Inheritance of Suri and Huacaya type of fleece in Alpaca

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

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Carlo Renieri¹, Alessandro Valbonesi¹, Vincenzo La Manna¹, Marco Antonini², Moises Asparrin³

¹Dipartimento di Scienze Ambientali. Università di Camerino, Italy
²Ente per le Nuove Tecnologie, l’Energia e l’Ambiente, C.R. Casaccia BAS-agro. Roma, Italy
³Michell 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

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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 pattern 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 4.78. 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’eredità 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 recessivi, 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.

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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 \times Suri dam from 62 paternal half sib families, and 2126 (1009 females and 1117 males) offspring by Huacaya sire \times 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 \times 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 |
Inheritance of fleece types in alpaca

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 mask 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, Gadj, 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 (Gp, on which the overall judgement is based) and to resolve it in its components: the pooled G (Gp, obtained by treating the different progenies as though they were a single large progeny), and the heterogeneity G (GH, 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 (Gp) or partitioned (Gp and GH) Williams’s correction was not applied, because the adjusted G-values (Gadj) are not additive. Values of G were compared to a chi-square distribution at the 0.05 level with: (a-1), b(x(a-1), and (a-1)x(b-1) degrees of freedom for Gadj and Gp, Gp and GH, 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 F₁ progeny of
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 2. Observed and expected frequencies on Suri x Suri segregating families in a tested 7 : 1 hypothesis.

| Males | Offspring | Observed frequency | Expected frequencya | $G_{adj}^b$ | 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.
Inheritance of fleece type in alpaca
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).

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

| Males | Offspring | Observed frequency | Expected frequency | \(G_{adj}^b\) | 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.
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 the 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
Inheritance of fleece types in alpaca 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 5. Observed and expected frequencies on Suri x Suri segregating families in a tested 9:7 hypothesis.

| Males | Offspring | Suri | Huacaya | Expected frequency | Gadj | P |
|-------|-----------|------|---------|-------------------|------|---|
|       |           |      |         | 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| 5        | 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 |

*According to the formula suggested by Andresen (1974).

*bAdjusted G-values according to William’s correction.
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.

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