Inheritance of Suri and Huacaya type of fleece in Alpaca

Carlo Renieri, Alessandro Valbonesi, Vincenzo La Manna, Marco Antonini & Moises Asparrin

Inheritance of Suri and Huacaya type of fleece in Alpaca

Carlo Renieri[1], Alessandro Valbonesi[1], Vincenzo La Manna[1], Marco Antonini[2], Moises Asparrin[3]

[1]Dipartimento di Scienze Ambientali. Università di Camerino, Italy

[2]Ente per le Nuove Tecnologie, l'Energia e l'Ambiente, C.R. Casaccia BAS-agro. Roma, Italy

[3]Michell y CIA S.A. Fundo Mallkini, Peru

Corresponding author: Prof. Alessandro Valbonesi. Dipartimento di Scienze Ambientali. Facoltà di Medicina Veterinaria, Università di Camerino. Via Circonvallazione 95, 62024 Matelica (MC), Italy - Tel. +39 0737 403451 - Fax: +39 0737 403402 - Email: alessandro.valbonesi@unicam.it

ABSTRACT

The inheritance of the two types of fleece, Suri and Huacaya, observed in Alpaca (*Lama pacos* L.) is still not clearly defined. The objective of this work is to investigate the patter of inheritance of these two phenotypes, throughout 588 Suri x Suri and 2126 Huacaya x Huacaya offspring. The single gene and the three two-phenotype epistatic models were tested in the 19 Suri x Suri segregating families. The single dominant gene hypothesis best fitted our segregation data and could be, therefore, accepted (G_T=20.276, P=0.378). The gene frequency of the recessive Huacaya allele was 0.295, being the frequency of the dominant Suri allele 0.705. The frequency of heterozygotes, estimated in the whole population and among dominant individuals, was 0.416 and 0.455, respectively, with a "carrier" Suri to Huacaya ratio of 4.780. In three Huacaya families, 3 Suri were born, as a result of a new dominant mutation on some germinal lines of Huacaya animals. The direct mutation rate can be estimated at 0.0014.

Key words: Alpaca, Suri, Huacaya, Segregation analysis, Epistasy.

RIASSUNTO

EREDITÀ DEI TIPI DI VELLO SURI E HUACAYA NEGLI ALPACA

*L'eredita dei due tipi di vello, Suri e Huacaya, osservati negli Alpaca (*Lama pacos L.*), non è ancora definita in modo univoco. Lo scopo di questo lavoro è quello di determinare il modello ereditario di questi due fenotipi basandosi sulla progenie risultante da incroci Suri x Suri (588 nati) e Huacaya x Huacaya (2126 nati). Su 19 famiglie Suri x Suri segreganti, in cui cioè sono comparsi dei probandi (individui Huacaya recessivi), sono state testate le ipotesi ereditarie di un gene singolo e quelle relative a tre modelli epistatici. L'ipotesi di un gene singolo dominante per il Suri è risultata la più consistente (G$_T$=20,276, P=0,378). La frequenza genica dell'allele Huacaya, recessivo, è risultata di 0,295, mentre quella dell'allele Suri, dominante, di 0,705. La frequenza degli eterozigoti, stimata sia sull'intera popolazione sia tra gli individui dominanti, è rispettivamente di 0,416 e 0,455, con un rapporto Suri eterozigoti/Huacaya di 4,78. In tre famiglie Huacaya sono nati tre Suri, che verosimilmente sono il frutto di una nuova mutazione dominante in alcune linee germinali di genitori Huacaya, il cui tasso di mutazione diretta è di 0,0014.*

Parole chiave: *Alpaca, Suri, Huacaya, Analisi di segregazione, Epistasi.*

Introduction

Alpaca (*Lama pacos* L.) is a South American camelid specialised in fibre production (Bustinza Choque, 1985; Flores Ochoa and Mac Quarry, 1995; Bonavia, 1996).

Two different types of fleece are described among alpaca, Huacaya and Suri (Calle Escobar, 1984; Novoa and Wilson, 1992). Huacaya represents 90% of alpaca fleece processed in Peru (Hoffman and Fowler, 1995). It is characterised by compact, soft and highly crimped fibres, with blunt-tipped locks which closely resemble those of Merinos sheep. By contrast, Suri has locks with a "cork-screw" shape and straight, less-crimped, lustrous, silky fibres, very similar to mohair from Angora goat but not as bright. Differences between fleece types in regarding cuticular scale frequency, follicular density and secondary to primary follicular ratio were described (Antonini *et al.*, 2001; Antonini *et al.*, 2004).

The genetic background of Huacaya and Suri is still not clearly defined because the segregation analyses carried out in the past do not show concordant data. Suri is inherited as a single recessive gene (Calle Escobar, 1984), a single dominant gene (Velasco, 1980), a single dominant gene or an haplotype (Ponzoni *et al.*, 1997; Baychelier, 2000). A review on the topic is presented in Frank *et al.* (2006).

The aim of the present work is to test the model of inheritance of Suri and Huacaya in a two-phenotypes system (one-gene two-alleles, and three epistatic models: duplicate gene action, dominant suppression and complementary action) in records of Suri by Suri and Huacaya by Huacaya matings.

Material and methods

Animals

Five hundred eighty eight (291 females and 297 males) offspring by Suri sire x Suri dam from 62 paternal half sib families, and 2126 (1009 females and 1117 males) offspring by Huacaya sire x Huacaya dam from 177 paternal half sib families, born in 4 years (2004, 2005, 2006, and 2007), were recorded. Animals were reared in 4 separate flocks (1 Suri flock and 3 Huacaya flocks), in a private farm located in the Peruvian Highlands. Being Suri and Huacaya early evident, the classification of the type of fleece was performed immediately at birth. Out of the 588 Suri x Suri offspring, 219 born from non segregating families and 369 (318 Suri and 51 Huacaya) from segregating families.

Statistical analysis

Segregation analysis was applied only to Suri segregating families which showed, at least, one proband, *i.e.* an individual sup-

Table 1. Segregation hypotheses tested.

Segregation	Phenotypic hypothesis	Hypothesis tested
Single gene	Dominance with complete penetrance of Suri over Huacaya	7 : 1
Epistasis: two- phenotypes	Duplicate gene action for Suri	15 : 1
Epistasis: two- phenotypes	Dominant suppression epistasis of gene for Suri over gene for Huacaya	13 : 3
Epistasis: two- phenotypes	Complementary action of dominant and recessive gene for Huacaya	9 : 7

posed recessive among the offspring (truncate selection) (Huston *et al.*, 1974) and with a total of offspring ≥ 5.

The segregation hypotheses tested in a two-phenotypes system were summarized in Table 1 (Cotterman, 1953). For the single gene hypothesis, a 7 Suri: 1 Huacaya *a priori* expectation hypothesis was tested (Huston *et al.*, 1974). In the duplicate gene action epistasis, two duplicate dominant genes were involved, either providing the Suri phenotype. The expected segregation is 15 Suri and 1 Huacaya. In the dominant suppression epistasis, the dominant gene for Suri is supposed to masks the genes at the Huacaya locus, with an expected segregation of 13 Suri and 3 Huacaya. Lastly, in the complementary gene action epistasis, two genes are required for the Huacaya phenotype, with an expected segregation of 9 Suri and 7 Huacaya.

For all tested hypotheses (single gene and epistasis), the expected frequencies for each family were statistically corrected with the "*a priori*" method proposed by Andresen (1974).

The goodness of fit for the hypotheses was evaluated applying both G-test (as the log-likelihood ratio test is also called), with Williams's correction, G_{adj}, for single segregation, and heterogeneity G-test for replicate segregations (Sokal and Rohlf, 2003). The G-test was preferred to the chi-square because the G-values are completely additive. This property allows us to obtain a total G (G_T, on which the overall judgement is based) and to resolve it in its components: the pooled G (G_P, obtained by treating the different progenies as though they were a single large progeny), and the heterogeneity G (G_H, which, by analogy with the analysis of variance, is also called "interaction" G, as it evaluates the effect of the replicated segregations on the overall deviation from the expected value). When G-values were summed (G_T) or partitioned (G_P and G_H) Williams's correction was not applied, because the adjusted G-values (G_{adj}) are not additive. Values of G were compared to a chi-square distribution at the 0.05 level with: (a-1), bx(a-1), and (a-1)x(b-1) degrees of freedom for G_{adj} and G_P, G_T, and G_H, respectively (where a is the number of phenotypical classes and b the number of the segregating families under investigation).

The hypothesis of a complete independence of the monofactorial segregation, related to both the Alpaca fleece types (Suri or Huacaya) and the sex of the animals, was tested by means of the G-test of independence (Sokal and Rohlf, 2003). This test was applied to segregation data displayed in the form of a two-way table (contingency table).

Assuming a single gene two-alleles genetic model, the gene frequency of both the recessive Huacaya and the dominant Suri alleles was estimated by means of the Modified Single Jackknife Estimator (MSJE) method, as suggested by Huether and Murphy (1980). Accordingly to these estimates, the frequency of heterozygotes in the whole population was calculated as $2q(1$-$q)$, and among dominant individuals as $2q/(1$+$q)$ (Falconer, 1993; Serre, 1997).

Lastly, the mutation rate of the recessive Huacaya allele was estimated by determining the incidence of dominant individuals whose parents were recessives. This method, which is known as a direct method, assumes complete penetrance of the dominant gene (Steinberg, 1959).

Results and discussion

Table 2 shows the results from 19 Suri (males and females) segregating families for a single gene tested hypothesis. Because the Suri phenotype is supposed to be dominant on the Huacaya, the occurrence of both Suri and Huacaya animals among the F_1 progeny of

Table 2. Observed and expected frequencies on Suri x Suri segregating families in a tested 7 : 1 hypothesis.

Males	Offspring	Observed frequency		Expected frequency[a]		G_{adj}[b]	P
		Suri	Huacaya	Suri	Huacaya		
190	32	31	1	27.943	4.057	3.630	0.057
239	18	16	2	15.526	2.474	0.111	0.739
65691	27	26	1	23.531	3.469	2.697	0.101
00-024	27	23	4	23.531	3.469	0.089	0.765
00-034	30	27	3	26.180	3.820	0.215	0.643
0-176	27	26	1	23.531	3.469	2.697	0.101
0-258	19	13	6	16.421	2.579	4.053	0.044
02-848	34	29	5	29.704	4.296	0.126	0.722
1-1-245	6	5	1	4.639	1.361	0.133	0.716
1-2-240	9	7	2	7.391	1.609	0.109	0.741
1-3-214	8	7	1	6.477	1.523	0.246	0.620
1-3-310	12	10	2	10.122	1.878	0.009	0.924
1-3-329	10	8	2	8.304	1.696	0.063	0.802
1-3-333	10	9	1	8.304	1.696	0.392	0.531
2-1-376	19	16	3	16.421	2.579	0.076	0.783
2-3-335	5	4	1	3.717	1.283	0.089	0.766
2-3-342	5	3	2	3.717	1.283	0.489	0.484
9-163	20	19	1	17.314	2.686	1.553	0.213
9-510	44	34	10	38.485	5.515	3.471	0.062
Pooled	362	313	49	316.750	45.250	0.347	0.556

[a] *According to the formula suggested by Andresen (1974).*
[b] *Adjusted G-values according to William's correction.*

each male, can be explained by the presence of heterozygous males and either heterozygous or homozygous females. Assuming that the percentage of the two female genotypes is the same (50%), the expected segregation is 7 Suri:1 Huacaya individual.

With the exception of the offspring of male 0-258, in all the remaining 18 segregations the differences between the observed and the expected frequencies, in the above tested hypothesis, are not statistically significant. The *G*-test values show a probability (P) of $0.057 \leq P \leq 0.924$. Similar results were obtained from aggregated data analysis; the heterogeneity *G*-test indicates that the total *G* (G_T=20.276, P=0.378), as well as its components (G_P= 0.347, P=0.556; G_H=19.929, P=0.337), do not deviate significantly from expectation.

In the 15 : 1 segregation hypothesis (Table 3) we have two progenies (the offspring of males 0-258 and 9-510), both with an excess of Huacaya and a low number of Suri, which resulted significantly different from expec-

Table 3. Observed and expected frequencies on Suri x Suri segregating families in a tested 15 : 1 hypothesis.

Males	Offspring	Observed frequency		Expected frequency[a]		G_{adj}[b]	P
		Suri	Huacaya	Suri	Huacaya		
190	32	31	1	29.710	2.290	0.977	0.323
239	18	16	2	16.363	1.637	0.083	0.773
65691	27	26	1	24.954	2.046	0.702	0.402
00-024	27	23	4	24.954	2.046	1.611	0.204
00-034	30	27	3	27.809	2.191	0.291	0.590
0-176	27	26	1	24.954	2.046	0.702	0.402
0-258	19	13	6	17.319	1.681	7.802	0.005
02-848	34	29	5	31.609	2.391	2.376	0.123
1-1-245	6	5	1	4.832	1.168	0.031	0.860
1-2-240	9	7	2	7.723	1.277	0.418	0.518
1-3-214	8	7	1	6.760	1.240	0.058	0.810
1-3-310	12	10	2	10.609	1.391	0.269	0.604
1-3-329	10	8	2	8.686	1.314	0.363	0.547
1-3-333	10	9	1	8.686	1.314	0.093	0.760
2-1-376	19	16	3	17.319	1.681	0.940	0.332
2-3-335	5	4	1	3.867	1.133	0.021	0.885
2-3-342	5	3	2	3.867	1.133	0.749	0.387
9-163	20	19	1	18.276	1.724	0.387	0.534
9-510	44	34	10	41.079	2.921	11.737	0.001
Pooled	362	313	49	339.375	22.625	25.051	0.000

[a]*According to the formula suggested by Andresen (1974).*
[b]*Adjusted G-values according to William's correction.*

tation (P=0.05 and 0.001, respectively). The resulting heterogeneity G is clearly not significant (G_H=4.56; P=0.999), indicating that most of the deviations from expectation of the progenies are in the same direction and are not significantly different from each other. The pooled G has a highly significant value (G_P=25.051; P<0.001) and the total G shows a border line value (G_T=29.65; P=0.056).

In the 13:3 segregation hypothesis (Table 4) we have three progenies (the offspring of males 190, 65691, and 0-176), each with an excess of Suri and a low number of Huacaya, which resulted significantly different from expectation (P=0.007, 0.018, and 0.018, respectively). Although none of the remaining segregations were significantly different from the expected one (the individual G-tests show a probability of 0.065≤P≤0.997), most of them deviate in the same direction and, hence, the resulting heterogeneity G is clearly not significant (G_H=23.00; P=0.191). The pooled frequencies show this deviation

Table 4. Observed and expected frequencies on Suri x Suri segregating families in a tested 13 : 3 hypothesis.

Males	Offspring	Observed frequency		Expected frequency[a]		G_{adj}[b]	P
		Suri	Huacaya	Suri	Huacaya		
190	32	31	1	25.992	6.008	7.338	0.007
239	18	16	2	14.543	3.457	0.867	0.352
65691	27	26	1	21.919	5.081	5.628	0.018
00-024	27	23	4	21.919	5.081	0.301	0.583
00-034	30	27	3	24.364	5.636	1.764	0.184
0-176	27	26	1	21.919	5.081	5.628	0.018
0-258	19	13	6	15.367	3.633	1.672	0.196
02-848	34	29	5	27.620	6.380	0.391	0.532
1-1-245	6	5	1	4.421	1.579	0.318	0.573
1-2-240	9	7	2	7.005	1.995	0.000	0.997
1-3-214	8	7	1	6.148	1.852	0.584	0.445
1-3-310	12	10	2	9.547	2.453	0.111	0.740
1-3-329	10	8	2	7.856	2.144	0.012	0.911
1-3-333	10	9	1	7.856	2.144	0.921	0.337
2-1-376	19	16	3	15.367	3.633	0.143	0.705
2-3-335	5	4	1	3.549	1.451	0.213	0.644
2-3-342	5	3	2	3.549	1.451	0.275	0.6000
9-163	20	19	1	16.190	3.810	3.406	0.065
9-510	44	34	10	35.749	8.251	0.434	0.510
Pooled	362	313	49	294.125	67.875	7.003	0.008

[a]*According to the formula suggested by Andresen (1974).*
[b]*Adjusted G-values according to William's correction.*

clearly and, being based on a larger sample size, yield a highly significant value of G (G_P=7.00; P=0.008). When all the individual G were added together to obtain a total G, however, the test yield to a value slightly above the critical one (G_T=30.00; P=0.052).

According to 9:7 segregation hypothesis (Table 5), 12 progenies, out of 19, resulted significantly different from expectation (0.0001<P≤0.045) because of an excess of Suri deviate in the same direction, the resulting heterogeneity G is clearly not significant (G_H=23.22; P=0.182). The pooled G, in view of the consistent trend in favour of Suri, is highly significant (G_P=153.951; P<0.0001); and the total G (G_T=177.388; P<0.0001) is highly significant as well.

On the basis of the total G value, on which the overall judgement is based, only the latter segregation hypothesis can be completely rejected.

At the phenotypic point of view, based on fitting hypotheses (7 dominant Suri:1 recessive Huacaya, 15 duplicate dominant Suri

Table 5. Observed and expected frequencies on Suri x Suri segregating families in a tested 9 : 7 hypothesis.

Males	Offspring	Observed frequency		Expected frequency[a]		G_{adj}[b]	P
		Suri	Huacaya	Suri	Huacaya		
190	32	31	1	18.000	14.000	28.387	0.000
239	18	16	2	10.125	7.875	9.148	0.002
65691	27	26	1	15.187	11.813	22.986	0.000
00-024	27	23	4	15.187	11.813	10.414	0.001
00-034	30	27	3	16.875	13.125	16.502	0.000
0-176	27	26	1	15.187	11.813	22.986	0.000
0-258	19	13	6	10.687	8.313	1.179	0.278
02-848	34	29	5	19.125	14.875	13.225	0.000
1-1-245	6	5	1	3.289	2.711	2.191	0.139
1-2-240	9	7	2	5.040	3.960	1.864	0.172
1-3-214	8	7	1	4.465	3.535	3.765	0.052
1-3-310	12	10	2	6.745	5.255	4.007	0.045
1-3-329	10	8	2	5.611	4.389	2.528	0.112
1-3-333	10	9	1	5.611	4.389	5.539	0.019
2-1-376	19	16	3	10.687	8.313	6.789	0.009
2-3-335	5	4	1	2.682	2.318	1.514	0.218
2-3-342	5	3	2	2.682	2.318	0.082	0.775
9-163	20	19	1	11.250	8.750	15.555	0.000
9-510	44	34	10	24.750	19.250	8.482	0.004
Pooled	362	313	49	203.625	158.375	153.951	0.000

[a]According to the formula suggested by Andresen (1974).
[b]Adjusted G-values according to William's correction.

genes:1 Huacaya, and 13 dominant suppression Suri:3 Huacaya; see Table 1), the dominance of Suri *vs* Huacaya seems clearly established, in agreement with the results of Velasco (1980) and Ponzoni *et al*. (1997).

About the genetic model of dominance, the observed offspring frequencies seem to better fit the single gene two-alleles model (*i.e.,* 7:1 segregation hypothesis; P=0.378). By contrast, the border line values of the total *G*, resulting from both the two-genes two-alleles (duplicate dominant genes and

dominant suppressor genes) models, do not provide any evidence either in favour nor against the 15:1 and the 13:3 segregation hypotheses. Further analyses of segregation data should contribute to a greater understanding of the genetic mechanisms.

Assuming a single gene two-alleles genetic model, the segregations were tested for independence of sexual chromosome segregation. The *G*-test of independence, applied to the segregation data, was clearly not significant (G=0.224; P=0.636). There-

Table 6.   Gene frequency, carrier frequency, and ratio estimated from Suri x Suri offspring.

Gene frequency		Carrier frequency in the whole population	Carrier frequency among Suri individuals	Carrier Suri to Huacaya ratio
q	p	2q (1-q)	2q / (1+q)	2 (1-q) / q
0.295	0.705	0.416	0.455	4.780

Table 7.   Huacaya families with new Suri mutation.

Males	Offspring				
	Huacaya		Suri		
	♀	♂	♀	♂	Total
661	4	2	0	1	7
2009	7	11	1	0	19
2308	3	7	0	1	11
Total	14	20	1	2	37

fore a Huacaya sire by Suri dam mating can be considered genetically equivalent to a Suri sire by Huacaya dam mating.

Keeping the single dominant Suri gene assumption: i) the gene frequency, of both the recessive Huacaya and the dominant Suri allele, ii) the frequency of heterozygotes, in the whole population and among dominant individuals, and iii) the "carrier" Suri to Huacaya ratio, were estimated and reported in Table 6.

Among the 2126 offspring by Huacaya sire x Huacaya dam, 2123 were Huacaya and 3 Suri, born from three different families (Table 7). The few-recorded Suri out of such mating cannot be regarded as recording errors. Also the hypothesis of a misclassification of heterozygous individuals, showing an incomplete penetrance, cannot be accepted, because the parents of these 3 Suri belonged to pure Huacaya lines. Hence, only the hypothesis of a new dominant mutation on some germinal lines of Huacaya animals can be taken into consideration. The mutation rate of this supposed new dominant mutation can be estimated as 3/2126=0.0014.

The new mutation can explain the segregation of Suri offspring in the Huacayas mating observed in the Australian Stud Book (about 0.13% of the cases) (Baychelier, 2000). Seemingly, this occurrence might be called upon to explain the misunderstanding Calle Escobar's (1984) hypothesis of Suri as recessive under Huacaya phenotype. Suri cannot be recessive because it seems expressed as a single gene in heterozygous animals. Hence, only a dominant mutation can be consistent with this peculiar situation.

Conclusions

Suri is dominant at the phenotypic point of view over Huacaya, but no information

could be obtained on the degree of penetrance because the mating Suri x Huacaya were not performed in the farm.

Suri and Huacaya inheritance can be described by a single gene two-alleles autosomic system. The tested two-genes two-alleles dominant hypotheses (epistasis) appear not completely consistent with the results of segregations.

The birth of 3 Suri by Huacaya x Huacaya mating should be explained as the occurrence of a new dominant mutation.

REFERENCES

Andresen, E., 1974. The effect of ascertainment by truncate selection on segregation ratios. Proc. 1st World Congr. on Genet. Appl. Livest. Prod., Madrid, Spain, 1:111-114.

Antonini, M., Gonzales, M., Frank, E., Hick, M., Pierdominici, F., Catalano, S., Castrignanò, F., 2001. Cuticle cell mean scale frequency in different type of fleece of domestic South American Camelids. In: M. Gerken and C. Renieri (eds.) Progress in South American Camelids Research. EAAP Publ. N. 105, Academic Press Ltd., London, UK, pp 110-116.

Antonini, M., Gonzales, M., Valbonesi, A., 2004. Relationship between age and postnatal skin follicular development in three types of South American domestic camelids. Livest. Prod. Sci. 90:241-246.

Baychelier, P., 2000. Suri and Huacaya: Two Alleles or Two Genes ? pp 79-85 in Proc. Australian Alpaca Ass. Nat. Conf., Camberra, Australia.

Bonavia, D., 1996. Los Camelidos Sudamericanos. IFEA-UPCH Publ., Conservation International, Lima, Peru.

Bustinza Choque, V., 1985. Razas de Alpacas del Altiplano: Suri y Wakaya. Universidad Nacional del Altiplano ed., Puno, Peru.

Calle Escobar, R., 1984. Animal Breeding and Production of American Camelids. Ron Hennig – Patience ed., Lima, Peru.

Cotterman, C.W., 1953. Regular two-allele and three-allele phenotype systems. Am. J. Hum. Genet. 5:193-235.

Falconer, D.S., 1993. Introduction to Quantitative Genetics. Longman Scientific and Technical, Longman House, Burnt Mill, Halow, UK.

Flores Ochoa, J., Mac Quarry, K., 1995. I Camelidi andini. In: F.O. Pathey and Sons (eds.) L'oro delle Ande, Vol. I, Soto Impresor, Madrid, Spain, pp 23-35.

Frank, E.N., Hick, M.V.H., Gauna, C.D., Lama, H.E., Renieri, C., Antonini, M., 2006. Phenotypic and genetic description of fibre traits in South American domestic camelids (llamas and alpacas). Small Ruminant Res. 61:113-129.

Hoffman, E., Fowler, M.E., 1995. The Alpaca Book. Clay Press, Clay, CA,USA.

Huether, C.A., Murphy, E.A., 1980. Reduction of bias estimating the frequency of recessive genes. Am. J. Hum. Genet. 32:212-222.

Huston, K., Chase, R., Waller, R., 1974. Identifying genes with visible effect in cattle: full, three-quarter, and half-sib; other methods. Proc. 1st World Congr. on Genet. Appl. Livest. Prod., Madrid, Spain, 1:39-46.

Novoa, C., Wilson, T., 1992. The management of global animal genetic resources. FAO ed., Animal Production and Health, Roma, Italy.

Ponzoni, R.W., Hubbard, D.J., Kenyon, R.V., Tuckwell, C.D., McGregor, B.A., Howse, A., Carmichael, I., Judson, G.J., 1997. Phenotypes Resulting From Huacaya by Huacaya, Suri by Huacaya and Suri by Sury Alpaca Crossings. pp. 11-13 in Proc. Int. Seminar on Alpaca Industry, Sydney, Australia.

Serre, J.L., 1997. Génétique des populations. Editions Nathan, Paris, France.

Sokal, R.R., Rohlf, F.J., 2003. Biometry. 3rd ed. Freeman and Company, New York, NY, USA.

Steinberg, A.G., 1959. Methodology in Human Genetics. J. Med. Educ. 4:315-334.

Velasco, J., 1980. Mejoramiento Genético de Alpacas. Page 156 in Anales III Reunion Cientifica Animal. Soc. Peruana de Prod. Anim., Lima, Peru.