Archivos de Zootecnia
Journal website: https://www.uco.es/ucopress/az/index.php/az/
NOTA BREVE

Dilute Modification of Color in Shetland and Ouessant Sheep

Wendelboe, L.[1]; Hemming, R.[2] and Sponenberg, D.P.[3@]

[1]P.O. Box 43, Site 2, RR 2, Sundre, AB, Canada T0M 1X0.
[2]La Ville Oreux, 22130, Pluduno, France.
[3]Department of Biosciences and Pathobiology, Virginia Maryland College of Veterinary, Medicine, Virginia Tech, Blacksburg, VA, 24061.

ADDITIONAL KEYWORDS

Coat color.
Genetics.
Ovine.
Color dilution.

SUMMARY

Shetland breeding sheep were classed into fleece colors that varied from dark to light in a black-based group (black, warm black, dark brown, pewter) and a brown-based group (brown, fawn, honey). These produced 257 lambs. Among the most dilute colors, honey x honey matings produced only honey lambs, pewter x pewter matings produced only pewter or honey lambs. These two dilute colors mated to darker colors produced varying colors in agreement with a system of control by two loci in which black is dominant to brown at one *locus* (B) and dilute colors are recessive to fully intense colors at a second *locus* (*Mod* for *Modified*). Both loci have some degree of incomplete dominance which accounts for the full range of fleece colors. Results from Ouessant sheep included 41 lambs, all of black-based colors. Ouessant results were similar to Shetland results and indicate that the recessive mechanism for diluting fleece color is present in multiple breeds.

Modificación Diluída de Colores en Ovinos Shetland y Ouessant

PALABRAS CLAVE ADICIONALES

Color de la capa.
Genética.
Ovino.
Dilución de color.

RESUMEN

Ovinos de la raza Shetland mostraban vellones de varios colores, los cuales variaban de oscuro a claro en un grupo basado en el negro (negro, negro cálido, café oscuro, y estaño) y otro basado en café (café, café claro, miel). Los ovinos produjeron 257 crias. Entre los colores mas diluidos, apareamientos de miel con miel solamente produjeron crias de color miel. Parejas estaño por estaño solamente produjeron crias de miel o estaño. Estos dos colores diluidos apereados con colores más oscuros, produjeron varios colores que concuerdan con un sistema de dos loci. En el cual el negro es dominante sobre el café en un locus (B), y los colores diluidos fueron recesivos respectos a los colores completamente intensos en un segundo locus (Mod que significa Modificado). Ambos loci tienen algún grado de dominancia incompleta, que representa la gama completa de colores de vellóon. Los resultados de la raza Ouessant incluyeron 41 crías, todos de colores del grupo basado en el negro. Los resultados de Ouessant son similares a ellos de Shetland, e indican que el mecanismo para la dilución del color de los vellones ocurre en varias razas.

INFORMATION

Cronología del artículo.
Recibido/Received: 13.08.2018
Aceptado/Accepted: 03.09.2019
On-line: 15.10.2019
Correspondencia a los autores/Contact e-mail:
dpsponen@vt.edu

INTRODUCTION

The study of color is an important part of the morphological characterization of domestic animals, which is in turn a very important aspect of livestock breed conservation (Alderson, 2018). Sheep color varies widely, although breeders targeting wools for industry have focused on white wool and have penalized colored fleeces (Adalsteinsson 1970, Sponenberg, 1997, Lundie 2011). Selection for whiteness has decreased the frequency of alleles that produce color, although these persist in many breeds as recessive variants. Production of colored wool persists and provides value to those breeders involved. Previous studies have documented various alleles at the highly variable *Agouti Signaling Protein* locus, *Melanocortin 1 receptor* locus, and *Tyrosinase Related Protein 1* locus (Adalsteinsson, 1970; Lundie, 2004, Lundie 2011, Sponenberg 1997).

Among the problems facing investigations on sheep color inheritance is the tendency for colored wool to fade dramatically with age, making the assessment of subtle influences on color quite difficult. Shetland sheep have a relatively high percentage of colored sheep, and a high percentage of these do not fade with age. These sheep are useful for studying genetic effects that would be undetectable in breeds with more dramatic fading.

Shetland sheep from nonfading bloodlines vary from black to brown in the color of skin and short-haired regions (face, lower legs), as well as fleeces that vary from black, dark brown, pewter grey, brown, and light yellowish-brown (honey). Anecdotal evidence from flock owners suggested that simple genetic mechanisms accounted for these differences. This study aims to identify the genetic differences between these fleece colors in Shetland sheep.

Additional data were available from Ouessant sheep, a breed that is generally black with minimal color fading but that occasionally produces other colors that are within the same range of shades as found in the Shetland sheep.

MATERIALS AND METHODS

A survey concerning the results of mating Shetland sheep with various fleece colors were available for study. Parental sheep all had minimal fading over time, so lamb colors could be accurately and consistently classified. The colors of interest were those caused by eumelanins, and included a black-based group all of which have black skin and short-haired regions (head, legs) and fleeces of these colors: black, warm black (not quite true black), dark brown (distinctly brown fleece from base to tip), and pewter (uniform grey).

A brown-based group of colors had skin and short-haired regions that were brown. Wool color varied: brown (dark clove to cinnamon, also called "moorit"), fawn (medium brown), and honey (light yellow brown, also called "mioget").

Lambs were classified at birth, and also at a few months old. Some lambs are born darker than their final color, but the final color is always obvious by two months. Changes in fleece color are minimal after that and never lead to changes in classification.

RESULTS AND DISCUSSION

The results of the matings are presented in **Table I**. A working hypothesis at the beginning of the stu-

Table I. Results of mating various colors of Shetland sheep, with Ouessant results in parentheses (Results of mating various colors of Shetland sheep, with Ouessant results in parentheses).

parent	parent	lamb color						
		black	warm black	dark brown	pewter	brown	fawn	honey
black	black	10 (23)	2 (1)	(2)		1		
	warm black	1	2	1		1		
	dark brown	1 (1)	1	2	(1)	1	1	
	pewter	(9)	6	7		1	1	
	brown	10	2	1		6		
	fawn		1			1		1
	honey	4	3	2	2	8	3	2
warm black	warm black		1					
	dark brown	1	1		2	1	1	1
	pewter	1	9	3	6 (1)	3	5	1
	brown		2					
	fawn		1				1	
	honey				1		2	2
dark brown	dark brown	1		3		1		
	pewter		4	4	15		1	4
	brown		2			1	1	
	fawn							4
	honey	1	2	5	6		3	6
pewter	pewter				6 (3)			5
	brown	1	3		1		1	
	fawn		1		6	1		
	honey				6			9
brown	brown							
	fawn							
	honey					4		
fawn	fawn					1		1
	honey					2	4	7
honey	honey							4

Table II. Color phenotypes of varying genotypes at the *Brown* and *Modified* loci (Color phenotypes of varying genotypes at the Brown and Modified loci).

Brown genotype	*Modified* genotype	Anticipated color phenotype	Actual range of colors, if different
	$Mod^+ Mod^+$	black	
$B^+ B^+$	$Mod^+ Mod^{mod}$	flat black	dark brown, warm black
	$Mod^{mod} Mod^{mod}$	cool pewter	
	$Mod^+ Mod^+$	warm black	warm black, black
$B^+ B^b$	$Mod^+ Mod^{mod}$	dark brown	dark brown, warm black, black
	$Mod^{mod} Mod^{mod}$	warm pewter	
	$Mod^+ Mod^+$	brown (moorit)	
$B^b B^b$	$Mod^+ Mod^{mod}$	fawn	fawn, brown
	$Mod^{mod} Mod^{mod}$	honey (mioget)	

dy was that brown was recessive to black, which is already well established to be at the *Brown* (*Tyrosine related protein 1*) locus (Adalsteinsson, 1970). The data reveal no discrepancy from this, and all matings involving only brown-based phenotypes produced only lambs in the brown-based family of colors.

An additional recessive modifier of both brown and black is proposed. Animals homozygous for this modifier are lightened to honey (from a brown background) or pewter (from a black background). Honey sheep mated to honey sheep only produced honey lambs, consistent with sheep of this color being homozygous recessive at both loci. Pewter sheep mated to either pewter or honey sheep only produced pewter or honey lambs. These results agree with the expectation that honey and pewter are recessive modifications of brown and black base colors. The modifier is proposed as *modified* at the *Modified* locus (Mod^{mod}).

Some level of incomplete dominance at both loci was anticipated because of previous observations that many black-based sheep that are heterozygous for brown are a warm black with some brown aspects to it instead of the true black expected if dominance is complete. Similarly, sheep heterozygous for the diluting modifier were anticipated to be lighter than those lacking this modifier. The anticipated color phenotypes of the various genotypes are outlined in **Table II**, which also indicates the range of colors actually observed in the genotype. All dark brown sheep were mated sufficiently to demonstrate that each of them produced at least one brown offspring, and at least one pewter or honey offspring. This indicates that these sheep were consistently heterozygous at both loci.

The results generally follow the hypothesis of moderately incomplete dominance at both loci, but with enough deviation to reveal that the relationships among the darker colors are more complicated than a straightforward incomplete dominance at both loci. Black sheep can carry the *brown* or *modified* alleles, which is impossible if incomplete dominance is uniformly expressed. Matings involving only brown-based sheep are too few to draw firm conclusions, but the 10 black lambs produced by black to brown matings indicate that complete dominance is common because all of these lambs are obligate heterozygotes for brown. The 5 brown lambs from black to brown matings indicate that some black sheep carry brown with no phenotypic evidence.

The matings of brown, fawn, and honey sheep indicate that incomplete dominance also occurs for the dilute modifier, but is also not uniform throughout all matings. Brown to brown matings were unfortunately not accomplished; they would have helped to indicate levels of complete dominance of the heterozygous modified sheep. Honey to honey yielded only honey, as expected. Fawn to honey matings should have been unable to yield brown lambs if dominance is incomplete, and yet these matings provide 2 brown, 4 fawn, and 7 honey lambs. The ratio of honey:other is 7:6, as close to the expected 1:1 as can be had. The ratio of 2 brown to 4 fawn might indicate the relative frequency of incomplete dominance within this population.

Black to honey matings indicate that the full range of colors is possible from this mating, which would be impossible if dominance is incomplete in every instance because black would be lightened to dark brown in these lambs, which are obligate heterozygotes at both loci. The results indicate that complete dominance is common but not invariable.

The results of matings within the Ouessant breed are similar, and are presented in **Table I** in parentheses. The Ouessant is a short-tailed French breed, within the same breed group as the Shetland. Pewter to pewter matings only produce pewter offspring, while pewter to black matings consistently produce black offspring. This indicates a tendency for complete dominance of the dilution mechanism, although the few warm black and dark brown lambs do suggest some level of incomplete dominance. This is further supported by the one pewter lamb produced from a pewter to warm black mating.

Even though the expression of straightforward incomplete dominance is variable, this genetic mechanism can still be usefully exploited. The two-locus system provides for a range of wool colors in two categories. The black-based colors include black, warm black, dark brown, and pewter, while the brown-based range is brown, fawn, and honey. Their expression early in life, with minimal change thereafter, provides a reliable source for this range of shades in all classes of wool from soft lambs' wool to mature adult wool. The finding that dark brown sheep were heterozygous at both loci indicates that they can be used to produce the complete range of colors. The two-locus mechanism detailed here is most effective when coupled with a genetic background with minimal age-related fading, for it then provides the complete and predictable range of shades over the lifetime of the sheep.

BIBLIOGRAPHY

Adalsteinsson, S 1970, 'Colour Inheritance in Icelandic Sheep and Relation between Colour, Fertility, and Fertilization', *Journal of Agricultural Research in Iceland,* vol. 2, pp. 3-135.

Alderson, G.L.H. 2018. Conservation of breeds and maintenance of biodiversity: justification and methodology for the conservation of Animal Genetic Resources. *Arch. Zootec* 67 (258): 300-309.

Lundie, RS 2004, 'The Genetics of Colour in Sheep – Some Basics', in: *The World of Colored Sheep. 6th World Congress on Coloured Sheep* (edited by RS Lundie & EJ Wilkinson), pp. 111-122. BCSBANZ, Christchurch, New Zealand.

Lundie, RS 2011, 'The genetics of colour in fat-tailed sheep: a review', *Tropical Animal Health and Production* vol. 43, pp. 1245-1265. doi 10.1007/s11250-011-9850-0.

Sponenberg, DP 1997, 'Genetics of Colour and Hair Texture', in: *The Genetics of Sheep* (edited by L Piper & A Ruvinsky) pp 51-86. CAB International, Wallingford and New York.