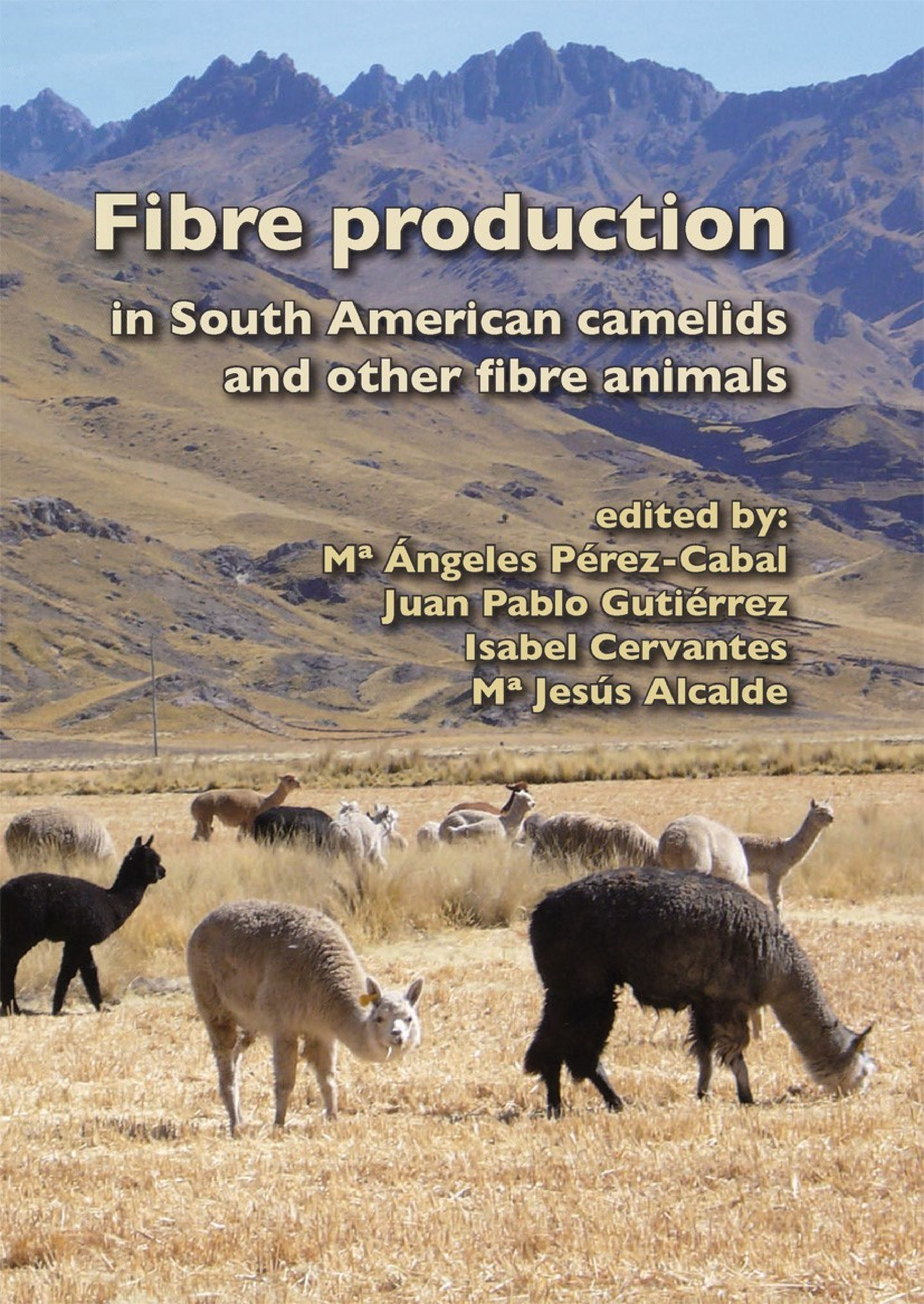

Fibre production

in South American camelids and other fibre animals

edited by:
Mª Ángeles Pérez-Cabal
Juan Pablo Gutiérrez
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Preface

The main objective of these European meetings is to promote the exchange of scientific information among international groups dedicated to the production of animals producing textile fibre. They are organised under the umbrella of the European Association of Animal Production (EAAP) and claims for relaunching the meeting activities of the Animal Fibre Working Group organised within the EAAP. The previous European Symposium was held in Göttingen (Germany) in 2006 and our main aim was to set a 3-year frequency for the following meetings to continue with the debates about South American Camelids and Fibre Animals.

The 5th European Symposium on South American Camelids and First European Meeting on Fibre Animals was jointly organised by the Complutense University of Madrid (UCM) and the University of Seville (US) in Seville (Spain). Dr. Juan Pablo Gutiérrez (UCM) was the Chairman of the Organising Committee which was formed by Mª Jesús Alcalde (US), Mª Ángeles Pérez-Cabal (UCM), Ester Bartolomé (US), Rocío Álvarez (US), Mercedes Valera (US) e Isabel Cervantes (UCM). We wish to thank especially Andrés Pérez and Meritxell Justicia, students from both universities, who helped us during the Symposium.

The Symposium was held at the 'Diputación of Seville'. We thank the administration of the Diputación for providing the lecture and posters halls and all the staff for their help.

We are grateful to the 'Ministerio de Ciencia e Innovación' (Spanish Ministry of Science and Technology) for supporting the attendance of the invited speakers. ETSIA and Vicerrectorado de Relaciones Institucionales of University of Seville, Barclays Bank, Diputación of Seville, Turismo of Seville Convention Bureau, Ministerio de Medio Ambiente y Medio Rural y Marino, and Consejería de Agricultura y Pesca of Junta de Andalucía funded the organisation of the Symposium. We would also like to acknowledge the 'Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria' (INIA, Spanish Institute of Agricultural Technology and Research) who funded these proceedings (AC2010-000002-00-00), that were printed from the manuscripts supplied by the authors. We would like to thank the editors of Wageningen Academic Publishers. Here are the studies presented in Seville that the contributors wanted to be published in these proceedings.

Mª Ángeles Pérez-Cabal, Juan Pablo Gutiérrez, Isabel Cervantes, and Mª Jesús Alcalde
The editors

Table of contents

Setting the scene: animal fibre

Meat and fibre production

Breeding and genetics

Nutrition and reproduction

Management

Health

Abstracts

Round tables

Keyword index

Setting the scene: animal fibre

Genetic variability of fleece shedding in the Martinik hair, Romane sheep breeds and their crossbreds

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Abstract

From the ancestral pelage of the domestic sheep which looks like the protective double coat of the wild sheep, changes following domestication and the development of textile industry resulted in the development of the modern woolled sheep with a large decrease in the tendency to moult and extension of wool fibre at the expense of coarse hair leading to a single coat where all fibres are similar in dimension and grow permanently. Wool production is still the main purpose of sheep farming in the southern hemisphere, but in Europe wool production is often unprofitable and there is an interest in the use of breeds that have no wool or shed their wool due to the relative value of meat and wool, and increasing shearing costs. In the present paper investigations were made to evaluate genetic variability of moulting or fleece shedding including QTL detection in the French Romane, the Martinik Hair, a hairy sheep without wool close to Barbados-Black-Belly and a Martinik Hair-Romane backcross population. In the Romane breed, 43.2% of adult ewes shed at least part of their fleece once a year during spring. Heritability estimate of moulting aptitude is high (0.46) but prevalence of total fleece shedding is low (1.5% of ewes shed all their fleece). In the Martinik Hair-Romane backcross population 72% of animals shed their fleece. It was proposed to introgress gene pool from the Martinik Hair in the Romane breed through an experimental design combining QTL detection and introgression of QTL for fleece shedding in the Romane breed.

Keywords: sheep, fleece shedding, genetic variability, QTL detection, gene introgression

Introduction

The wild ancestor of sheep was a hair sheep which evolved into modern woolled breeds through domestication, migration of people from the Middle East and artificial selection. The first important migration was of hair sheep; the present-day tropical hair sheep and some other hair breeds (Wiltshire Horn, Soay, …) are descendants of these sheep. Later, migrations of people from the Middle East outwards to south-east Asia, Africa and Europe were accompanied by domestic animals, including the more recently developed woolled sheep. In time, these sheep displaced hair sheep everywhere, except the humid tropics (Zygoyiannis, 2006).

The needs of humans for clothing, and of the sheep for protection from cold, were undoubtedly responsible for the evolution of the many woolled breeds and their dominance in both Europe and the arid regions of Asia and Africa. In particular, the Romans introduced a white woolled sheep into Western Europe and this was a major contributor to the British breeds of sheep, and probably also fine woolled sheep. The development of true fine wool began in the Middle East probably soon after 1000 BC (Ryder, 1969). But the emergence of the Merino as a distinct breed occurred in the late Middle Ages in Spain (Ryder, 1984). Wool production based on the Merino-breed was then developed in the New World and southern hemisphere from the 19th century.

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Along with domestication and selection process in response to the human needs for clothing and development of the textile industry, the coat of the wild sheep evolved into the merino fleece. The coat of the wild sheep and derived hair sheep comprises a hairy outer coat (composed of kemp) and a woolly undercoat. This coat has a simple cycle of active growth from spring to autumn followed by inactivity in winter, which is annually driven by seasonal changes in daylight. The whole coat moults every spring with replacement of outer coat only from spring to summer and then replacement of the undercoat from summer to autumn. Changes following domestication and selection have resulted in (1) an increasing period of hair growth leading to a growth phase longer than a year and subsequently a decrease in the tendency to moult, and (2) the development of the wool at the expense of the hair and kemp. As a consequence for textile use, the lengthening of the hair growth phase provides the necessary fibre length for spinning while extension of the wool undercoat leads to the modern fine woolled sheep owning a single coat where all fibres are similar in dimensions and grow permanently (Rougeot, 1982).

Today wool production remain the main purpose of sheep farming in the southern hemisphere, mainly Australia, New Zealand, Argentina, Uruguay, South Africa and Asia. In contrast, in Europe wool production is now generally unprofitable and may indeed be undesirable compared to meat or milk production. This is mainly because the income from wool is less than the costs associated with shearing and the removal of soiled wool (‘dagging’) from lambs prior to slaughter or to prevent fly strike (Vipond, 2006). Consequently with increasing shearing costs, there is a new interest in Europe for the use of breeds that have no wool or shed their wool. Some farmers in the UK or Germany are experimenting by crossing their sheep with other breeds that either shed their wool annually, or are recognised ‘hair’ sheep breeds, such as the Wiltshire Horn, the Dorper, Khatardin and Barbados Blackbelly, with varying degrees of success (Conington, 2010). To date no similar experiments have been undertaken in France. The present paper describes experimental designs with first results aiming (1) to investigate genetic variability including QTL detection of fleece shedding aptitude in the Martinik Hair sheep breed, the French Romane breed and their crossbred and (2) to evaluate genetic strategies for gene introgression of fleece shedding in the Romane breed in France.

Fleece shedding aptitude in the Romane breed

Material and methods

The Romane breed is a composite line of 50% Romanov (prolific breed) and 50% Berrichon du Cher (meat breed), considered as a new breed at the 4th intercross generation (Ricordeau *et al.*, 1992). Selection objectives of this breed are mostly maternal traits (prolificacy, growth of the lambs between 10 and 30 days) and meat production traits. This breed is known to have a high productive potential but shows a large variability in its fleece type due to the variability of coat structure in parental lines. Romanov breed has a coarse fleece with some fibre shedding (Bykova, 1973) while Berrichon du Cher derived from Merino by crossbreeding during the 19th century has a fine medium crossbred fleece. The Romane breed, shows a large variability in its fleece type with a high variable birthcoat type in lambs related to lamb survival and a kemp wool fleece of a poor quality with some aptitude for fleece shedding (Allain *et al.*, 2010b).

General experimental conditions

A flock of 350 ewes of the Romane breed has been used as experimental support since 2000 at the INRA farm of La Fage on the Causses-du-Larzac, a calcareous plateau at an altitude of 800 m in the south of France. This flock was maintained in permanent outdoors conditions on rangelands with arid conditions despite an abundant annual rainfall of 1000 mm, due to an important permeability of the soil, which feeds deep subterranean rivers. Seasons are highly contrasted with cold winter due to the altitude, hot summer due to the southern latitude and intermediate seasons showing high variations in temperature, wind and rainfall. The breeding system thus described (Bouix *et al*., 2002) is characterised by a short lambing period in outdoors conditions from end-March to mid-April. Climate conditions in that period can vary abruptly from severe conditions of low temperature, wind and rain or snow to warm and sunny conditions. The annual shearing time for ewes is the beginning of July, just after weaning the lambs. A total of 3,051 observations on fleece shedding aptitude were made once a year from the age of 14 months on 1,359 ewes from 79 sires just prior to the annual shearing at the end of June.

Fleece shedding measurement

Fleece shedding or moulting aptitude was determined in adult animals once a year at the end of June just before shearing time. In a first step, at farm level, the part of the animal body area denuded or without wool was drawn on a standard sheep profile. Then this figure was analysed using image software to estimate the extent of moulting or fleece shedding as a percentage of the total body area.

Data analysis

Data were analysed by ANOVA with the GLM procedure of the SAS package. In the analysis model, the considered fixed effects were year of observation (from 2000 to 2009), age (4 levels from 1 year to 4 years old and more), litter size (4 levels from none to 3) and number of suckling lambs. Genetic parameters of fleece shedding aptitude in the adult Romane ewe were estimated using a TM (Threshold Model) programme[1] using a Bayesian analysis and performing numerical integration through the Gibbs sampler. Fleece shedding rate was considered as a continuous trait[2].

Results and discussion

Fleece shedding rate and moulting pattern

Annual fleece shedding aptitude in the 1,359 adult Romane ewes observed once a year (3,051 records) is reported in Figure 1. Mean fleece shedding rate is 17.0% with 43.2% and 1.4% of adult ewes which shed at least part of and all their fleece once a year during spring, respectively. As a general pattern of moulting over body regions, wool shedding was first observed from neck and belly, then moved progressively in a dorso-posterior direction to end on the rump. The Romane breed being a composite line of 50% Romanov and 50% Berrichon du cher, gene pool involved in fleece shedding aptitude is probably originated from the Romanov breed where fibre shedding has been reported (Bykova, 1973) while no fleece shedding has ever been reported in the Berrichon du Cher breed.

Non-genetic effects and heritability of fleece shedding in the adult Romane ewe

Age of the ewe, reproductive activity and year of observation have a highly significant effect on fleece shedding aptitude. Young ewes of 1-year old shed significantly less ($P<0.001$) their fleece than older ewes. Increase of wool shedding with age has also been reported in Wiltshire-Merino crosses (Rathie *et al*., 1994). At one year of age hog ewes shed less ($P<0.05$) than breeding ewes. Such a difference in fleece shedding aptitude in young ewes can be due either to gestation and

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[1] Available at http://snp.toulouse.inra.fr/~legarra or upon request to the author at: andres.legarra@toulouse.inra.fr.

[2] Authors thank Andres Legarra for help in using the TM programme.

Figure 1. Fleece shedding in the Romane breed categorised by percentage classes of body surface where fleece is shed in adult ewes (3,051 records from 1,359 ewes).

reproductive activity or to body growth development at the age of 7 months as the decision for the age of first mating (7 or 19 months) is conditioned by a minimum live weight of 35 kg at 7 months of age. But in breeding ewes, whatever the age, there was no effect of the litter size on fleece shedding.

High heritability (0.46±0.06) estimate of fleece shedding aptitude was observed in the Romane breed (Figure 1). Genetic variability of fleece shedding aptitude has never previously been reported in a woolled sheep. It offers opportunities to implement selection leading to a moulting sheep requiring no shearing and thus creation of genetic progress by improving adaptive traits in a breed with a high production potential (Francois *et al*., 2010).

In addition to fleece shedding, the Romane breed shows another fleece adaptive trait to be selected in extensive management under permanent exposure outdoors and harsh environments. At birth lambs exhibit a high variability of coat type from a long hairy coat to a very short woolly coat and lamb survival rate is related to birthcoat type (Allain *et al*., 2009). Lambs bearing a long hairy double coat have a higher survival rate than lambs with a short woolly coat. This difference in lamb survival (4 points; 93% vs. 89%) could be explained by a lesser thermal protection with higher heat losses and a lesser resistance to cold and wet weather conditions in lambs bearing a short woolly coat (Allain *et al*., 2010a). High heritability estimates of both birthcoat type (0.58) and fleece shedding (0.47) were observed but there were no genetic correlations between these two fleece adaptive traits (Allain *et al*., 2010b) suggesting that different genes are controlling determinism of fleece shedding and birthcoat hairiness.

Fleece shedding aptitude in Martinik hair and Martinik hair-Romane backcross

Material and methods

General experimental conditions

A flock of 50 Martinik Hair ewes and a flock of 800 Romane ewes breeds were used as experimental support at the INRA farm of La Sapinière (Domaine experimental de Bourges). Animals are raised in a barn with open shed. Depending on grazing availabilities and season, animals are fed indoors and go to pasture during the day from spring to autumn. As concerns the reproduction cycle, Romane ewes were mated for the first time at the age of 7 months in July, at the age of 16 months in April for the second time and then once a year in April. Martinik Hair ewes were mated once a year in July.

Martinik Hair sheep

The Martinik Hair sheep is a typical double coat hair sheep with no wool, originated from the French West Indies but related (origins and history) to the other hair sheep populations present in the Caribbean Islands and Central America (Barbados Blackbelly, Pelibuey, West African Dwarf) (Leimbacher *et al*., 2010). The Martinik Hair sheep has a high production potential (prolificacy, low susceptibility to endoparasites) and was introduced in the form of embryos in France during the nineties. A small flock of 50 ewes was created at the INRA farm of La Sapinière (Domaine de Bourges) for experimentation. As in tropical conditions, this hair sheep also moults and renews its whole fleece annually from spring to summer in temperate conditions.

Creation of a backcross Martinik Hair-Romane sheep population

In 2001, 4 Martinik Hair rams were mated with 100 Romane ewes to produce F1 rams. 4 sons of the different Martinik Hair sires were mated with 180 Romane ewes to produce 228 backcrossed animals born in December 2006. All these backcrossed animals were measured for fleece shedding aptitude in late spring at 7 months. Thereafter within this population, 83 animals were also measured for fleece shedding aptitude once a year in late spring for 2 years, i.e. at 19 and 31 months of age.

An inter-backcross population was also created in 2008. 8 backcross sires were mated to backcross ewes to create 102 individuals of the inter-backcross population which were also measured for fleece shedding aptitude at 7 months of age in late spring. Fleece shedding aptitude was measured in a similar way to that previously for Romane ewes.

Results and discussion

Annual fleece shedding aptitude in Martinik hair - Romane backcross animals

Figure 2 shows fleece shedding aptitude at 7 months of age in the 228 backcross animals. 71.9% of individuals shed at least 30% of their fleece during spring and 2 animals shed all their fleece with a mean fleece shedding rate of 36.4%. Non-genetic effects such as sex, age of dam or litter size were tested but any significant effect was not observed. In contrast, a highly significant sire effect was observed. Within the sire family (44 to 75 halfsibs/sire family), the mean proportion of fleece shedding varies from 18.6 to 47.0% between the 4 family sires studied. The general pattern of wool shedding over body regions is similar to that observed in the pure Romane breed.

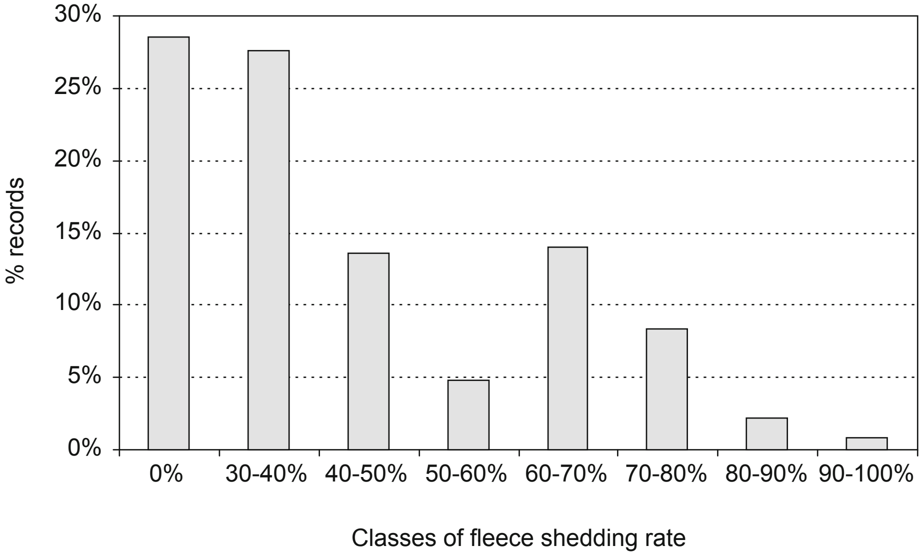

Figure 2. Fleece shedding categorised by percentage classes of body surface where fleece is shed at 7 months of age in 228 Martinik Hair-Romane backcross animals.

Fleece shedding was then observed in 83 animals of both sexes over 3 consecutives years. Data were analysed using GLM and then Varcomp SAS procedures to determine variability and animal variance components of fleece shedding in the 83 animals observed 3 times at yearly intervals. Age and sex-age interaction effects were observed. Fleece shedding increases with age from a rate of 30.3% at both 7 and 19 months of age to 45.0% at 31 months of age as previously observed in the Romane breed and Wiltshire-merino crosses (Rathie *et al.*, 1994). There was no sex effect at 7 months of age but thereafter highly significant differences were observed according to sex at 19 and 31 months of age. Compared to males, a higher and a lower fleece shedding were observed in females at 19 and 31 months of age, respectively. As a possible explanation, sex hormones and/or genes on the sexual chromosome could be involved in determining fleece shedding. Repeatability estimated using the SAS VARCOMP procedure was 0.59.

Fleece shedding in the inter-backcross population of Martinik Hair-Romane animals

Figure 3 shows the fleece shedding rate in the 102 animals of the inter-backcross population. 60.8% of individuals shed at least 30% of their fleece during spring and 4 animals shed all their fleece. Compared to backcross animals, a smaller proportion of animals shed part of their fleece but a larger part shed all their fleece.

In agreement with Slee (1959), who studied different crosses between the Wiltshire Horn and the Scottish Blackface, at least two components of the shedding process can be distinguished: (1) the ability to shed and, (2) the extent of shedding or proportion of the body area defleeced. In the present work, by comparing backcross population to parental pure breed lines, there is evidence that genetic determinism of the fleece shedding extent is a polygenic effect but the existence of major genes for the ability to shed cannot be excluded. The mean fleece shedding rate observed in backcross animals (owning ¾ of the Romane gene pool) is close to expected value estimate of the shedding rate in parental lines (36.4%, 100% and 17% in Martinik Hair-Romane backcross, Martinik Hair and Romane respectively), but the proportion of animals that shed at least a

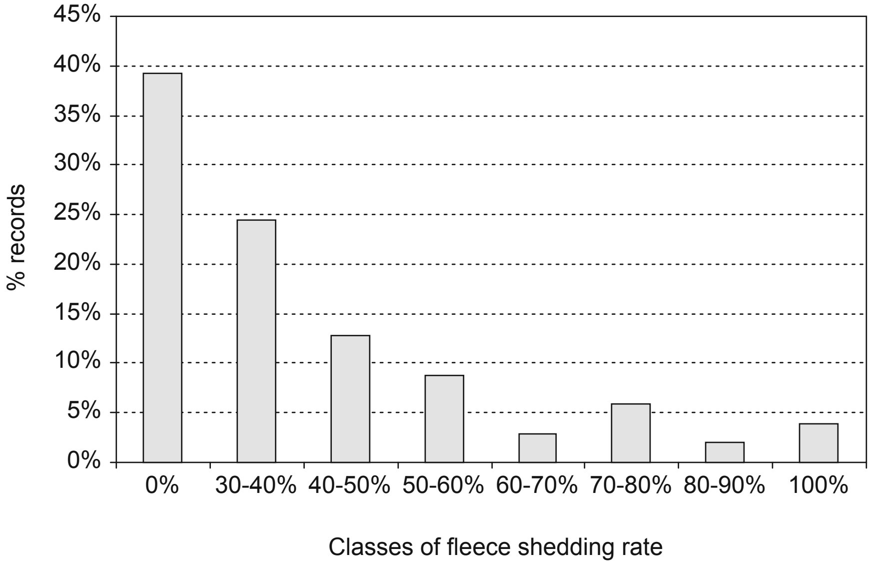

Figure 3. Fleece shedding categorised by percentage classes of body surface where fleece is shed at 7 months of age in 102 inter-backcross Martinik Hair-Romane animals.

part of their fleece in backcross animals is intermediate between the two parental lines (100%, 43.2% and 71.9% in Martinik Hair, Romane and backcross animals, respectively) suggesting a deviation from additivity with major gene and/or dominant effects of the ability to shed.

QTL detection for fleece shedding

In parallel to these investigations, two experimental designs for QTL detection of fleece shedding aptitude through whole genome scans were initiated from 2004. The first one using the Romane breed population at INRA La Fage experimental farm comprises 10 sire families of 100 halfsibs/sire for QTL detection of birthcoat type, fleece shedding and maternal behaviour traits (Boissy *et al*., 2007). Within this experimental design, a total of 600 adult ewes from 10 sire families were observed once a year for fleece shedding aptitude just prior to the annual shearing at the end of June.

The second one is based on the Martinik Hair-Romane backcross population at La Sapinière Inra experimental farm and comprised 4 sire families of 60 halfsibs/sire for QTL detection of resistance to parasitism and fleece shedding (Moreno *et al*., 2006). Animals of these QTL experimental designs have been genotyped with the OvineSNP50 bead chip (Moreno *et al*., 2009), and analyses are in progress to detect QTL and then to fine-map relevant genes controlling fleece shedding aptitude in these 2 population resources as well as birthcoat type in the Romane breed.

Genetic strategies for gene introgression of fleece shedding gene in the Romane breed

Under European conditions where the value of wool is often lower than shearing costs and other costs associated with managing wool, selection for fleece shedding in order to suppress shearing represents an alternative opportunity for improving the profitability of sheep farming. However, as for any other adaptive trait, selection strategies for fleece shedding in the Romane breed could be selecting together with production traits according to two different strategies.

The first strategy could be to select within the Romane breed as according to our results, a genetic variability with a high heritability estimate of fleece shedding aptitude was observed offering opportunities for within-breed selection leading to a moulting sheep requiring no shearing. However, it is not easy to measure this trait and prevalence of total fleece shedding is low. An alternative method could be to introgress gene pool controlling fleece shedding from the Martinik Hair, a 'hair sheep'.

In order to valorise results observed up to now on fleece shedding in both the Romane breed and the Martinik Hair-Romane backcross population, an experimental design aimed at introgressing gene pool for fleece shedding from the Martinik hair breed into the Romane breed through 4 successive backcrossing generations was initiated in 2009. The experimental design is similar to those combining detection and introgression QTL in outbred populations recently proposed by Yazdi *et al*. (2008, 2010) as an efficient method for saving time and cost in an introgression process. For instance, 6 Martinik Hair-Romane backcross rams with total or near total fleece shedding phenotype from the QTL experimental design described above, were mated with 120 hog Romane ewes expressing partial fleece shedding at 7 months of age in late spring. Measurements made with 360 hog ewes showed that about 40% of hog Romane ewes shed part of their fleece at 7 months of age. Similar mating schemes will also be used for producing the last backcrossing generation. The use of molecular information with QTL introgression will be very helpful in the near future, as QTL detection through a whole genome scan with the OvineSNP50 bead chip is in progress in both the Romane breed and the Martinik Hair-Romane backcross population.

Conclusions

Genetic variability of fleece shedding was investigated in the Romane breed and a Romane-Martinik hair backcross population. The high heritability estimate of fleece shedding observed in the Romane breed offers opportunities to implement selection, leading to a moulting sheep requiring no shearing as a new adaptive trait, together with production traits in this breed known to have a high productive potential.

Despite high genetic variability of fleece shedding in the Romane breed, it was proposed to increase efficiency by introgressing a moulting gene pool with the use of molecular markers from the Martinik Hair breed, a hair sheep with no wool, due to low prevalence of total fleece shedding in the Romane breed. The experimental design scheme will combine detection and introgression of QTL for fleece shedding in the Romane breed.

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Suri/Huacaya phenotype inheritance in alpaca (*Vicugna pacos*)

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Abstract

The Suri/Huacaya phenotype inheritance in alpaca was tested on two independent Peruvian sources of records: the Registry of Mallkini farm (588 offspring by Suri sire × Suri dam from 62 paternal half sib families, and 2,126 offspring by Huacaya sire × Huacaya dam from 177 paternal half sib families) and the results of the Quimsachata INIA ILPA Puno experimental trial (two reciprocal experimental test-crosses, involving a total of 17 unrelated males and 149 unrelated females). The data support a genetic model in which two linked loci must simultaneously be homozygous for recessive alleles in order to produce the Huacaya phenotype. The estimated recombination rate between these loci was 0.099 (95% C.L. = 0.029-0.204). The birth of 3 Suri offspring from Huacaya x Huacaya mating is explained by a new dominant mutation on some germinal lines of Huacaya animals. The direct mutation rate can be estimated at 0.0014.

Keywords: alpaca, Suri, Huacaya, segregation analysis, linkage

Introduction

This paper summarises the results of the research on Suri/Huacaya phenotypes inheritance carried out at the Italian University of Camerino, School of Environmental Sciences in collaboration with the Peruvian private Michel Group and the Peruvian National Institute for Agronomic Innovation (INIA, ILLPA Puno). The results are published in Renieri *et al*. (2009) and Presciuttini *et al*. (2010).

The inheritance of Suri/Huacaya phenotypes: a review

The inheritance mode of the Suri/Huacaya phenotype is unclear. A hypothesis of Suri recessivity has been abandoned in favour of a more widely accepted simple Suri dominance. Velasco (1980) proposed a single locus model with a dominant allele for Suri. Similarly, Ponzoni *et al*. (1997) suggested a model with a single gene with two alleles, though they also noted that the data were compatible with a model in which the trait was controlled by a group of closely linked alleles (haplotype). Baychelier (2000) tested three inheritance hypotheses using the records of the Australian Alpaca Association Herd Book: the model of a single gene with three alleles can be rejected, whereas the two-gene model is more suitable than the one-locus model. Finally, Sponenberg (2010) proposed a single autosomal dominant gene, with an additional genetic mechanism that can suppress the Suri phenotype in some animals. It should be noted that 4 Suri offspring have been observed among the offspring of 19,637 Huacaya × Huacaya crosses.

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Experimental designs

Two sets of records were analysed. The first source is the Registry record of the Mallkini farm, the private farm of Michell Group. In this case, 588 (291 females and 297 males) offspring by Suri sire × Suri dam from 62 paternal half sib families, and 2,126 (1,009 females and 1,117 males) offspring by Huacaya sire × Huacaya dam from 177 paternal halfsib families, born over 4 years (2004, 2005, 2006, and 2007), were analysed.

The second set of data was recorded in the crosses carried out at the experimental station of the INIA located in Quimsachata, Peru. The trial involved a total of 17 unrelated males and 149 unrelated females. Two reciprocal experimental test-crosses were carried out: Suri males × Huacaya females and Huacaya males × Suri females: 64 total Suri animals and 102 total Huacaya animals.

Results and discussion

Single gene hypothesis

The single gene hypothesis was tested in both data sets. In the Mallkini records, assuming that the percentage of the two female genotypes is the same (50%), the expected segregation 7 Suri: 1 Huacaya individual was tested. The results are presented in Table 1.

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 are not statistically significant ($0.057 \leq P \leq 0.924$). 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=0.33).

Considering first the Suri males in the Quimsachata experimental trial (Table 2), for the eight segregating animals it was possible to estimate the segregation ratio R of the Huacaya phenotype among their offspring assuming a truncated binomial distribution. With this model the maximum likelihood estimate of R was 0.290, with 95% C.L.=0.184-0.409. Clearly, a value of R=0.5, which is expected for a testcross of a recessive single-locus model can be rejected.

With regard to the reciprocal cross a similar analysis cannot be carried out. When one offspring only can be obtained from a Suri animal (the female in this case), the observed segregation ratio for a number of animals of unknown genotype is a function of two parameters: (1) the probability R that a segregating animal generates a Huacaya offspring (e.g. the Mendelian transmission probability), and (2) the probability H that an animal is segregating. A practical approach could be to estimate the value that each parameter assumes, once the other parameter is fixed on a value representing a reasonable choice. Assuming the segregation ratio R=0.5 (the probability that a Suri female mated to a Huacaya male produces a Huacaya offspring for a simple recessive genetic model), the maximum likelihood estimate of H is 0.582. Conversely, if we assume that H among the Suri females has the same value as that observed among Suri males (= 8/9, or 0.88), the maximum likelihood estimate of R is 0.331. The similarity of this last value with that estimated for the crosses of Suri males is certainly interesting. The results are for the rejection of the single-locus recessive model for the Huacaya phenotype.

Table 1. Observed and expected frequencies of Suri × Suri segregating families in a tested 7:1 hypothesis.

Males	Offspring	Observed frequency		Expected frequency[1]		G_{adj}^2	P
		Suri	Huacaya	Suri	Huacaya		
190	32	31	1	27.9	4.1	3.630	0.057
239	18	16	2	15.5	2.5	0.111	0.739
65691	27	26	1	23.5	3.5	2.697	0.101
00-024	27	23	4	23.5	3.5	0.089	0.765
00-034	30	27	3	26.2	3.8	0.215	0.643
0-176	27	26	1	23.5	3.5	2.697	0.101
0-258	19	13	6	16.4	2.6	4.053	0.044
02-848	34	29	5	29.7	4.3	0.126	0.722
1-1-245	6	5	1	4.6	1.4	0.133	0.716
1-2-240	9	7	2	7.4	1.6	0.109	0.741
1-3-214	8	7	1	6.5	1.5	0.246	0.620
1-3-310	12	10	2	10.1	1.9	0.009	0.924
1-3-329	10	8	2	8.3	1.7	0.063	0.802
1-3-333	10	9	1	8.3	1.7	0.392	0.531
2-1-376	19	16	3	16.4	2.6	0.076	0.783
2-3-335	5	4	1	3.7	1.3	0.089	0.766
2-3-342	5	3	2	3.7	1.3	0.489	0.484
9-163	20	19	1	17.3	2.7	1.553	0.213
9-510	44	34	10	38.5	5.5	3.471	0.062
Pooled	362	313	49	316.8	45.3	0.347	0.556

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

Double genes, independent segregation (epistasy)

Three independent two loci-two phenotype hypothesis were tested through the Mallkini records. In the 15:1 segregation hypothesis for duplicate Suri dominant gene action (Table 3), two progenies (the offspring of males 0-258 and 9-510), both with an excess of Huacaya and a low number of Suri, showed significantly different results than expected (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 borderline value (G_T,=29.65; P=0.056).

In the 13:3 segregation hypothesis (Table 4) for dominant suppression epistasis (the dominant gene for Suri is supposed to mask the genes at the Huacaya locus) three progenies (the offspring of males 190, 65691, and 0-176), each with an excess of Suri and a low number of Huacaya, displayed significantly different results than expected (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 $0.065 \leq P \leq 0.997$), 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 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