obtained previously in the same population from 0.32 to 0.41 (Gutiérrez et al., 2009, 2014; Cervantes et al., 2010; Cruz et al., 2015, 2019; Mancisidor et al., 2021) probably because dealing with only one record per animal, the permanent environmental effect cannot be fitted, and this one and the additive genetic effect were confounded. Thus, for example, the estimated FDM and SDM heritabilities were both 0.53 ± 0.04, even lower than those estimated by Cruz et al. (2020b) using random regression models that ranged from 0.56 to 0.61 for FD and from 0.56 to 0.70 for SD. Considering the possible overestimation of the heritabilities in this case, SDF provided even the highest estimated heritability (0.61 ± 0.05), confirming the presence of important genetic variability for uniformity that would predict sound genetic response if selecting against fleece variability. Genetic correlations of SDF with the other traits also led to optimism about the expectable correlated responses in FD and SD, but to less extent than the HE model, given that the genetic correlations ranged from 0.35 to 0.51 for fiber diameter and from 0.11 to 0.35 for standard deviations depending on location. Therefore, genetic correlations between the trait measuring the variability between locations (SDF) and variability within location (SDM, SDS, and SDT) were moderate but not high showing that the within variability is a poor indicator of the lack of fleece uniformity. The conclusion by Aguilar et al. (2019) would not be supported. However, those correlations of SDF with traits addressing thickness (FDM, FDS, and FDT) were also moderate but some were higher than the previous ones, suggesting that selection to reduce the fiber diameter will also bring about an increase in the uniformity.

The phenotypic correlations of the FD between FDM and other parts (0.85–0.88) were similar to those reported by McGregor et al. (2012) in Peruvian alpacas (0.902) and Aylan-Parker and McGregor (2002) in Australian alpacas (0.89). These authors concluded that although there is phenotypic variability, the mid side can be the body location of choice to evaluate the quality of an alpaca (Aylan-Parker and McGregor, 2002; McGregor et al., 2012). Similar reasoning was made for other species such as goats (Taddeo et al., 2000; McGregor and Butler, 2008), sheep (Scobie et al., 2015), and vicugnas (Quispe et al., 2014). However, no phenotypic correlations between sampling sites for standard deviation were reported so far.

Another interesting point of view is derived from the phenotypic and genetic correlations between different locations. Fiber diameter trended to appear as measures of the same trait (genetic correlations between 0.86 and 0.88), but standard deviation within samples seems to be less related (genetic correlations between 0.33 and 0.67).

Estimated partial means for fiber diameter and for heritability depending on the levels of the location systematic effect obtained by the HE model, can help to understand the traits behavior in different locations. Differences between systematic effects existed but they were not dramatic for the mean or for the variability (Figures 2 and 3), with the exception of the age on the variability, even more if it is noted that the age range in the sampled animals did not include youngest animals that are by far the finest (Gutierrez et al., 2011; Cruz et al., 2020b) and most uniform. Concerning FD, mid side was the location with the lowest value, but differences were neither important nor significant. However, residual variance appeared higher at the shoulder location than the others, leading to a sensitive reduction in the estimated heritability at this location. Causes of variability in this location seemed to be somehow different than the others and less related to fleece variability, highlighted also by the low genetic correlation of SDS with SDF (0.11 ± 0.05) under the HO multivariate model, and by the lowest heritability of SDS among the SD traits in this same model. Summarizing, consistency seemed to exist among FD in different locations but it was much lower among SD measures in the same fleece.

Uniformity heritability was clearly appreciable and even higher than that for other fiber traits, showing that there were genetic differences in uniformity across the population. However, to our knowledge, fleece uniformity has not been used as a selection criterion in fiber industry for any species. However, the decision of including the uniformity as a selection criterion has to be carefully studied. First, the inclusion of the uniformity among the main selection objectives is doubtful when the industry and the national and international markets do not financially incentivize it at present. Second, the decision to partially select for uniformity would entail an opportunity cost by losing the possibility of selecting for other traits that are economically valued, such as fineness or reducing medullation. Third, selecting for uniformity multiplies the cost of registering and mainly analyzing several samples. In addition, it must be noted that the estimated high genetic correlation between fleece uniformity and fineness informs about the expected favorable correlated response in uniformity when selecting for fineness. And finally, the high genetic correlation between fiber diameter in different locations supposes that selecting to reduce the diameter in one location will bring about the reduction in all the other locations, even when this reduction will vary across animals according to the high heritability estimated in the uniformity. Consequently, efforts to increase uniformity seem not worthy.

Conclusion

Considerable genetic variation has been found in fleece uniformity in alpacas. Although this is very encouraging to develop a breeding program to reduce the variability of the fiber diameter within the fleece, a highly correlated genetic response is expected to reduce the fiber diameter in a unique location, due to the high genetic correlation between fiber fineness in a unique sample. Fleece uniformity and the high genetic correlation between diameter in different locations could save the cost of taking and analyzing several samples of the same fleece.

Conflict of Interest Statement

The authors declare no conflict of interest.

References

Aguilar, H., G. Gutiérrez, and M. Wurzinger. 2019. Parámetros genéticos de caracteres asociados a la uniformidad del diámetro de fibra en alpacas Huacaya en Puno, Perú. *Rev. Inv. Vet. Perú*. 30:1150–1157. doi:10.15381/rivep.v30i3.15370.

Aylan-Parker, J., and B. A. Mcgregor. 2002. Optimising sampling techniques and estimating sampling variance of fleece quality attributes in alpacas. *Small Rumin. Res.* 44:53–64. doi:10.1016/S0921-4488(02)00038-X.

Blasco, A., M. Martínez-Álvaro, M. L. García, N. Ibáñez-Escriche, and M. J. Argente. 2017. Selection for environmental variance of litter size in rabbits. *Genet. Sel. Evol.* 49:48–55. doi:10.1186/s12711-017-0323-4.

Cervantes, I., M. A. Pérez-Cabal, R. Morante, A. Burgos, C. Salgado, B. Nieto, F. Goyache, and J. P. Gutiérrez. 2010. Genetic parameters and relationships between fibre and type traits in two breeds of Peruvian alpacas. *Small Rumin. Res.* 88:6–11. doi:10.1016/j.smallrumres.2009.10.016.

Cruz, A. 2017. *Parámetros genéticos de caracteres funcionales y secundarios en alpacas* [*Doctoral thesis*]. Madrid, España: Universidad Complutense de Madrid.

Cruz, A., I. Cervantes, A. Burgos, R. Morante, and J. P. Gutierrez. 2015. Estimation of genetic parameters for reproductive traits in alpacas. *Anim. Reprod. Sci.* 163:48–55. doi:10.1016/j.anireprosci.2015.09.017.

Cruz, A., I. Cervantes, A. Burgos, R. Morante, and J. P. Gutierrez. 2017. Genetic parameters estimation for preweaning traits and their relationship with reproductive, productive and morphological traits in alpaca. *Animal*. 11:746–754. doi:10.1017/S175173111600210X.

Cruz, A., J. P. Gutierrez, R. Torres, N. Formoso-Rafferty, R. Morante, A. Burgos, and I. Cervantes. 2020a. Calving date and its variability as a potential trait in the breeding objective to account for reproductive seasonality in alpacas. *Reprod. Domest. Anim.* 55:814–821. doi:10.1111/rda.13689.

Cruz, A., A. Menéndez-Buxadera, G. Gutiérrez, R. Morante, A. Burgos, and J. P. Gutiérrez. 2020b. Genetic (co)variance across age of fiber diameter and standard deviation in Huacaya alpacas, estimated by repeatability, multi-trait and random regression models. *Livest. Sci.* 231:103863. doi:10.1016/j.livsci.2019.103863.

Cruz, A., R. Morante, J. P. Gutiérrez, R. Torres, A. Burgos, and I. Cervantes. 2019. Genetic parameters for medullated fiber and its relationship with other productive traits in alpacas. *Animal*. 13:1358–1364. doi:10.1017/S1751731118003282.

Formoso-Rafferty, N., I. Cervantes, N. Ibanez-Escriche, and J. P. Gutierrez. 2016a. Correlated genetic trends for production and welfare traits in a mouse population divergently selected for birth weight environmental variability. *Animal*. 10:1770–1777. doi:10.1017/S1751731116000860.

Formoso-Rafferty, N., I. Cervantes, N. Ibanez-Escriche, and J. P. Gutierrez. 2016b. Genetic control of the environmental variance for birth weight in seven generations of a divergent selection experiment in mice. *J. Anim. Breed. Genet.* 133:227–237. doi:10.1111/jbg.12174.

Formoso-Rafferty, N., I. Cervantes, N. Ibañez-Escriche, and J. P. Gutiérrez. 2017. Modulating birth weight heritability in mice. *J. Anim. Sci.* 95:531–537. doi:10.2527/jas.2016.1169.

Formoso-Rafferty, N., K. N. Chavez, C. Ojeda, I. Cervantes, and J. P. Gutierrez. 2020. Selection response in a divergent selection experiment for birth weight variability in mice compared with a control line. *Animals*. 10:1–12. doi:10.3390/ani10060920.

Formoso-Rafferty, N., J. P. Gutierrez, A. Garcia-Alvarez, T. Perez, and I. Cervantes. 2022. Impact of selection for birth weight variability on reproductive longevity: a mice model. *J. Anim. Breed. Genet.* 139:370–379. doi:10.1111/jbg.12676.

Gutiérrez, J. P., I. Cervantes, M. A. Perez-Cabal, A. Burgos, and R. Morante. 2014. Weighting fibre and morphological traits in a genetic index for an alpaca breeding programme. *Animal*. 8:360–369. doi:10.1017/S1751731113002358.

Gutiérrez, J. P., F. Goyache, A. Burgos, and I. Cervantes. 2009. Genetic analysis of six production traits in Peruvian alpacas. *Livest. Sci.* 123:193–197. doi:10.1016/j.livsci.2008.11.006.

Gutierrez, J. P., B. Nieto, P. Piqueras, N. Ibanez, and C. Salgado. 2006. Genetic parameters for canalisation analysis of litter size and litter weight traits at birth in mice. *Genet. Sel. Evol.* 38:445–462. doi:10.1186/1297-9686-38-5-445.

Gutierrez, J. P., L. Varona, A. Pun, R. Morante, A. Burgos, I. Cervantes, and M. A. Perez-Cabal. 2011. Genetic parameters for growth of fiber diameter in alpacas. *J. Anim. Sci.* 89:2310–2315. doi:10.2527/jas.2010-3746.

Hill, W. G., and H. A. Mulder. 2010. Genetic analysis of environmental variation. *Genet. Res.* 92:381–395. doi:10.1017/S0016672310000546.

Ibañez-Escriche, N., M. García, and D. Sorensen. 2010. GSEVM v.2: MCMC software to analyze genetically structured environmental variance models. *J. Anim. Breed. Genet.* 127:249–251. doi:10.1111/j.1439-0388.2009.00846.x.

Mancisidor, B., A. Cruz, G. Gutiérrez, A. Burgos, J. Moron, M. Wurzinger, and J. P. Gutiérrez. 2021. ssGBLUP method improve the accuracy of breeding value prediction in Huacaya alpaca. *Animals*. 11:3052. doi:10.3390/ani11113052.

Mcgregor, B. A., and K. L Butler. 2008. Variation of mean fibre diameter across mohair fleeces: implications for within flock animal selection, genetic selection, fleece classing and objective sale lot building. *Small Rumin. Res.* 75:54–64. doi:10.1016/j.smallrumres.2007.08.003.

Mcgregor, B. A., H. E. Ramos, and E. C Quispe Peña. 2012. Variation of fibre characteristics among sampling sites for Huacaya alpaca fleeces from the High Andes. *Small Rumin. Res*. 102:191–196. doi:10.1016/j.smallrumres.2011.07.016.

Neumaier, A., and E. Groeneveld. 1998. Restricted maximum likelihood estimation of covariances in sparse linear models. *Genet. Sel. Evol*. 30:3–26. doi:10.1186/1297-9686-30-1-3.

Pinares, R., G. A. Gutiérrez, A. Cruz, R. Morante, I. Cervantes, A. Burgos, and J. P. Gutiérrez. 2018. Heritability of individual fiber medullation in Peruvian alpacas. *Small Rumin. Res*. 165:93–100. doi:10.1016/j.smallrumres.2018.04.007.

Quispe, E., A. Poma, and A. Purroy. 2013. Características productivas y textiles de la fibra de alpacas de raza huacaya. *Rev. Complut. Cienc. Vet*. 7:1–29. doi:10.5209/rev_RCCV.2013.v7.n1.41413.

Quispe, E., F. Sánchez, J. B. Filella, and L. A. Ruiz. 2014. Variation of commercially important characteristics among sampling sites for vicuña (vicugna vicugna mensalis) fleeces. *J. Camelid Sci*. 7:1–14.

Sancristobal-Gaudy, M., J. -M. Elsen, L. Bodin, and C. Chevalet. 1998. Prediction of the response to a selection for canalisation of a continuous trait in animal breeding. *Genet. Sel. Evol*. 30:423–451. doi:10.1186/1297-9686-30-5-423.

Scheiner, S. M., and R. F. Lyman. 1991. The genetics of phenotypic plasticity. II. Response to selection. *J. Evol. Biol*. 4:23–50. doi:10.1046/j.1420-9101.1991.4010023.x.

Scobie, D. R., A. J. Grosvenor, A. R. Bray, S. K. Tandon, W. J. Meade, and A. M. B. Cooper. 2015. A review of wool fibre variation across the body of sheep and the effects on wool processing. *Small Rumin. Res*. 133:43–53. doi:10.1016/j.smallrumres.2015.10.025.

Spiegelhalter, D. J., N. Best, B. P. Carlin and A. Van Der Linde. 2002. Bayesian measures of model complexity and fit. *J. R. Statist. Soc. B*. 64:583–639. doi:10.1111/1467-9868.00353.

Taddeo, H. R., L. Duga, D. Almeida, P. Willems, and R. Somlo. 2000. Variation of mohair quality over the body in Angora goats. *Small Rumin. Res*. 36:285–291. doi:10.1016/s0921-4488(99)00116-9.

Tao, J., H. Zhou, H. Gong, Z. Yang, Q. Ma, L. Cheng, W. Ding, Y. Li, and J. G. H. Hickford. 2017. Variation in the KAP6-1 gene in Chinese Tan sheep and associations with variation in wool traits. *Small Rumin. Res*. 154:129–132. doi:10.1016/j.smallrumres.2017.08.001.

Tatliyer, A., I. Cervantes, N. Formoso-Rafferty, and J. P. Gutiérrez. 2019. The statistical scale effect as a source of positive genetic correlation between mean and variability: a simulation study. *G3*. 9:3001–3008. doi:10.1534/g3.119.400497.