

Genetic parameters for growth of fiber diameter in alpacas¹

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ABSTRACT: The alpaca is the most important fiber producer of the South American camelid species, and is an important source of income for the Andean communities. Nowadays, fiber diameter is considered the main selection objective in alpaca populations throughout the world. However, fiber diameter increases with the age of the animals, and it would be preferable to select those animals that maintain a thin fiber throughout their life span. The goal of this study was to describe the genetic relationship between fiber diameter at weaning age (6 mo) and the evolution of fiber diameter along the life span. The analysis of the evolution of fiber diameter was studied as a useful model for canalization and as a longitudinal trait by hierarchical Bayesian analysis. The results suggested that substantial genetic variation exists for fiber diameter and also for the variability and linear growth of the fiber diameter. Thus, a genetic selection program is plausible to modify the evolution of fiber diameter with time, together with a favorable correlated decrease in fiber diameter.

Key words: alpaca, Bayesian analysis, camelid, fiber diameter

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INTRODUCTION

Fiber diameter is currently considered the main selection goal in alpaca populations throughout the world. However, fiber diameter increases with age, and it would be preferable to select those animals with the thinnest fiber that also maintain this fiber diameter throughout their life span. There is thus an interesting double variability to be reduced: the variability within the fleece and the variability between different shearing periods. The first is easily measured by the SD or the CV of the fiber diameter. However, the variability between different shearings has not yet been addressed. Although estimates of genetic parameters are required to design effective genetic improvement programs, no genetic relationship between fiber diameter and its variability has been ascertained in alpacas (Gutiérrez et al., 2009).

Heterogeneity has been analyzed based on the hypothesized existence of one pool of genes controlling the mean of performance and another controlling the homogeneity of performance when the environment is

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modified (Schneider and Lyman, 1991). SanCristobal- Gaudy et al. (1998) developed a model to deal with the genetics of variability, which has been widely used (Yang, 2010). The evolution of fiber diameter can be also studied as a longitudinal trait by the Bayesian procedure for the analysis of production functions described by Varona et al. (1997), which allows each performance to be modeled as a function of time. This procedure has been used in several studies (Forni et al., 2007).

Thus, the aim of this study was to estimate the genetic parameters of the variability of different performances of the mean fiber diameter by using 2 models, one based on the heterogeneity of environmental variability and the second based on describing the growth of the fiber.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because data were obtained from an existing database (Paco_pro, Pacomarca S.A.).

Data

Production data and pedigree information on a Huacaya breed population were obtained from the experimental Pacomarca ranch, as registered in the performance-recording software Paco Pro (http://www.pacomarca.com/pacomarca/paco_pro_en.htm) developed by Pacomarca S.A., which can be used to gather relevant production and genealogical data. Details about the farm can be found in Cervantes et al. (2010). Records obtained from the Paco Pro database were edited to exclude animals with identification errors or ambiguous birth dates. The data set consisted of a pedigree of 4,173 individuals of the Huacaya breed and 8,405 records of fiber diameter corresponding to 3,257 individuals, which corresponds to 2.6 records/animal. The distribution of the fiber diameter by microns is shown in Figure 1. The numbers of sires and dams with progeny in the data were 95 and 888, respectively, with 92 sires and 841 dams also having their own records. The average fiber diameter was (mean \pm SD) $23.05 \pm 4.23 \mu\text{m}$. Animals were classified into 3 classes according to coat color: white (69%), cream (17%), and others (14%). The availability of age (age) at recording was mandatory and ranged from 12 to 6,150 d. The relationship between age and fiber diameter is presented in Figure 2.

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Methodology

Two different models were designed and solved independently. First, we developed a model that accounted for genetic determinism of the residual variability based on the model developed by SanCristobal-Gaudy et al. (1998), which we called the heterogeneity model (HE). Second, we used the model developed by Varona et al. (1997) to fit the growth of traits, which we called the growth model (GR). They are described briefly below.

HE. The HE model assumes that the environmental variance is heterogeneous and partly under genetic control:

additive genetic variance affecting the environmental variance of the trait; ρ is the coefficient of the genetic correlation, and \otimes denotes the Kronecker product. The vectors c and c^* were also assumed to be independent,

$$y = x'b + z'u + w'c + e \quad i \quad i \quad i \quad \epsilon,$$

$$(x'b^* + z'u^* + w'c^*) \quad iii \quad i$$

ijk

$y_{ijk} = f_i + a_j + g_j x_{ijk} + r_{ijk}$. The vector of residuals (r) was assumed to be Gauss-

zian and identically distributed such that $r \sim N(0, \sigma_r)$, where σ_r is the residual variance. Fiber diameter at birth and the slope of the increase in fiber diameter were assumed to be determined by the other systematic effects in the HE model (sex, with 2 levels; color, with 3 levels), the additive genetic effect, and the environmental effect:

where an asterisk (*) indicates the parameters associated with environmental variance; b and b^* are the vectors associated with the systematic effect; u and u^* are the vectors associated with the direct genetic effect; c and c^* are the vectors associated with the permanent environmental effect; x_i , z_i , and w_i are the incidence vectors for the fixed effects, animal effect, and permanent environmental effect, respectively; and ϵ is the residual. The fitted systematic effects were the year-by-month effect with 44 levels, the color effect with 3 levels (white, cream, and others), and the sex effect with 2 levels.

The genetic effects u and u^* were assumed to be Gaussian, such that

$$\begin{pmatrix} a \\ g \end{pmatrix} = \begin{pmatrix} X & Z \\ 0 & 0 \end{pmatrix} \begin{pmatrix} b \\ b^* \end{pmatrix} + \begin{pmatrix} u \\ u^* \end{pmatrix} + \begin{pmatrix} e \\ e^* \end{pmatrix},$$

where a is the vector of fiber diameters at birth; g is the vector of slopes of linear growth for fiber diameter, b and b^* are the vectors associated with the systematic effects; u_a and u_g are the vectors associated with the direct genetic effect; e_a and e_g are the corresponding vectors of residuals; X is the incidence matrix for

$u \sim N(0, \sigma_u^2 A + \sigma_e^2 I)$ where A is the additive genetic relationship matrix; σ_u^2 is the additive genetic variance of the trait; σ_e^2 is the

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2222 with $c \sim N(0, \sigma_c)$ and $c^* \sim N(0, \sigma_{c^*})$, where

$$\begin{pmatrix} c \\ c^* \end{pmatrix} \sim N \left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_c^2 & 0 \\ 0 & \sigma_{c^*}^2 \end{pmatrix} \right)$$

is the identity matrix of equal order to the number of permanent environmental variances affecting the trait and its variation, respectively. Several estimations of heritability for the traits exist under this procedure because residual variance varies among levels of the b effects (Ros et al., 2004; Gutiérrez et al., 2006; Ibáñez-Escriche, 2006). Because of this, heritability was not obtained in this study.

The vectors b and b^* were assigned bounded uniform prior distributions. Scaled inverted χ^2 ($\nu = 4$, and $S = 0.45$) distributions were assigned for the variance parameters σ_a^2 , σ_g^2 , σ_e^2 , $\sigma_{e^*}^2$, and a uniform prior bounded

between -1 and 1 was assigned for ρ . The results were computed by averaging the results obtained after running 2,000,000 iterations of the Markov chain Monte Carlo algorithms described by Sorensen and Waagepetersen (2003), with a burn-in of 1,000,000 and a thinning rate of 100. Convergence was checked by visual inspection of the trace plots. The program used was GSEVM (genetically structured environmental variance model) version 2, and further details of the estimation process can be found in Ibáñez-Escriche et al. (2010).

GR. The statistical model assumed that the j th measure of the fiber diameter for the i th individual (y_{ijk}) was determined by the effect of the year-by-month of recording (f_i , with 44 levels), the fiber diameter at birth (a_j), and the slope of linear growth for fiber diameter (g_j) times the age at the j th measure (x_{jk}), plus a residual (r):

individuals having records, and σ_c and σ_{c^*} are the per-

$$y_{ijk} = f_i + a_j + g_j x_{jk} + r_{ijk}$$

b and b^* , and Z is the incidence matrix for u and u^* .

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Figure 1. Distribution of the fiber diameter by microns.

The additive genetic and the environmental effects and were assumed to be distributed with the following mul- tivariate Gaussian distributions: $\begin{bmatrix} u \\ e \end{bmatrix} \sim N(\mathbf{0}, \mathbf{I} \otimes \begin{bmatrix} \sigma_u^2 & \rho\sigma_u\sigma_e \\ \rho\sigma_u\sigma_e & \sigma_e^2 \end{bmatrix})$, where \mathbf{A} is the additive genetic relationship matrix; \mathbf{I} is

$$\begin{bmatrix} \sigma_u^2 & \rho\sigma_u\sigma_e \\ \rho\sigma_u\sigma_e & \sigma_e^2 \end{bmatrix}$$

$$u \sim N(\mathbf{0}, \mathbf{A} \otimes \begin{bmatrix} \sigma_u^2 & \rho\sigma_u\sigma_e \\ \rho\sigma_u\sigma_e & \sigma_e^2 \end{bmatrix})$$

$$e \sim N(\mathbf{0}, \mathbf{I} \otimes \begin{bmatrix} \sigma_u^2 & \rho\sigma_u\sigma_e \\ \rho\sigma_u\sigma_e & \sigma_e^2 \end{bmatrix})$$

the identity matrix; σ_u^2 is the additive genetic variance

Figure 2. Evolution of fiber diameter along the life span of an alpaca. Downloaded from jas.fass.org at Universidad Complutense De Madrid on August 2, 2011

$$u \sim N(\mathbf{0}, \mathbf{A} \otimes \begin{bmatrix} \sigma_u^2 & \rho\sigma_u\sigma_e \\ \rho\sigma_u\sigma_e & \sigma_e^2 \end{bmatrix})$$

$$e \sim N(\mathbf{0}, \mathbf{I} \otimes \begin{bmatrix} \sigma_u^2 & \rho\sigma_u\sigma_e \\ \rho\sigma_u\sigma_e & \sigma_e^2 \end{bmatrix})$$

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Table 1. Posterior mean and SD of the additive genetic variance for fiber diameter σ_u^2 and its variability $\sigma_{u^*}^2$, the environmental permanent variance for fiber diameter σ_e^2 and its variability $\sigma_{e^*}^2$, and the genetic correlation (ρ) between both additive genetic (c^*) effects under the heterogeneity model

Item	σ_u^2	$\sigma_{u^*}^2$	σ_e^2	$\sigma_{e^*}^2$	ρ	c^*
Posterior mean	2.321	1.250	0.150	0.146	0.912	0.025
SD	0.025	0.033	0.021	0.023	0.046	

of the fiber diameter at birth, σ_e^2 is the additive ge-

netic variance $\sigma_{u^*}^2$ is the additive genetic variance of the fiber diameter at birth, σ_e^2 is the additive ge- heritability was not feasible. The posterior mean esti- mates of the genetic and residual correlations between fiber diameter at birth and its growth were high and positive, at 0.74 and 0.93, respectively. This high ge- netic correlation suggests that the genetic background involved in both the fiber diameter and its growth is the same to a great extent (Figure 3). Therefore, ge- netic selection based on fiber diameter will lead to a favorable correlated genetic response on its growth.

DISCUSSION

This is the first time these types of parameters in- volving variability between shearings have been esti- mated in an alpaca population. However, an estima- tion of heritability for fiber diameter in this species has been carried out before (e.g., see Frank et al., 2006), and also in the same population (Gutiérrez et al., 2009; Cervantes et al., 2010). Note that the estimation of heritability is not possible under the models used here. Therefore, the discussion of parameters was done on the variance components. However, previous estimates have been obtained using different models and different (although closely related) data sets. Therefore, these comparisons should be interpreted with caution. The estimated additive genetic variances with the HE mod- el (2.32) and the GR model (1.29) for the trait of fi- ber diameter were moderately less than those obtained before for the same population (with values of almost 3 or 4) as a consequence of an important change in the model with a more dissected residual effect. How- ever, they were very close to the value of 1.71 found by Pérez-Cabal et al. (2010) for the polygenic component when a model fitting a major gene was used, in contrast to the value of 3.19 when the major gene was not fitted. Difficulties in assigning variability caused by the major gene could be related to these differences between the netic variance of the linear growth; σ_{ea} and σ_{eg} are the respective residual variances; ρ_u and ρ_e are the respec- tive additive genetic and environmental correlations, and \otimes denotes the Kronecker product. Therefore, the models for the parameters of the linear growth are nest- ed within the model above for the fiber diameter re- corded.

Prior distributions for b , b , σ_e^2 , $\sigma_{u^*}^2$, σ_e^2 , $\sigma_{e^*}^2$, and σ_{ag}^2 were assumed to be flat between bounded limits. The Bayesian analysis was implemented with a Gibbs sam- pler algorithm with a single long chain of 1,000,000 it- erations after discarding the first 250,000 samples.

RESULTS

HE

The results of the posterior distributions of the variance components and the genetic correlation between fiber diameter and its variability are shown in Table 1. The estimates of genetic parameters, such as heritabilities, are, in this case, unfeasible because of the way the trait is modeled. A high positive genetic correlation (0.91) was found between the trait and its environmental variability.

GR

The results of the posterior distributions of the variance components are presented in Table 2. The posterior mean (and SD) estimates for the additive genetic variances were 1.293 (0.144) and 0.048 (0.011), respectively, for the fiber diameter at birth and its posterior growth. Given that the global environmental variances are split into 2 nested components, estimating their

Table 2. Posterior mean and SD of the additive genetic variance for fiber diameter at birth σ^2_{ug} and its growth σ^2_{ue} , the environmental variance for fiber diameter at birth σ^2_{ua} and its growth σ^2_{ue} , the additive genetic correlation (ρ), the environmental correlation (ρ), and the remaining residual variance σ^2_{er} under the growth model $e(r)$

Item	σ^2_{ug}	σ^2_{ue}	σ^2_{ua}	σ^2_{ue}	ρ	ρ	σ^2_{er}	SD				
Posterior mean	1.293	0.048	0.133	0.125	0.738	0.934	4.705		0.144	0.011	0.054	0.015
	0.130	0.073	0.093									

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Figure 3. Posterior mean estimates of breeding values for fiber diameter at birth and its linear growth.

classical model and the HE model. In the case of the GR model, the additive genetic variance corresponded to a different trait (i.e., fiber diameter at birth), with a smaller mean value and also a smaller variance as the result of a scale effect.

The HE model developed by SanCristobal-Gaudy et al. (1998) has been widely used with different traits and species (Sorensen and Waagepetersen, 2003; Ros et al., 2004; Gutiérrez et al., 2006; Rowe et al., 2006; Ibáñez et al., 2007, Ibáñez-Escriche et al., 2008a,b; Wolc et al., 2009), but this is the first time it has been applied to fiber diameter. When this HE model was fitted, a high positive genetic correlation (0.91) was found between the trait and its environmental variability. This would allow genetic selection to be carried out in the direction of decreasing the trait mean because this would lead to a correlated decrease in its variability. However, the skewness of the marginal distribution of the data under the HE model has been shown to lead to unreal genetic correlations between the trait and its variability, being an artifact of the scale of measure (Yang, 2010). In fact, the distribution of the data is highly skewed in a positive direction. Thus, the high genetic correlation found might not be a consequence of a real genetic relationship; therefore, a different model, the GR model, was fitted to analyze the trait.

The GR model has also been used previously with a linear model in the Pirenaica beef cattle breed (Varona et al., 1997), and with nonlinear models for milk production (Varona et al., 1998; Rekaya et al., 2000) and chicken growth (Mignon-Grasteau et al., 2000), Iberian pigs (Fernandez et al., 2002), rabbits (Blasco et al., 2003), and beef cattle (Forni et al., 2007). However, this is the first time it has been applied to fiber diameter. Results from the GR model suggest that substantial genetic variation exists for fiber diameter at birth and also for the linear growth of fiber diameter. This implies that a genetic program is plausible to modify the evolution of the fiber diameter over time. However, the posterior mean estimate of the additive genetic correlation between fiber diameter at birth and its linear growth was 0.74, with a posterior SD of 0.13. This result was confirmed with a scatter plot of the posterior mean estimates of the breeding values for both traits. Therefore, selection to increase the growth of the fiber diameter without a substantial reduction in the fiber diameter at birth does not seem possible. Fortunately, farmers prefer to

decrease the fiber diameter even when it would be preferable to select those animals with the thinnest fiber that also maintain this fiber diameter throughout their life span because of their economic value. Alpacas stay at the ranch of the farmer as long as they produce fine-quality fiber, after which they are culled. Thus, the increase in fiber diameter with age affects the herd size and is one of the reasons for the increased culling rate of Andean farmers.

As a global result, high genetic correlations have been found between the trait and its variability, as well as between the trait and its growth with age. Therefore, an important relationship seems to exist between these concepts, the mean value of the trait and its modification along the life span. Pérez-Cabal et al. (2010) found evidence of the existence of a major gene for both fiber diameter and the SD of the trait in the same population. If both concepts are so narrowly related, it might be possible that a unique major gene could be influencing both traits.

Genetic programs for fiber characteristics have been implemented in Peru, such as the one developed by Pacamarca S.A. (Morante et al., 2009), which uses the textile value index combining the amount of each quality type and its economic value (Gutiérrez et al., 2009;

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Cervantes et al., 2010) to simultaneously reduce the fiber diameter and its variability. In general, the textile industry in Peru sufficiently considers the present thinness of the fiber, but requires decreased variability in diameter values between different shearings. Modeling of data to find the selection criteria to achieve this objective does not appear to be easy. One approach could be analysis based on the HE model (SanCristobal-Gaudy et al., 1998), but the skewed distribution of data does not ensure that the genetic correlation found between the trait and its variability would not be an artifact (Yang, 2010). With such a high genetic correlation as estimated here, the breeding values for variability are probably greatly influenced by the mean of the trait, which is much more accurately measured, and they might not be a clear, accurate reflection of the real genetic background. On the other hand, the HE model ignores this variability between fiber diameters at different shearing periods and depends partly on physiological growth according to age. The GR model fitted here deals with the fiber diameter and its variability as independent traits and seems to be an important alternative. However, again, a high genetic correlation was estimated between these concepts, and the GR model also might not be well adapted to the real genetic background. Given that the GR model is not used very often, it cannot be considered sufficiently validated, and it should be contrasted with other data sets working on the same or different traits.

Another reason for the inconclusive results from the HE and GR models could be the limited amount of information that exists, but the opportunities to check it are limited. The important issue is that with both models, the estimated genetic correlation between the trait and the concept theoretically involved in its variability was high. Therefore, if this is a good reflection of reality, selection to diminish the fiber diameter would lead to a reduction in its variability, but further research on this relationship is still needed.

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