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Research Article

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Inheritance patterns of coat colouration and horn number in Jacob sheep

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Abstract: The allele for black coat colour is dominant relative to the allele for lilac in Jacob sheep and is affected by a single gene locus. The percentage of this colouration, as opposed to white fleece, across the body has a heritability value of 0.255. The mode of inheritance for horn number in these animals is less clear, with neither the trait for 2 horns, nor for 4 horns being totally dominant, based on crosses of 2 x 2-horned parents and 4 x 4-horned parents; although in these examples the majority of lambs had the same number of horns as their parents. However, when one parent had 2 horns and the other had 4 horns, the gender of the 4-horned parent appeared to influence the frequency of 4-horned offspring; 77% of lambs born to a 4-horned dam being 4-horned, but only 50% when the 4-horned parent was the sire. These data suggest evidence for sex-limiting factors being involved in determining the number of horns in this breed.

Keywords: Jacob sheep; horn number; coat colour

1 Introduction

Jacob sheep are a hardy breed which are believed to have originated from the Mediterranean area but are now kept throughout the world (Jacob Sheep Society 2014: http://www.jacobsheepsociety.co.uk). They have recently attracted medical interest due to the observation of a genetic disorder in the breed which can be used as an animal model for Tay-Sachs disease (e.g. Torres et al. 2010). As a breed they have been farmed for meat production but are probably best known for their characteristic patched black and white, or lilac and white, fleece with the colouring being distributed across the body of the animal. This patched appearance means that the fleece has a premium associated with it for spinning of wool, and also that the sheepskin can be sold as a rug after an animal has been killed. However the extent and distribution of the colouration within the fleece varies from animal to animal (Figure 1). It has been suggested that alleles for black colouration are dominant and that alleles for lilac colouration are recessive, although evidence for this has not yet been reported in the scientific literature.

Another characteristic trait is the presence of horns in both males and females, with those in the males being particularly prominent (Figure 2). They are defined as being polycerate and the breed standard dictates that all animals should have either two or four horns. As in other breeds which can be multiple-horned (e.g. Manx and Hebridean) it is generally believed that those animals with four horns may be more susceptible to splits in the eyelid (Herrera et al. 2007), a trait regarded as undesirable, as it is thought to increase dangers of eye problems. The nature of this apparent association between multiple horns and split eyelids remains unclear.

This paper investigates the genetic relationship between three different factors which are regarded as important in the Jacob breed: the genetic relationship between black and lilac colouration; the relationship between numbers of horns in individual sheep relative to the number of horns in the parents of these sheep; and the heritability of the extent of the black/lilac colouration.

2 Materials and Methods

All data were accessed using historical data publically available at The Jacob Sheep Breeders Association webpages (http://www.jsba.org/search.html).

To investigate the mode of inheritance of the black versus lilac colouration, the database was searched using “lilac” as a search term and data were collated from

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Figure 1: Example of Jacob ewes showing the variation in extent and distribution pattern of colouration across the body

Figure 2: Example of the gender difference relative to horn size in the male (left) and female (right) within the Jacob breed

the first 50 animals where the pedigree was available. The outcome of all crosses within two generations of the original animal were examined (i.e. parental, grandparental, F1 and F2 generations) and recorded for lilac x lilac crosses and also between lilacs and animals believed to be heterozygotes (based on the observation that they were listed as black, but had either a lilac parent, or had produced lilac offspring).

To investigate the heritability of the extent of colouration 500 entries were selected at random and for each animal the following values were tabulated: percentage of coat colouration (irrespective of black or lilac colouration) for each animal and also for both parents. Heritability of the degree of colouration was assessed by calculating the correlation of the degree of colouration of the lambs relative to the mid-parent mean value. Heritability values were also determined based on the correlation to that of the sire and dam individually. In addition, the mean and median values were calculated for percentage colouration of lambs, sires and dams. Data were checked to ensure values were normally distributed and paired t-tests were performed on sire-lamb and dam-lamb values.

For each of the 500 animals used for the analysis of percentage of coat colouration, the number of horns present was recorded for both it and also for both parents. The relationship between the following crosses was investigated: 2-horned males x 2-horned females; 2-horned males x 4-horned females; 4-horned males x 2-horned females; and 4-horned males x 4-horned females. Data

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were compared by using a Chi-squared test to determine if the values for 2-horned or 4-horned lambs was equivalent when crossing a 4-horned male and 2-horned female relative to crossing a 2-horned male and 4-horned female.

Ethical approval: The conducted research is not related to either human or animal use.

3 Results

3.1 Inheritance of coat colouration (lilac versus black)

In total 24 lilac x lilac crosses were identified and in all cases the resulting lamb was lilac. This is in keeping with the observations expected where lilac sheep are homozygous for a recessive lilac allele. In the case of the lilac x assumed heterozygotes 43 of the 82 (i.e. 52%) offspring were lilac. Based on a Chi-squared calculation this value is not significantly different from the 50% expected from a backcross F1 population arising from crosses between homozygous recessive individuals and known heterozygotes. Thus these data are supportive of the hypothesised relationship between the black and lilac alleles, with black being dominant relative to lilac.

3.2 Heritability of extent of coat colouration

The mean and SEM (shown in parenthesis) values of the percentage of colouration on the fleece of the animals was 38.2 (0.60) for lambs, 38.7 (0.51) for sires and 37.2 (0.59) for dams, with median scores of 40% in all cases. Paired t-tests for values for both lambs versus sires and lambs versus dams showed no significant differences in values ($P>0.05$)

The heritability value for extent of colouration, based on a plot of percentage colouration in lambs versus the mid-parent mean value, was 0.255. When compared against a single parent the value was 0.184 for the sire and 0.325 for the dam.

3.3 Inheritance of horn number (2 horns versus 4 horns)

The pattern of horn numbers observed in lambs relative to the number of horns seen in their parents is shown in Table 1. These data do not help to elucidate the mode of inheritance regarding 2 versus 4 horns in these animals, other than to support hypotheses that there are likely to be polygenic interactions between genes in terms of the number of horns an animal possesses.

The fact that 4 x 4 crosses and 2 x 2 crosses both result in combinations of lambs with both 2 and 4 horns suggests that this is not a simple single locus Mendelian relationship with a pair of alleles, as neither is completely dominant over the other. In both cases, the majority of the lambs had the same number of horns as the parents; 63% of the lambs from a 2 x 2 cross had 2 horns, and 72% of the lambs from a 4 x 4 cross had 4 horns.

It is interesting to note that crosses where one parent has 2 horns and the other has 4 horns shows a pattern which varies depending upon the gender of the parent with 4 horns and the one with 2 horns. For example, where the sire had 4 horns and the dam had 2 horns, 50% of the lambs had 4 horns, but where the sire had 2 horns and the dam had 4 horns, 77% of the lambs had 4 horns. These values were significantly different ($P<0.05$).

It is interesting to note that when the sire has 2 horns, there is little difference between the proportion of males and females having 2 horns; 0.62 versus 0.64 (where the dam had 2 horns) and 0.21 versus 0.25 (where the dam

Table 1: Proportion of lambs born with either 2 or 4 horns, relative to the number of horns for each parent. Numbers shown in parenthesis are actual values

	Lambs with 2 horns			Lambs with 4 horns		
	All	Male	Female	All	Male	Female
2-horned sire						
2-horned dam	0.63 (29)	0.62 (13)	0.64 (16)	0.37 (17)	0.38 (8)	0.36 (9)
4-horned dam	0.23 (16)	0.21 (6)	0.25 (10)	0.77 (53)	0.79 (23)	0.75 (30)
4-horned sire						
2-horned dam	0.50 (38)	0.42 (13)	0.56 (25)	0.50 (38)	0.58 (18)	0.44 (20)
4-horned dam	0.28 (52)	0.23 (19)	0.32 (33)	0.72 (136)	0.77 (65)	0.68 (71)

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had 4 horns) respectively. However when the sire had 4 horns the proportion of males and females having 2 horns appeared to be lower in males than in females; 0.42 versus 0.56 (where the dam had 2 horns) and 0.23 versus 0.32 (where the dam had 4 horns) respectively. However, after performing a Chi-squared calculation neither difference was found to be significant ($P > 0.05$).

4 Discussion

Breeders of Jacob sheep have generally regarded the relationship between black and lilac colouration as being present at a single locus, with black being the dominant allele. However, to the best of our knowledge, this is the first time that this pattern has been investigated in the scientific literature and the data here are supportive of the predicted mode of inheritance. The inheritance of colouration has been investigated previously in other breeds and the pattern varies with black fleeces being recessive in the Xalda breed (Royo et al. 2008) and Ryelands (http://www.ryelandfbs.com/) but the black colouration is dominant in Welsh Black Mountain sheep (Roberts and White, 1930). However the data here do not compare colouration versus non-colouration, but rather they compare the type of colouration (black versus lilac) and it is likely that this is a comparison involving some sort of dilution factor, with black being dominant relative to the diluted lilac.

As a breed one of the most important traits of the Jacob breed is the appearance and colour pattern of the coat, with the fleece being desirable for wool production and the pelt or hide being used for sheepskin rugs. In part this is why societies for the breed recommend that the extent of colouration should ideally be between 40% and 60%, with anything less than 15% or more than 85% being considered undesirable. Therefore information regarding the heritability value for extent of colouration in this breed is useful to breeders. In the case of this investigation, a relatively high heritability value ($h^2 = 0.255$) was observed. Thus a breeder who is aiming to achieve the recommended extent of coat colouration would be strongly advised to breed from sheep with around half of the fleece being coloured. However, a stronger correlation was seen between the values for the dam and the offspring ($h^2 = 0.325$) than were seen for the sire versus the offspring ($h^2 = 0.184$). This may suggest some form of epigenetic influence, although it is unclear why the extent of pigmentation would be influenced by epigenetic factors.

Previous investigations into the genetics of horn development in Soay sheep have identified either a three allele model (Coltman and Pemberton 2004: 321-327) or an example of incomplete expression of different alleles (Johnston et al. 2011) when investigating the presence or absence of horns, or the possibility of scurs (vestigial or deformed horns). More recently the analysis of polyceraty has been investigated using SNP markers in Damara sheep (Greyvenstein et al. 2016), suggesting a number of SNPs significantly associated with horn formation lie on ovine chromosome 2. However, the current data make use of archived records, rather than designed experiments where mating choices are planned using animals of known phenotypes, and so provides no access to genetic information. As such only the phenotypes, and not the genotypes, of the parents are known. Nevertheless it is clear that the number of horns in Jacobs is not determined by a single locus where there is complete dominance of one allele over the other and that there is some form of gender discrimination involved in the resulting phenotype.

Within the current work, we have identified two different areas where there appears to be some degree of difference associated with the gender of the corresponding parent. Firstly there is the issue of a higher heritability value when comparing the percentage of colouration of the dam to the offspring relative to the equivalent value for the sire and offspring. Secondly there is the issue of a difference in the presence of 2 or 4 horns in lambs resulting from a cross of a 2-horned and a 4-horned parent, with the horn number of the mother being more likely to influence the number of horns in the offspring.

Influences from either the mother or the father showing a bias have already been reported for other genetic factors in sheep (Cockett et al. 1997; Smit et al. 2005). However in the absence of more detailed information it remains unclear how exactly this influence is being exerted in the current examples.

It is concluded as follows: the relationship between black and lilac follows a classical single allele pattern with black being dominant; there is a high heritability in the extent of fleece colouration, with lambs having higher similarity to their mothers relative to their fathers for this trait; and although there is some degree of similarity in horn numbers between parents and offspring, the trait is almost certainly polygenic and the mode of inheritance remains unclear.

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