Analysis of the existence of major genes affecting alpaca fiber traits[1]

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ABSTRACT: The aim of this study was to determine the presence of major genes for fiber diameter (FD), SD of FD (SDFD), CV of FD, and comfort factor (CF) in Huacaya (HU) and Suri (SU) Peruvian alpaca breeds. Bayesian segregation analyses with relaxed transmis- sion probabilities were performed using 1,906 and 6,592 available records for SU and HU breeds. Evidence for the presence of major genes was statistically supported when the 95% posterior density did not include zero. Significant major genes were found associated with de- creased FD, SDFD, CV values, and increased CF val- ues. Additive effects of the major genes were 4.18 and 4.23 μm for FD, 1.67 and 1.61 μm for SDFD, 3.32 and 3.76% for CV, and 15.03 and 14.90% for CF in HU and SU breeds, respectively. Dominance effects were −1.98 and −2.03 μm for FD, −0.88 and −1.11 μm for SDFD, −1.37 and −2.17% for CV, and 13.0 and 11.8% for CF in HU and SU breeds, respectively. Major gene variance was larger than the polygenic variance for all traits. Major gene allelic frequencies for FD, SDFD, and CV ranged from 0.81 to 0.86 for HU breed and from 0.70 to 0.77 for the SU breed and were 0.24 and 0.36, re- spectively, for CF. It can be concluded that a major gene affecting these traits could be segregating. Then, molecular identification and monitoring of animals car- rying favorable genes throughout the worldwide alpaca population would allow for a quick genetic improve- ment.

INTRODUCTION

The alpaca is the most important fiber producer of South American camelid species. Its fiber production is the main income for many rural Andean communities because alpaca flocks can graze at more than 4,000 m above sea level with daily temperature ranging from −15 to 20°C (Morante et al., 2009). There are 2 alpaca breeds with different fleece characteristics: Huacaya (HU) and Suri (SU). The HU breed represents more than 85% of the alpaca population in Peru (Quispe et al., 2009).

Few genetic selection programs have been imple- mented to improve fleece characteristics. The Pacomar- ca S.A. research farm has developed some technological

improvements and is becoming an elite alpaca flock. It developed a selection program for the HU breed using a textile value index as the selection criterion. Genetic parameters estimated from both breeds at this farm showed that estimated heritabilities for fiber traits were moderate for HU and high for SU (Gutiérrez et al., 2009; Cervantes et al., 2010), which may suggest segre- gation of a major gene (Zhang et al., 2000).

The existence of major genes in livestock has been reported in several studies (e.g., in pigs, Kadarmideen and Janss, 2005; in dairy cattle, Karacaören et al., 2006; and in laying hens, Hagger et al., 2004). Renieri et al. (2009) and Sponenberg (2010) reported that HU and SU inheritance can be described by a single dominant gene. The identification of major genes in alpaca is of great interest because identifying animals carrying al- leles with important positive effects on economic traits would allow for quicker genetic improvement given the general lacking of recording organizations. Our hypoth- esis is that a major gene is segregating in both alpaca breeds, and the objective of this study was to determine if major gene effects were present in 4 fiber quality traits in 2 Peruvian alpaca breeds.

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MATERIALS AND METHODS
The animal welfare guidelines of the Peruvian gov- ernment were followed.

Data
The production and pedigree data from 2001 to Au- gust 2009 of 2 Peruvian alpaca breeds, SU and HU, were provided by Pacomarca S.A. All animals of both breeds were managed together. The alpacas are manu- ally shorn once a year, and the fleece of each animal is individually analyzed and classified according to color and a textile value index (Gutiérrez et al., 2009). On the international textile market, greater value is placed on alpaca fleeces with the thinnest fiber diameters.

Pacomarca S.A. is an experimental farm run by the Inca group in the department of Puno since 1992. It is located at an altitude of 4,060 m above sea level, on the Altiplano. The alpaca breeding program implemented by Pacomarca S.A. started in 1992 with 2 main goals: to decrease fiber diameter of Peruvian alpaca fleeces and to provide genetically superior alpacas throughout the Peruvian Altiplano. Initial genetic stock was composed of the animals selected and bought according to the information available from the purchasing fiber activity of the Inca group for 50 yr. Animals were individu- ally identified from the beginning, and Pacomarca S.A. developed software called Paco Pro to manage animal performances, mating, and health. Further information can be found in Morante et al. (2009).

Traits analyzed were fiber diameter in μm (FD), SD of FD (SDFD), CV of FD, and comfort factor (CF). Mean FD was computed using an Optical Fiber Diam- eter Analyzer by the IWTO-47-95 test method (IWTO, 1995) on washed 2-mm snippet minicore samples taken by extraction. Comfort factor is defined as the percent- age of fibers less than 30 μm (Frank et al., 2006).

Two independent data sets were used in the current study. After editing, 1,906 records were available for the SU breed and 6,592 records for the HU breed (for further details, see Cervantes et al., 2010). Pedigree files included 1,119 and 3,468 animals for SU and HU breeds, respectively. Inbreeding was not taken into ac- count because pedigrees involved about 3 generations and inbreeding coefficients were therefore not meaning- ful.

Polygenic and Mixed Inheritance Models

The polygenic model and the mixed inheritance mod- el were used to compare results with and without the effect of the major gene. The polygenic model used was y=Xb+Zu+Qp+e,whereyisthevectorofobserva- tions; β is the vector of fixed effects including month-year of recording as contemporary group (26 levels in SU breed; 36 levels in HU breed), color (3 levels in both breeds), sex (male or female), and the age at shearing in days as a linear and quadratic covariate; u is the vec- tor of random polygenic effects; p is the vector of ran- dom permanent environmental effects; X, Z, and Q are the incidence matrices for β, u, and p, respectively; and e is the vector of random residuals.

The joint distribution of random effects was as fol- lows:

éæ2 ê çAs$_{polyg}$ 0

æö çu÷
öù 0 ÷ú
çp÷ ⫿ N ê0,ç 0   Is2 ç ÷ ê ç   perm
0 ÷ú, ÷ú
çe÷ ê ç 0 0 Is2÷ú èøç÷ êè   eØú
ëû

where s2   , s2   , and s2 are the variance of the poly- polyg   perm   e genic, permanent environmental, and residual effects; A is the numerator relationship matrix; and I is an identity matrix.

The previous model assumes that additive genetic effect aggregates the effect of a large number of loci. Segregation analysis is a statistical method to identify a major gene using only phenotypic data and without DNA marker information (Kadarmideen and Janss, 2005). In a mixed inheritance model a trait is influ- enced by a polygenic effect and by the genotype at a single locus, which is assumed to be an additive, bi- allelic, autosomal locus with Mendelian transmission probabilities (Janss et al., 1995).

The mixed inheritance model used added the effect of the major gene to the polygenic model as follows:
y=Xb+Zu+Qp+ZWm+e, where y, β, u, p, X, Z,
Q, and e were described above; m is the vector of gen- éù
otype means   m ' = (-a,d,a) ,   where a   is   the   additive êë úû
effect and d is the dominance effect, respectively; W is a matrix that contains the genotype of each individual (i.e., A1A1, A1A2/A2A1, A2A2). Both W and m are unknown and have to be estimated from data by using segregation analyses.

For all analyses Monte Carlo Markov Chain algo- rithm based on Gibbs sampling was assessed using MaGGic 4.0 software (Janss, 1998). Uniform prior dis- tributions were assumed such as (-¥, +¥) for nonge-
netic effects and the major locus, (0, +¥) for variance components, and é0,1ù for allele frequency (Janss et al.,
was computed as h2 = m

S2   + S2 polyg*   m   ,
S2   +S2 +S2 2 polyg*   m   perm*   e*
êë   úû
1995). Heritabilities for the polygenic component were
s2 estimated as h2   =   polyg   from the poly-
polyg   S2   + S2   + S2 polyg   perm   e
s2 genic model and h2   =   polyg*
polyg*   S2   +S2 +S2 +S2 polyg*   m   perm* e*
from the mixed inheritance model. Heritability estimate for the sum of the polygenic and major gene variances

2 2 where s_{polyg*}, s_{perm*}, and s_{e*} are the variance of the polygenic, permanent environmental, and residual ef-

Table 1. Mean and SD of the traits for Huacaya and Suri breeds

Trait	Breed[1]	Mean	SD
Fiber diameter, µm	HU	22.97	4.18
	SU	24.71	4.88
SD of fiber diameter, µm	HU	5.36	1.17
	SU	6.40	1.61
CV of fiber diameter, %	HU	23.35	3.66
	SU	25.95	4.16
Comfort factor, %	HU	88.12	14.97
	SU	81.04	18.99

[1]HU: Huacaya breed; SU: Suri breed.

fects from the mixed inheritance model, respectively; s_{2m} is the major gene variance obtained from 37% of the SU fleece reached that quality. This may be due either to the selection program that is being implemented in the HU breed or the inherent differ- ences between the breeds.

Polygenic Model

Estimations of variances and heritabilities from the polygenic model are shown in Table 2. All fiber traits showed greater variability in the SU breed than in the HU breed as expected. This is because HU has been involved in selection programs for a long time and its variability has consequently been reduced. Estimated heritabilities of all traits were greater for SU than for HU. Values of 0.36 and 0.46 were estimated for FD, 0.51 and 0.43 for SDFD, 0.25 and 0.27 for CV, and 0.23 and 0.26 for CF, for HU and SU, respectively. Es- timated heritabilities were similar to those reported by Cervantes et al. (2010) for the HU breed, but from 35 to 55% less for the SU breed. The decrease in heritabili- ties for the SU breed with respect to previous studies could probably be due to the fixed effect color, also in- cluded in the model for SU in the present study, which absorbed part of the genetic variability. Heritabilities for the SU breed were greater than those for HU breed, which may be a consequence of a smaller data set.

Mixed Inheritance Model

Results for segregation analyses of the HU and SU breeds are shown in Table 3 and Table 4, respectively. A major gene effect was associated with the 4 studied traits. Partial dominance effects were estimated in the desired direction of the traits, which is a decrease in FD, SDFD, CV, and an increase in CF.

Fiber Diameter. The variance estimate of the ma- jor gene variance was almost 5 times greater than the variance estimate of the polygenic effect for the HU and SU breeds and explained 52 and 57% of the total variance, respectively. Because 95% HPDR did not in- clude 0, it can be concluded that there is evidence of a major gene for FD. The differences between homozy- gous individuals were 8.36 and 8.46 µm, for HU and SU breeds, respectively. Estimated frequencies of the major gene allele were 0.85 for the HU breed and 0.77 for the SU breed. This implies that, assuming Hardy-Weinberg equilibrium, 72% of HU and 59% of HU individuals can be considered as sire and dam candidates in a breed- ing program emphasizing production of homozygous individuals. The average effect of the gene substitution toward a finer fiber was −5.6 µm for the HU breed and −5.3 µm for the SU breed.

SD of Fiber Diameter. Polygenic variance was less than major gene variance, and 95% HPDR sup- port the presence of a segregating major gene in both breeds. Major gene variance explained approximately 64% of the total variance. The effects of substitution of the major gene for SDFD were −2.3 and −2.1 µm, for the HU and SU breeds, respectively.

$$s_m^2 = 2pqa + d(q-p) + (2pqd),$$

where p is the allele frequency of the major gene, a the additive effect, and d the dominance effect. The average effect of the gene substitution was obtained based on Falconer and Mackay (1996) as $a + d(1 - 2p)$.

The existence of a major gene for FD, SDFD, CV, and CF was tested independently for each breed with the interval of the 95% high posterior density regions (HPDR), such that the significance of the major gene was determined if the HPDR of the major gene vari- ance excluded zero (Box and Tiao, 1973). Convergence was improved by using the relaxation of allele trans- mission probabilities to

slightly non-Mendelian prob- abilities (Janss et al., 1997; Sánchez et al., 2003). From a Gibbs chain with relaxed transmission probabilities, cycles with a Mendelian genotype configuration were filtered out to provide a correct set of samples for infer- ences on a strict Mendelian model (Sheehan and Thom- as, 1993). An initial chain with relaxed transmission probability 0.5 was annealed by slowly decreasing to 0.001. Marginal posterior distributions were obtained using boa package (Smith, 2007) with version 2.9.0 of R (R Development Core Team, 2009). Convergence of variance parameters were assessed by visual inspection of the Gibbs samples.

RESULTS AND DISCUSSION

Means and SD of the 4 traits for both breeds are shown in Table 1. According to previous studies in the same Peruvian population (Gutiérrez et al., 2009; Cer- vantes et al., 2010), the HU breed produced finer fleece than SU breed. Average fleece trait values for the HU were 22.97 µm for FD, 5.36 µm for SDFD, 23.35% for CV, and 88.12% for CF. Averages values for SU breed were 24.71 µm for FD, 6.40 µm for SDFD, 25.95% for CV, and 81.04% for CF. More than 52% of fiber from HU alpacas were finer than 22.5 µm, the most desir- able categories for the textile industry, whereas only

Table 2. Posterior means and 95% highest posterior density regions (in parentheses) of parameters from the polygenic model for Huacaya and Suri breeds[1]

Item[2]	FD	SDFD	CV	CF
HU[3] h_2	0.36	0.38	0.25	

0.23 (0.10/0.28) 90.47
(86.90/94.10) 32.76
(25.71/39.84) 18.83
(13.39/24.27)
0.26 (0.18/0.35)
102.43 (94.72/110.44)
52.18 (33.30/71.53)
42.60 (27.46/58.02)

	FD	SDFD	CV	CF		
polyg	(0.31/0.41)	(0.33/0.43)	(0.20/0.29) s_{2e}	4.54	0.51	6.58
	(4.35/4.72)	(0.48/0.53)	(6.30/6.86) s_2	3.19	0.40	2.58
polyg	(2.66/3.74)	(0.33/0.46)	(2.03/3.14) s_2	1.18	0.14	1.25
perm	(0.82/1.54)	(0.10/0.19)	(0.83/1.69) SU[3]			
h_2	0.46	0.43	0.27 polyg	(0.36/0.55)	(0.33/0.53)	(0.18/0.37)
s_{2e}	4.52	0.68	8.90 (4.12/4.89)	(0.62/0.73)	(8.21/9.60)	
s_2	5.24	0.75	3.90 polyg	(3.87/6.65)	(0.53/0.96)	(2.39/5.48)
s_2	1.69	0.30	1.40 perm(0.83/2.56)	(0.16/0.44)	(0.24/2.55)	

[1]FD: fiber diameter; SDFD: SD of FD; CV: CV of FD; CF: comfort factor. [2]h_2 : heritability for polygenic variance; s_2: residual variance; s_2 : variance of the polygenic effect; s_2 :
polyg   e   polyg   perm
variance of the permanent environmental effect. [3]HU: Huacaya breed; SU: Suri breed.

CV of Fiber Diameter. The magnitude of the major gene variances and the 95% HPDR imply a large major gene effect on CV for HU and SU breeds. However, 95% HPDR of polygenic and permanent en- vironmental variances for SU included values close to 0 (shown as 0.00 in Table 4) and, therefore, were not significant. Although apparently all the genetic vari- ance is due to a major gene (40 and 47% from total variance for HU and SU, respectively), the most likely reason is the large residual variance given that CV is a composite trait. Further studies with larger data sets will be needed to confirm this.

The power of detecting polygenic and permanent en- vironmental variance was low. The ratio between major gene variance and polygenic variance was 22% larger in SU than in the HU breed. This between-breed differ- ence was likely because of the selection process imple- mented in the latter. Homozygous individuals for the

Table 3. Posterior means and 95% highest posterior density regions (in parentheses) of parameters from mixed-inheritance model for the Huacaya breed[1]

Item[2]	FD	SDFD	CV	CF
$S^2 e^*$				
$S^2 polyg^*$				
$S^2 perm^*$				

4.50   0.50 (4.32/4.69) (0.48/0.52)
1.71   0.16 (1.17/2.31) (0.10/0.21)
0.96   0.10 (0.61/1.30) (0.06/0.13)
7.86   1.28 (5.55/10.43)   (1.00/1.58)
0.24   0.21 (0.17/0.31) (0.15/0.27)
0.63   0.71 (0.57/0.70) (0.66/0.75)
4.18   1.67 (3.11/5.23) (1.46/1.87)
−1.98   −0.88 (−2.60/−1.34)   (−1.02/−0.72)
0.85   0.86 (0.77/0.91) (0.83/0.90)
6.54 (6.26/6.82)
0.72 (0.26/1.24)
1.08 (0.68/1.47)
5.50 (4.02/6.99)
0.09 (0.03/0.14)
0.45 (0.38/0.52)
3.32 (2.84/3.81)
−1.37 (−1.87/−0.87)
0.81 (0.75/0.87)
87.63 (84.22/90.99)
15.51 (10.99/20.04)
4.38 (0.19/8.01)
194.14 (169.46/220.74)
0.14 (0.10/0.18)
0.69 (0.67/0.72) 15.03
(13.85/16.23) 13.00
(11.41/14.69) 0.24
(0.19/0.28)

S^2m h^2
$polyg^*$ h^2m
a d p

[1]FD: fiber diameter; SDFD: SD of FD; CV: CV of FD; CF: comfort factor. [2]$S^2 e^*$: residual variance; $S^2 polyg^*$: variance of the polygenic effect; $S^2 perm^*$: variance of the permanent environmen-tal effect; $S^2 m$: variance of the major gene; $h^2 polyg^*$: heritability for polygenic variance; h^2m: heritability for poly-genic and major gene variance; a: additive effect; d: dominance effect; p: allele frequency of the major gene.

Table 4. Posterior means and 95% highest posterior density regions (in parentheses) of parameters from mixed inheritance model for the Suri breed[1]

Item[2]	FD	SDFD	CV	CF
$S^2 e^*$	4.48 (4.13/4.84)			
$S^2 polyg^*$	2.29 (1.11/3.54)			
$S^2 perm^*$	1.27 (0.54/2.00)			
S^2m	10.54 (7.13/14.16)			
$h^2 polyg^*$	0.28 (0.16/0.41)			

0.67 (0.62/0.72)
0.33 (0.17/0.50)
0.11 (0.02/0.20)
1.97 (1.55/2.39)
0.30 (0.17/0.42)
0.75 (0.70/0.79)
1.61 (1.36/1.85)
−1.11 (−1.38/−0.84)
0.70 (0.63/0.77)
8.86   99.66 (8.18/9.55) (92.30/107.31)
1.05   17.02 (0.00/2.23) (5.46/28.63)
0.89   16.67 (0.00/1.66) (6.17/27.22)
9.72   182.22 (6.55/13.17) (143.66/220.63)
0.10   0.13 (0.00/0.20) (0.04/0.21)
0.52   0.63 (0.43/0.62) (0.57/0.69)
3.76   14.90 (3.02/4.50) (13.09/16.71)

h2m
a d p
0.69 (0.61/0.76)
4.23 (3.45/5.03)
−2.03 (−2.81/−1.29)
0.77 (0.66/0.84)
−2.17 (−3.10/−1.34)
0.70 (0.61/0.79)
11.80 (9.63/14.02)
0.36 (0.29/0.42)

[1]FD: fiber diameter; SDFD: SD of FD; CV: CV of FD; CF: comfort factor. [2]s^2_e: residual variance; s^2_{polyg}: variance of the polygenic effect; s^2_{perm}: variance of the permanent environmental effect; s^2_m: variance of the major gene; h^2_{polyg}: heritability for polygenic variance; h^2_m: heritability for polygenic and major gene variance; a: additive effect; d: dominance effect; p: allele frequency of the major gene.

major gene (A1A1), with 65 and 49% frequency in the HU and SU populations, showed 6.64 and 7.52% less variability of fiber diameter than A2A2 animals, re- spectively. The major gene in the HU breed showed −4.2% of effect of substitution and was −4.6% in the SU breed.

Comfort Factor. Major gene variance was much greater than polygenic variance, and 95% HPDR did not include 0. Therefore, a major gene effect on CF is involved in both breeds. The effect of the major gene is estimated to account for 64 and 58% of the total vari- ance, respectively. Whereas the effects of substitution for FD, SDFD, and CV were similar in both breeds, for CF in the HU breed there was a greater effect of gene substitution than in the SU breed (21.9 and 18.3%, respectively). Marginal posterior distributions of polygenic and major gene variances (including polygenic variance from the polygenic model) and heritabilities have been graphically represented in Supplemental Figure 1 for the HU breed and in Supplemental Figure 2 for the SU breed (http://jas.fass.org/content/vol88/issue12/). In all traits, the ratio between polygenic variances from the polygenic model and from the mixed inheritance model was less than 50%, and the major gene variance was greater than polygenic variance. Then, heritabil- ity including the major gene variance was greater than polygenic heritability (Table 3). All estimated herita- bilities were significant except the heritability for poly- genic and major gene variances for CV in SU, given that its 95% HPDR included 0 (Table 4).

This study confirmed our hypothesis that segregat- ing major genes are affecting fiber traits (FD, SDFD, CV, and CF) in the HU and SU alpaca breeds. Given the genetic correlations reported by Cervantes et al. (2010), maybe 2 major genes would be involved. One major gene would be affecting fiber diameter (FD and CF) because the antagonistic and strong genetic corre- lation (−0.97 and −0.98 for HU and SU, respectively) between them shows that the prickliness is associated with finer fibers. Diameter variability (SDFD and CV) may depend on a second major gene because of the high genetic correlation between them in addition to the low correlation between FD and CV (0.09 for both breeds). Partial dominance effect was obtained assum- ing a single biallelic and autosomal locus.

These results have economic implications on fleece. That is, an individual with fiber diameter 8 µm thinner or with comfort factor 30% greater would have a consid- erably increased value. Although all the results referred to that experimental farm, it should be noted that the allelic distribution may be present on a broader popula- tion because those animals came from diverse origins. Therefore, molecular identification and monitoring of favorable genes throughout worldwide alpaca popula- tion may lead to a more favorable genetic response.

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