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The inheritance of coat colours and patterns in the Dutch Landrace Goat

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Abstract

In the last decades, the Dutch Landrace goat has successfully been re-established in the Netherlands. This involved crossing in exotic breeds and with that losing the authentic genetic diversity. The goal of the LFNL is to conserve the Dutch Landrace goat and all its colours and patterns. This research has shown that over the years, the amount of colour combinations grew, creating a larger diversity of combinations. When looking at the proportions of colours, some colours percentwise occur more or less in the population over the years. To make certain phenotypes more prevalent in the population, the goat's genetic characteristics can be looked at. In this research pedigree data suggests a recessive black and a dominant brown pigment type within the Dutch Landrace. As for the two pattern types, the characteristic dorsal stripe pattern shows mostly dominant inheritance, but the white markings inherit in a more complicated way. This information can be compared to research that already was performed in goats. As previous research suggests, multiple loci, i.e., Agouti, Extension, TYRP1, EDNRA and KIT, are involved with the inheritance of goat phenotypes. To find out which CNVS are present on which loci, further research is necessary. After that, a choice can be made when crossing in breeds that are known to dominantly inherit certain phenotypes.

Introduction

History of the Dutch Landrace goat

The Dutch Landrace goat is an endangered breed of livestock species, that in the last decades successfully has been re-established in the Netherlands by the National Breeders Club of the Dutch Landrace goat (LFNL). The current studbook breeding population consists of approximately 2700 animals (2000 females and 700 males), that are kept by hobby breeders and are used in nature management systems.

First documentation of the goat was in paintings from the 16th century, these show a Nordic type of goat with long horns, long hair, and a multi-coloured coat. This type of goat is similar to the Norwegian coastal goat and the Finnish, Danish and Icelandic landraces. Up until the beginning of the 20th century this type of goat was most common used as a backyard goat for smallholders. Due to the upscaling in the animal husbandry after World War II, smallholders disappeared and with them the Dutch Landrace. In the year 1958 the breed almost completely disappeared, which made it necessary to cross in different exotics to create a phenotypically similar type of goat, that was strong and healthy (Frankenhuis and Hazenbroek 1984).

From previous research it appears that by a combination of mixed origin and a population bottleneck, the Dutch landrace goat has an extremely low genetic diversity and is the second most inbred population. Also, it was found that compared to the other Nordic type of goats, the Danish and Dutch races are separated from those and are linked to the network close to the central European cluster with a shared genetic history with the Swiss Saanen. The Dutch Landrace goat is known for its multi-coloured appearance and for that a lot of colours and combinations. Which indicates that a low genetic diversity in an isolated population can still result in a considerable variation in coat colours (Lenstra et al. 2017).

Pigment types

By selecting goats for their unique coat colour phenotypes and keeping them in closed populations, different breeds have emerged with breed specific colours and patterns. Multiple studies have investigated the genetic inheritance and origin of goat coat colours and patterns in different breeds. The diversity of coat colours that can be seen in mammalian species is due to the presence, distribution, and biochemical activity of melanocytes. Melanocytes produce two pigment types, the brown/black eumelanin and the red/yellow/pale pheomelanin. Due to a lack of melanocytes, white markings, spotting, or completely white phenotypes can be seen. Very light to white colours also occur in animals with a normal set of melanocytes that synthesize a very pale pheomelanin (Russell 1968; Sponenberg 1990).



Fig 1: Two Dutch landrace goats with white markings



Fig2 : Dutch landrace goat with a dorsal stripe

Two main loci are known to control the distribution-pattern of the pigment types. The first being the Extension locus that encodes the melanocortin 1 receptor (MC1R), dominant alleles in this locus induce eumelanin and with that black/brown pigmentation, in contrast to recessive alleles that induce pheomelanin to the production of red/yellow/pale pigmentation. The second locus, the Agouti locus that encodes the agouti signalling protein (ASIP), will generally have the opposite model of action, where dominant alleles induce pheomelanin and recessive alleles induce eumelanin (Fontanesi et al. 2009). This effect of melanocytes producing eumelanin or pheomelanin is called pigment type switching and is affected by the activation or inactivation of MC1R (Figure 3).

If MC1R is activated by its ligand α -melanocyte stimulating hormone (α -MSH), eumelanin will be produced, but if α -MSH is absent or outcompeted by binding of the competitive antagonist ASIP pheomelanin will be produced. The Extension locus does not seem to play a major role in goat colour expression, only in a few breeds the existence of a dominant black (E^D), a recessive red (e) and a wild type (E^+) allele has been suggested (Fontanesi et al. 2009; Sponenberg 1990). Another gene that has been mentioned in different studies to influence the pigment expression in goats is TYRP1 (Dietrich et al. 2015; Henkel et al. 2021). The two alleles that have been found are the recessive wild black type ($TYRP1^{496Gly}$) allele and the dominant brown type ($TYRP1^{496Asp}$) allele that has been found in Toggenburg goats.

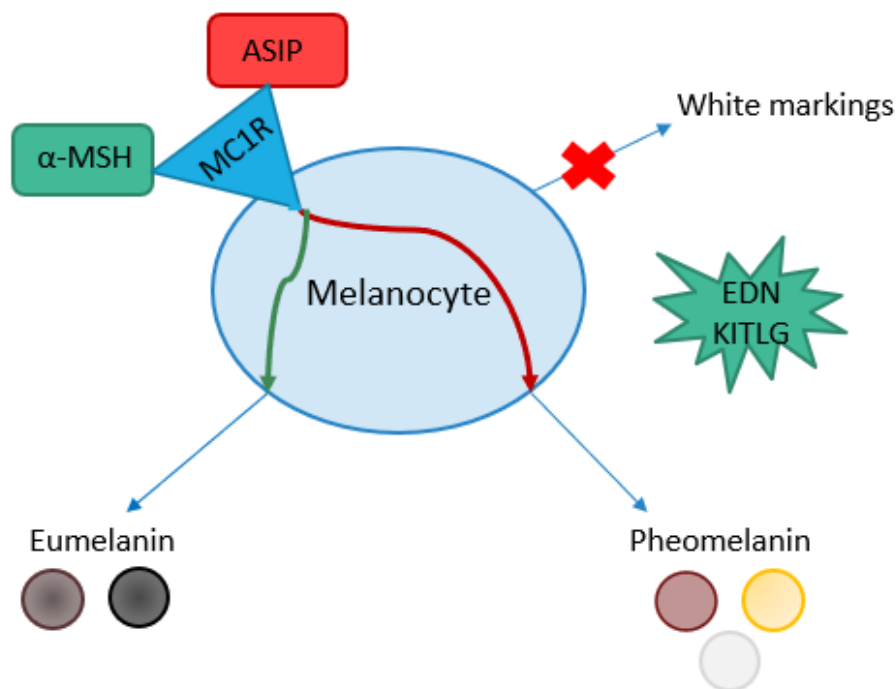


Figure 3: Pigment type switching in a melanocyte. MC1R binding α -MSH making the melanocyte produce eumelanin, while binding ASIP producing pheomelanin. When the melanocyte is not stimulated enough by EDN and/or KITLG it will not survive creating a pigment-less white area.

Patterns and markings

As for the Agouti locus in goats, alternative promoters of the ASIP allele will cause spatially regulated ASIP expression, that result in characteristic patterns of eumelanin and pheomelanin synthesis. Multiple copy number variants (CNVs) of the Agouti locus are researched that create unique coat colour phenotypes, that are described in Table 1 (Adalsteinsson et al. 1994; Henkel et al. 2019; Sponenberg et al. 1998). Several of these are found to be co-dominant intermediate alleles, with an exception of the top allele A^{wt} , that is responsible for a complete phaeomelanin coat and the bottom allele A^a , that is responsible for a complete eumelanin coat (Sponenberg 1990). This large amount of CNVs at the Agouti locus is therefore in goats responsible for a wide variability in coat colours. At the previously mentioned Extension Locus, the supposed to be most common, E^+ allele should make the phenotypical effects of the different Agouti alleles possible (Fontanesi et al. 2009).

In addition to these colour patterns determined by the agouti locus, white markings due to loss of pigmentation can be seen in multiple goat breeds. Melanocytes are derived from melanoblasts, which are precursor cells that originate from the neural crest. During the development these melanoblasts migrate over the surface of the foetus and settle in the epidermis as hair-follicle associated or interfollicular melanocytes. These melanocytes need stimulating signalling for survival (Figure 3). Endothelin's ($EDN1-EDN3$) and KIT ligand ($KITLG$) are melanocyte survival promoting factors. $EDNs$ provide multiple effects, including the activation of two different G-protein coupled receptors, $EDNRA$ and $EDNRB$. $EDNRB$ signalling is required for melanocyte development. Therefore, loss of function variants in $EDNRB$ lead to white spotting phenotypes. In Boer goats a mutant of $EDNRA$ is found to create an ectopic overexpression that clears $EDN3$, with that disrupting $EDNRB$ signalling and normal melanocyte development. In this research there has been found a CNV at the $EDNRA$ locus. In this analysis three alleles with one, two or three copies of this CNV were found, this copy number is correlated with the degree of white spotting. Pedigree data in this Boer goats, show a dominant inheritance of the white spotting (Menzi et al. 2016).

$KITLG$ is known as a mast cell growth factor and stem cell factor, mutations are found to disturb the melanocyte development and create a so-called roan pattern. In goats this has been supported by research in two Pakistani goat breeds (Talent et al. 2018). $KITLG$ binds the KIT -receptor, which is encoded by the KIT -gene and is involved with melanoblast and melanocyte development, migration, and survival. Mutations on the KIT gene itself lead to unfunctional KIT protein in melanoblasts or melanocytes and with that to apoptosis of these cells that result in white spotting phenotypes. This creates precise regulation of its spatial expression. Two CNVs were found in the goat KIT locus in a completely white and a white spotted breed (Henkel et al. 2019).

Locus name	Allele symbol	Allele name	References	Comments
Agouti	A^{wt}	White or tan (Most dominant)	1,2,4,5	All tan, red or white, sometimes with slightly darker face or shoulder.
	A^{blm}	Black mask (Intermediately dominant)	1,2	Tan or white phenotype, a black face mask with longitudinal stripes.
	A^{bz}	Bezoar (Intermediately dominant)	1,2,4	Produces a phenotype like the bezoar goat (wild colour). A tan body with dark head and stripes. Males are darker than females.
	A^b	Badger face (Intermediately dominant)	1,2,4	Most often tan, with a dark dorsal stripe, belly, lower legs, and face stripe. Males are darker than females.
	A^g	Grey (Intermediately dominant)	1,2	Uniform mix of black and white, creating a grey phenotype.
	A^{lb}	Light belly (Intermediately dominant)	1,2	Dark phenotype whit a tan to white belly.
	A^{sm}	Swiss markings (Intermediately dominant)	1,2,4	Dark/ brown with pale legs, ears, and facial stripes.
	A^{ls}	Lateral Stripes (Intermediately dominant)	1,2	Black with tan markings on the belly, back of the legs and head.
	A^{pck}	Peacock (Intermediately dominant)	2,4,5	Tan/white front half, black rear end, belly, legs, and face markings.
	A^{sc}	San Clemente (Intermediately dominant)	2	White/tan rear end belly and legs, a black front half with pale markings on the face and front.
	A^t	Black and tan (Intermediately dominant)	2	Black phenotype with tan belly, legs, inside of the ears and facial markings
	A^{mh}	Mahogany (Intermediately dominant)	1,2	Dark mix of black and tan hairs .
Extension	A^{rc}	Red cheek (Intermediately dominant)	1,2	Black with tan patches on cheeks, back and top of the ears.
	A^a	Nonagouti (Most recessive)	1,2	Completely solid coloured, brown/black/red.
	E^D	Black (dominant)	2,7	Completely black, not often found in goats.
TYRP1	E^+	Wild type (dominant)	2,7	Most common in goats, makes expression of agouti-alleles possible
	e	Red (recessive)	2,7	Red coat colour can be combined with patterns or markings.
TYRP1	^{496}ASP	Brown (dominant)	3, 5	Isolated out of the Toggenburg goats and creates a brown phenotype or a combination with brown.
	^{496}Gly	Wild Black (recessive)	3, 5	A completely black phenotype or a pattern combination with black. Also, solid white coloured goats can have this allele.
EDNRA	$EDNRA^{1\ CNV}$	Spotted (dominant)	6	Lightly spotted
	$EDNRA^{2\ CNVs}$	Spotted + (dominant)	6	More spotted
	$EDNRA^{3\ CNVs}$	Spotted ++ (dominant)	6	Most spotted
	$EDNRA$	Not spotted (recessive)	6	Not spotted
KIT	KIT^{BAR}	White spotted (dominant)	4,8	Roan pattern phenotype with small white markings all over.
	KIT^{ANG}	White not spotted (dominant)	4,8	Found in Angora goats, completely white.
	KIT^{BEZ}	Wild type (recessive)	4,8	Found in the bezoar goats

Table 1: Researched goat coat-colour alleles at different loci

1. (Adalsteinsson et al. 1994), 2. (Sponenberg et al. 1998), 3. (Dietrich et al. 2015), 4. (Henkel et al. 2019), 5. (Henkel et al. 2021), 6. (Menzi et al. 2016), 7. (Fontanesi et al. 2009), 8. (Talenti et al. 2018)

All these genetic factors together can contribute to the unique colour phenotypes that are shown in goats. As for the Dutch landrace, all colours can be seen, but only two of the patterns are described. The white markings (BO), Figure 1 that are seen in the Dutch landrace are extremely varied, as white markings are described as something white somewhere and therefore not easy to assign to a particular pattern. The dark dorsal stripe (AA), Figure 2 is most like the badger face (A^b) or the lateral stripes (A^{ls}) phenotype and with that found to be intermediately dominant.

Research goal

The main goal of this research is to learn how phenotypical characteristics are spread and inherited in the Dutch Landrace goat over several generations. In the first place the overall spread of colours and patterns will be discussed, afterwards the inheritance of the two most common colours i.e., black, and brown and the two different patterns i.e., white markings and dorsal stripe will be researched.

To keep conserving the breed and its phenotypical characteristics, it is necessary to know how these inherit over different generations. The outcome of this study will help the LFNL with its decisions in breeding further generations to keep re-establishing a population that is phenotypically similar to the original breed with its range of colours and patterns.

Hypothesis

H_0 = There is a level of inheritance of colours and patterns over several generations.

H_A = There is no level of inheritance of colours and patterns over several generations.

Materials and methods

The National Breeders Club of the Dutch Landrace goat (LFNL) is an organisation that aims to conserve the Dutch Landrace goat for cultural heritage. The current population consists of approximately 2700 animals (2000 females and 700 males), that are kept by hobby breeders and are used in nature management systems. As of the year 1960 the LFNL has collected data during the examination from all animals that were admitted to the herd-book. Since 2009, the LFNL has been using the online herd book-program ZooEasy. In that year all known data was collected and added. From then on, also a birth book was kept in which breeders could register their lambs themselves. When the lambs are present at the annual examination, the status can be changed to: register book, assistant book or herd book.

In total data of 20806 animals has been collected by the LFNL as of the year 1960. The dataset contains multiple variables that are; registration number, sex, name, colour, registration number of the parents, name of the parents, colour of the parents, birthdate, date of death, inbreeding coefficient, breed percentage, complete generations, and some information from the examinations.

The colour of the animals is listed as colour-codes that consists of a combination of abbreviations. For the colours they are: ZW= Black, GR= Grey, BE= Beige, BR= Brown and WIT= Solid White. For the colour patterns the following abbreviations are added: BO= White markings, AA= dorsal stripe pattern and TOG= Swiss markings. These colours and patterns can be combined in every way possible. In this data a total of 28 unique combinations of colours and patterns were described. Of 518 animals the colour-code was unknown: <onbekend> or ONB. Goats that have Swiss markings are nowadays completely excluded from the herd-book, as they were not typical for the Dutch Landrace and are a result of in cross with the Toggenburg goats in the early years of the re-establishment.

The variable "birth year" was divided in to birthyear-periods of five years, taken together the first twenty years due to the small number of animals and separate the last year for comparison and to have a complete overview. Creating categories: "1961-1980", "1981-1985", "1986-1990", "1991-1995", "1996-2000", "2001-2005", "2006-2010", "2011-2015", "2016-2020", "2021".

For analysing the colour-variables "Brown", "Black", "Dorsal stripe" and "White markings", these were recoded to present and not present.

The 518 animals that did not have a colour code were recoded as "unknown". During the inheritance analysis this group was assigned once to the group in which the variable was present and once in the group in which the variable was not present. The outcome of the first analyses, unknown is not present, will be described in the results (Table 3,4,6,7). The outcome of the second, unknown is present, will be described in the appendix (Appendix 1-4).

The data have been analysed using R Version 4.1.1.

Results

Over the years the number of newborn lambs increased drastically (Figure 4) up until 2009, in which 1259 animals were born. After 2009 the quantity decreased and stagnated at an average between 700 and 800 newborn animals per year. Figure 5 shows the distribution of females and males in the population. This ratio is about 3 to 7 until the year 2009, from then on it is approximately 1 to 1.

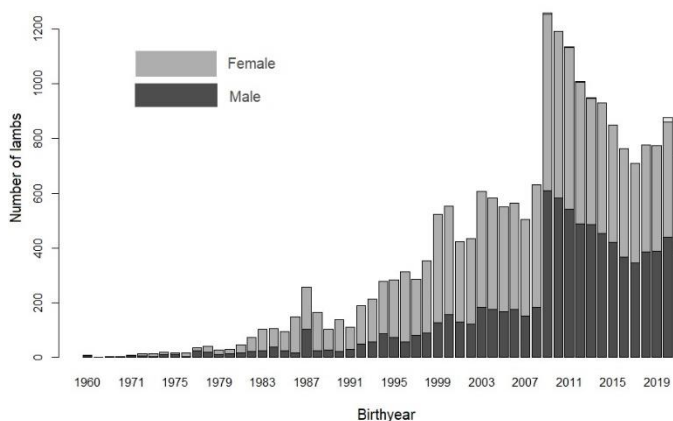
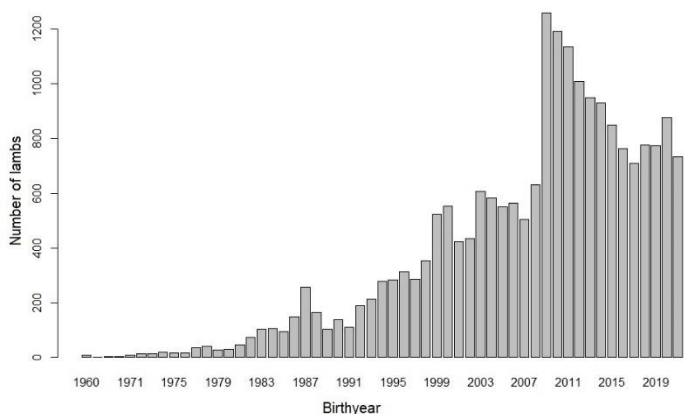


Figure 4: Number of lambs registered within each birthyear

Figure 5: Number of females and males registered within each birthyear

Coat colours

Table 2 gives an overview of all colour combinations that occurred in the animals divided over birthyear-periods of five years, taken together the first twenty years due to the small number of animals. The last year is separated to create a complete overview and to compare to the previous years. Table 2 shows both the number of animals in each colour combination group and the percentage of these colour combinations within these birth periods.

As can be seen, there is a big difference in the proportion in which the colours occur. Some of them contain only a few animals (ten or less in all years), i.e., solid beige (BE), brown with a dorsal stripe (BRAA), grey with a dorsal stripe (GRAA) and combinations that contain the Swiss markings (TOG, BRTOG, ZWTOG). The most common colour combinations (thousand or more in all years) all contain some sort of white markings, i.e., beige with white markings and a dorsal stripe (BEBOAA), brown with white markings (BRBO), grey with white markings (GRBO), black with white markings (ZWBO) and a combination of black and grey with white markings (ZWGRBO).

When looked in to the proportions in which the colours occur, great differences can be seen. The most common colour being black, with 12556 animals containing some sort of black, second being grey with 7671 animals, after that comes brown with 4517 animals, followed by beige with 2319 animals and lastly white with 235 animals. However, when combining the white animals with the animals with white markings, white will be the most common colour with a total of 19684 animals containing some sort of white.

Colour	Birthyear-Period	1961-1980	1981-1985	1986-1990	1991-1995	1996-2000	2001-2005	2006-2010	2011-2015	2016-2020	2021	Total
		% (N)	% (N)	% (N)	% (N)	% (N)	% (N)	% (N)	% (N)	% (N)	% (N)	(N)
<Unknown>		4,29 (10)	23,57 (99)	4,84 (39)	0,65 (7)	1,09 (22)	0,54 (14)	1,57 (65)	1,81 (88)	4,34 (169)	0,81 (6)	519
BE		1,29 (3)	0,24 (1)	0,50 (4)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,02 (1)	0,03 (1)	0,00 (0)	10
BEAA		2,58 (6)	0,48 (2)	0,00 (0)	0,28 (3)	0,35 (7)	0,12 (3)	0,10 (4)	0,64 (31)	0,62 (24)	1,36 (10)	90
BEBO		1,72 (4)	2,86 (12)	7,38 (31)	2,15 (23)	1,97 (40)	1,12 (29)	0,60 (25)	0,88 (43)	0,95 (37)	0,54 (4)	248
BEBOAA		0,00 (0)	0,48 (2)	2,73 (22)	5,13 (55)	9,03 (183)	5,62 (146)	4,10 (170)	5,42 (264)	7,83 (305)	9,35 (69)	1216
BEBRAA		0,00 (0)	0,48 (2)	0,00 (0)	0,00 (0)	0,15 (3)	0,58 (15)	0,51 (21)	0,57 (28)	0,39 (15)	0,68 (5)	89
BEBRBO		0,43 (1)	0,48 (2)	1,24 (10)	0,47 (5)	1,18 (24)	1,19 (31)	0,82 (34)	0,51 (25)	0,74 (29)	0,41 (3)	164
BEGRBO		0,00 (0)	0,24 (1)	1,19 (5)	0,75 (8)	0,10 (2)	0,08 (2)	0,12 (5)	0,12 (6)	0,21 (8)	0,27 (2)	39
BR		0,86 (2)	0,00 (0)	0,00 (0)	0,09 (1)	0,15 (3)	0,69 (18)	1,54 (64)	0,90 (44)	0,51 (20)	0,81 (6)	158
BR-TOG		0,86 (2)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,02 (1)	0,00 (0)	0,00 (0)	3
BRAA		0,86 (2)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,02 (1)	0,10 (4)	0,14 (1)	8
BRBEBOAA		0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,02 (1)	0,14 (7)	0,54 (21)	1,22 (9)	38
BRBO		3,43 (8)	3,33 (14)	7,33 (59)	12,22 (131)	19,29 (391)	21,87 (568)	22,04 (914)	16,90 (823)	13,24 (516)	13,69 (101)	3525
BRBOAA		0,00 (0)	0,24 (1)	0,00 (0)	0,09 (1)	0,15 (3)	0,19 (5)	0,58 (24)	0,39 (19)	0,26 (10)	0,68 (5)	68
BRGRBO		0,86 (2)	0,24 (1)	1,12 (9)	0,84 (9)	0,30 (6)	0,54 (14)	0,94 (39)	1,44 (70)	1,75 (68)	0,95 (7)	225
GRAA		0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,04 (2)	0,05 (2)	0,00 (0)	4
GRBO		37,34 (87)	32,14 (135)	31,06 (250)	14,65 (157)	5,72 (116)	3,62 (94)	3,28 (136)	6,53 (318)	6,67 (260)	7,18 (53)	1606
TOG		0,86 (2)	0,00 (0)	0,25 (2)	0,00 (0)	0,05 (1)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	5
WIAA		0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,02 (1)	0,48 (20)	0,13 (5)	0,54 (4)	30
WIT		22,75 (53)	9,76 (41)	3,60 (29)	0,93 (10)	0,59 (12)	0,04 (2)	0,19 (8)	0,62 (30)	0,44 (17)	0,54 (4)	205
ZW		0,43 (1)	0,00 (0)	0,12 (1)	0,00 (0)	0,30 (6)	0,46 (12)	0,75 (31)	1,48 (72)	1,08 (42)	1,36 (10)	175
ZW-TOG		0,86 (2)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,02 (1)	0,00 (0)	0,00 (0)	0,00 (0)	3
ZWBEAA		0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,05 (1)	0,35 (9)	1,17 (7)	0,55 (27)	0,33 (13)	0,14 (1)	58
ZWBEBO		0,86 (2)	0,24 (1)	1,49 (12)	3,17 (34)	2,22 (45)	1,42 (37)	0,77 (32)	1,42 (69)	0,87 (34)	0,81 (6)	272
ZWBEBOAA		0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,02 (1)	0,53 (26)	1,33 (52)	2,17 (16)	95
ZWBO		18,03 (42)	13,33 (56)	20,12 (162)	20,99 (225)	24,47 (496)	30,80 (800)	31,35 (1300)	29,32 (1428)	30,01 (1169)	28,73 (212)	5890
ZWBOAA		0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,00 (0)	0,04 (1)	0,17 (7)	0,23 (11)	0,21 (8)	0,14 (1)	28
ZWBRBO		0,43 (1)	0,95 (4)	0,99 (8)	0,93 (10)	0,64 (13)	0,81 (21)	1,16 (48)	1,56 (76)	1,09 (53)	0,54 (4)	238
ZWGRBO		1,29 (3)	10,95 (46)	20,12 (162)	36,66 (393)	32,22 (653)	29,92 (777)	29,15 (1209)	27,53 (1341)	26,03 (1014)	26,96 (199)	5797
Total*		100% (233)	100% (420)	100% (805)	100% (1072)	100% (2027)	100% (2597)	100% (4147)	100% (4871)	100% (3896)	100% (738)	20806

Table 2: Number and proportions of animals with the variety of colour-combinations divided into birth year groups of five years. Taken together the first twenty years, due to the small number of animals and separate the last year, for comparison and to have a complete overview.

* Total amount of lambs that were registered within each birthyear-group, taken in consideration that in the early years of reestablishment only a herd book was kept and as of 2009 a register book and assistant book were kept to.

Inheritance of colours black and brown

With black being the most increasing, brown the most decreasing pigment type in this population and these being the most researched pigment types in goats, the heredity of these is displayed in Tables 3 and 4.

Offspring	Parents						Total N
		No Black % (N)	1 Black % (N)	2 Black % (N)			
No Black		72,5 (2806)	51,0 (4308)	13,4 (1136)			8250
Black		27,5 (1063)	49,0 (4134)	86,6 (7359)			12556
Total		100 % (3869)	100 % (8442)	100 % (8495)			20806

Table 3: Heredity of black in one generation

The black pigment type seems to be inherited recessively (Table 3). As two black parents over 85% receive black lambs, 1 black parent has almost 50% chance of receiving a black lamb and parents that are both not black have received a black lamb over 25% of times.

Offspring	Parents						Total N
		No Brown % (N)	1 Brown % (N)	2 Brown % (N)			
No Brown		95,6 (12338)	55,6 (3547)	26,6 (404)			16289
Brown		4,4 (563)	44,4 (2838)	73,4 (1116)			4517
Total		100 % (12901)	100 % (6385)	100 % (1520)			20806

Table 4: Heredity of brown in one generation

The brown pigment type seems to be inherited dominant (Table 4). Parents that are not brown have a very low change, less than 5%, of receiving a brown lamb. If there is one brown parent, the chance of receiving a brown lamb is around 45% and the chance of receiving a brown lamb from two brown parents is almost 75%.

This outcome suggests that most animals in the Dutch Landrace population are heterozygous for both brown and black.

Colour patterns

In total 1724 (8,3%) animals had the dorsal stripe pattern and 19449 (93,5%) had white markings (Table 5). Over the years, a fluctuation can be seen in the proportion of animals that contain a dorsal stripe or white markings, but overall, the proportion of animals with patterns did increase which can also be seen in Figure 6 and 7. Furthermore, the percentage of animals with a dorsal stripe has never been so high as the most recent year. Table 5 shows no significant difference in the ratio of these patterns in males and females, which suggests that there is no sex-linked inheritance.

	Dorsal stripe		No Dorsal stripe		White Markings		No White Markings		Total	
	%	(N)	%	(N)	%	(N)	%	(N)	%	(N)
Total	8,3	(1724)	91,7	(19082)	93,5	(19449)	6,5	(1357)	100 %	(20806)
Sex										
Male	8,1	(680)	91,9	(7708)	92,7	(7775)	7,3	(613)	100 %	(8388)
Female	8,4	(1044)	91,6	(11351)	94,1	(11658)	5,9	(737)	100 %	(12395)
Unknown	0	(0)	100	(23)	69,6	(16)	30,4	(7)	100 %	(23)
Birth year period										
1959-1980	3,4	(8)	96,6	(225)	64,4	(150)	35,6	(83)	100 %	(233)
1980-1985	1,7	(7)	98,3	(413)	65,5	(275)	34,5	(145)	100 %	(420)
1985-1990	2,7	(22)	97,3	(783)	90,7	(730)	9,3	(75)	100 %	(805)
1990-1995	5,5	(59)	94,5	(1013)	98,0	(1051)	2,0	(21)	100 %	(1072)
1995-2000	9,7	(197)	90,3	(1830)	97,3	(1972)	2,7	(55)	100 %	(2027)
2000-2005	6,9	(179)	93,1	(2418)	97,2	(2525)	2,8	(72)	100 %	(2597)
2005-2010	5,7	(236)	94,7	(3911)	95,1	(3945)	4,9	(202)	100 %	(4147)
2010-2015	9,0	(436)	91,0	(4435)	92,9	(4526)	7,1	(345)	100 %	(4871)
2015-2020	11,9	(459)	88,2	(3437)	92,0	(3584)	8,0	(312)	100 %	(3896)
2020-2021	16,4	(121)	83,6	(617)	93,6	(691)	6,4	(47)	100 %	(738)

Table 5: Number of animals with patterns divided by birth year period and sex. Taken together the first twenty years, due to the small number of animals and separate the last year for comparison and to have a complete overview.

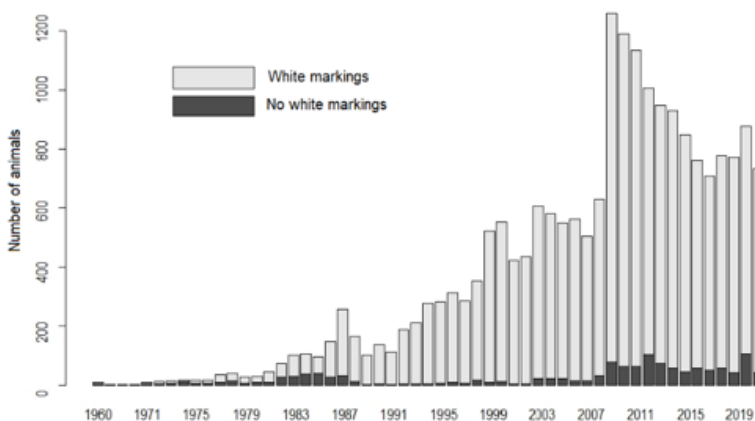


Figure 6: Number of lambs with white markings per birth year

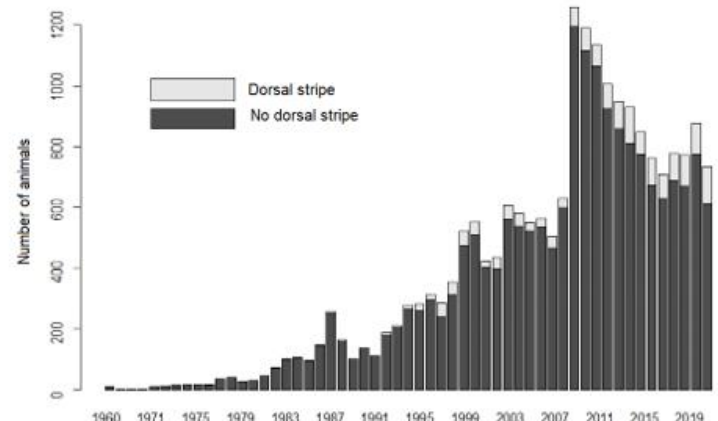


Figure 7: Number of lambs with a dorsal stripe per birth year

Inheritance of colour patterns

The heredity of white markings is shown in Table 6. It shows that parents without white markings, still have over 77% change to receive an offspring with white markings. This percentage does not become much higher if one of the parents has white markings. If both parents have white markings, over 95% of offspring's will get white markings.

Offspring	Parents						Total N	
		No white markings		1 White markings		2 White markings		
		%	N	%	N	%		N
No white markings	23,4	(88)	21,4	(363)	4,8	(906)	1357	
White markings	76,6	(288)	78,6	(1336)	95,2	(17825)	19449	
<i>Total</i>	100 % (376)		100 % (1699)		100 % (18731)		20806	

Table 6: Heredity of white markings in one generation

Table 7 shows the heredity of the dorsal stripe pattern, it shows close to 3% inheritance in an offspring that was born from two parents that do not have a dorsal stripe. In an offspring that was born from parents of which one has a dorsal stripe, almost 40% have a dorsal stripe pattern. If both parents have a dorsal stripe, around 72% of offspring's has a dorsal stripe pattern.

Offspring	Parents						Total N	
		No dorsal stripe		1 Dorsal stripe		2 Dorsal stripes		
		%	(N)	%	(N)	%		(N)
No dorsal stripe	97,6	(17441)	60,8	(1514)	28,2	(127)	19082	
Dorsal stripe	2,7	(424)	39,2	(977)	71,8	(323)	1724	
<i>Total</i>	100 % (17865)		100 % (2491)		100 % (450)		20806	

Table 7: Heredity of the dorsal stripe pattern in one generation

Most of the animals (87%) with a dorsal stripe pattern are beige or a colour combination with beige. Therefore there might be some evidence of co-dominance of these two factors. As can be seen in Table 8 the heredity of the combined factors is not much different of the heredity of the dorsal stripe by itself (Table 7).

Offspring	<i>Parents</i>						Total N
		Not BEAA % (N)	1 BEAA % (N)	2 BEAA % (N)			
Not BEAA		97,8 (17627)	65,0 (1551)	31,6 (131)			19309
BEAA		2,2 (380)	35,0 (834)	68,4 (283)			1497
<i>Total</i>		<i>100 % (1800)</i>	<i>100 % (2385)</i>	<i>100 % (414)</i>			<i>20806</i>

Table 8: Heredity of the dorsal stripe pattern in combination with a beige coat colour

Some dorsal stripes may be missed by interruption of white markings. To find out, the number of dorsal stripes in a group of animals with white markings and a group without white markings were compared (Table 9). This Table shows that there are percentwise significant less dorsal stripes in the group with white markings, approximately 7 %, compared to 21 %.

Dorsal stripe	<i>White markings</i>				Total N
		No white markings % N	White markings % N		
No dorsal stripe		79,4 (1078)	92,6 (18004)		19082
Dorsal stripe		20,6 (279)	7,4 (1445)		1724
<i>Total</i>		<i>100 % (1357)</i>	<i>100 % (19449)</i>		<i>20806</i>

Table 9: the dorsal stripe in a group with and without white markings

Discussion

In this study, a large dataset was used with data that has been collected over multiple years by multiple people. In the early years, most data were collected during annual exams of mostly animals that were committed to the herd book. This causes a lack of data before 2009, because not all animals were admitted to the herd book and mainly not all males went to the annual examinations. As of the year 2009, the LFNL used ZooEasy for online registering all animals that were born, which can explain the large number of animals that were given a birthdate in 2009. The administration nowadays is done by the breeders themselves when new animals are born and checked by the LFNL when an animal comes to one of the annual exams. This can result in an information bias, due to different opinions about naming certain phenotypes.

Pigment types

As can be seen in Table 2, the amount of colour combinations grew, creating a larger diversity of combinations, as multiple did not occur in the early years of the re-establishment. This creates a greater distribution of animals across the phenotypes and therefore a difference in the proportions in which combinations occur. White, beige and grey are the least common pigment types in the Dutch Landrace. The main difference, however, is that the amount of white and grey seem to be decreasing in the population, but the amount of beige seems to be increasing. The most common pigments are found to be black and brown, with black increasing and brown decreasing.

Pedigree data suggests a recessive black and dominant brown pigment type within the Dutch Landrace. This is equivalent to the previous research at the TYRP1 locus. At this locus two alleles have been found, the recessive wild black (*TYRP1*^{496Gly}) and the dominant brown (*TYRP1*^{496Asp}) allele. The brown type that has been researched is attributed to the Toggenburg goats, or a common ancestor (Dietrich et al. 2015; Henkel et al. 2019). By interbreeding with some of these goats, up to and including the last one in the year 2011, this same colour gene may be found in the current Dutch Landrace population.

The black pigment type, because of its recessive inheritance occurs homozygous in all black animals. The animals that are not black, are mostly heterozygous for black, therefore two non-black animals can receive a black lamb. For the brown pigment type, animals that are not brown are homozygous for not brown. The parents that are brown, seem to be heterozygous. This explains the increasing quantity of black and decreasing quantity of brown.

Patterns

For the white markings, the current definition of the LFNL is that there must be some white hairs somewhere. Whereas in previous research white markings were divided into different types, i.e., Belted, Spotted, Barbari, Flowery, Roan, Goulet, Algarve, Nigerian or Frosted. In most of which the mode transmission is likely to be dominant, but in others it is unknown or likely recessive (Adalsteinsson et al. 1994; Henkel et al. 2019, 2021; Sponenberg et al. 1998; Weaver 2021). This results in making it not clear which locus or allele contributes to the white markings in the Dutch Landrace.

This is in line with the outcome of the pedigree data in Table 6, which shows no clear line of inheritance. This can be due to the multiple variations that are seen in the white markings of the Dutch Landrace. Those white markings can be caused by specific CNVs at the ASIP locus, KIT locus and/or EDNRA locus. Because of there being multiple white pattern types, there are likely to be multiple different CNVs at multiple loci. To differentiate between goats that have very pale, phaeomelanin areas and goats that have white areas due to lack of melanocytes, an ASIP mRNA expression can be performed after biopsy of the white areas (Henkel et al. 2019).

The dorsal stripe pattern seems to occur in only one form but can be missed if there is a combination with white markings that interrupt the dorsal stripe. Therefore a comparison is made in table 9 of the number of dorsal stripes within a group of animals with white markings and a group without white markings. This Table shows that there are significantly less dorsal stripes in the group with white markings. This could be due to the interrupting of the genetically present dorsal stripe by the white markings. As there are animals that have both pattern-types, it does not seem that there is genetic suppression of the dorsal stripe by the white markings.

Table 7 indicates most animals that have a dorsal stripe pattern are heterozygous and it inherits mostly dominant. The dorsal stripe pattern that occurs in the Dutch Landrace is phenotypically mostly like the A^b or A^{ls} phenotypes that previously are described (Table 1) to be intermediately dominant in other breeds (Sponenberg 1990). But can also be a completely unresearched allele at the agouti locus or other loci. To ensure that the dorsal stripe pattern that can be found in the Dutch Landrace, the CNVs at the ASIP locus can be researched and compared with data from goats that are known to have either the A^b or the A^{ls} allele, i.e. the Swiss St. Gallen Booted goat or the Chamois Coloured goat (Henkel et al. 2019).

Most coat colour research, has been performed in Swiss, African or Pakistani breeds, not in Nordic goats. Therefore, it could be possible that other CNVs can occur in these types of goats. Research on the genetic diversity suggest genetic similarity to the Central European goat races, making it likely that the same loci and CNVs can be found by CNV analyses.

As this research is based on pedigree data and with that mainly focused on the level of heredity in one generation, it could be interesting to statistically estimate the heritability of phenotypical characteristics, such as patterns. With this also a breeding value from some of the most used animals could be calculated. This could help the breeders in making decisions on using certain animals.

To make sure all authentic colours and patterns appear in the population, historical paintings and data need to be reviewed. To make certain phenotypes occur or more prevalent in the population, other breeds with dominant characteristics can be introduced to this population. As the main goal is not the authentic genetic diversity, but conservation for cultural heritage.

Conclusion

From the pedigree data it can be concluded that in the Dutch landrace, colours and patterns have a level of inheritance. The black colour seems to inherit recessively, and the brown coat colour seems to inherit dominant, assumable by the alleles at the TYRP 1 locus. In line with the expectation, the data suggests the dorsal stripe pattern being mostly dominant. Therefore it is to expect that a known intermediately dominant allele (A^{ls} and/or A^b) or a yet to be researched allele can be found at the ASIP Locus of the Dutch Landrace. As for the white markings, the pedigree data shows a more complicated trend. This can be due to the multiple variations that are seen in the white markings of the Dutch Landrace.

As the main goal of the LFNL is to maintain conserving the Dutch landrace for cultural heritage and not to create a population that is similar in genes. Colours and patterns can be revived by crossing in breeds that are known to dominantly inherit certain phenotypical traits. Therefore it is important to know what phenotypical characteristics were present in the historic population.

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Appendix

Appendix 1

Comparison of two heredity analyses of the black pigment in one generation, firstly "unknown" coded as 'not black', secondly coded as 'black'.

		<u>Parents</u>						
<u>Offspring</u>		No Black		1 Black		2 Black		Total N
		%	N	%	N	%	N	
(unknown= No Black)	No Black	72,5	(2806)	51,0	(4308)	13,4	(1136)	8250
	Black	27,5	(1063)	49,0	(4134)	86,6	(7359)	12556
	Total	100 %	(3869)	100 %	(8442)	100 %	(8495)	20806
(unknown = Black)	No Black	69,5	(2610)	49,2	(4161)	11,2	(961)	7732
	Black	30,5	(1148)	50,8	(4296)	88,8	(7630)	13074
	Total	100 %	(3758)	100 %	(8457)	100 %	(8591)	20806

Appendix 2

Comparison of two heredity analyses of the brown pigment in one generation, firstly "unknown" coded as 'not brown', secondly coded as 'brown'.

		<u>Parents</u>						
<u>Offspring</u>		No Brown		1 Brown		2 Brown		Total N
		%	(N)	%	(N)	%	(N)	
(unknown= No Brown)	No Brown	95,6	(12338)	55,6	(3547)	26,6	(404)	16289
	Brown	4,4	(563)	44,4	(2838)	73,4	(1116)	4517
	Total	100 %	(12901)	100 %	(6385)	100 %	(1520)	20806
(unknown = Brown)	No Brown	92,7	(11791)	54,7	(3570)	26,5	(410)	15771
	Brown	7,3	(933)	45,3	(2962)	73,5	(1140)	5035
	Total	100 %	(12724)	100 %	(6532)	100 %	(1550)	20806

Appendix 3

Comparison of two heredity analyses of white markings in one generation, firstly “unknown” coded as ‘no white markings’, secondly coded as ‘white markings’.

Parents

Offspring

	No white markings		1 White markings		2 White markings		Total N
	%	N	%	N	%	N	
(unknown= No markings)							
No white markings	23,4	(88)	21,4	(363)	4,8	(906)	1357
White markings	76,6	(288)	78,6	(1336)	95,2	(17825)	19449
<i>Total</i>	<i>100 %</i>	<i>(376)</i>	<i>100 %</i>	<i>(1699)</i>	<i>100 %</i>	<i>(18731)</i>	<i>20806</i>
(unknown= markings)							
No white markings	16,4	(60)	17,9	(271)	2,7	(508)	839
White markings	83,6	(305)	82,1	(1243)	97,3	(18419)	19967
<i>Total</i>	<i>100 %</i>	<i>(365)</i>	<i>100 %</i>	<i>(1514)</i>	<i>100 %</i>	<i>(18927)</i>	<i>20806</i>

Appendix 4

Comparison of two heredity analyses of the dorsal stripe pattern in one generation, firstly “unknown” coded as ‘no stripe’, secondly coded as ‘stripe’.

Parents

Offspring

	No dorsal stripe		1 Dorsal stripe		2 Dorsal stripes		Total N
	%	(N)	%	(N)	%	(N)	
(unknown= No stripe)							
No dorsal stripe	97,6	(17441)	60,8	(1514)	28,2	(127)	19082
Dorsal stripe	2,7	(424)	39,2	(977)	71,8	(323)	1724
<i>Total</i>	<i>100 %</i>	<i>(17865)</i>	<i>100 %</i>	<i>(2491)</i>	<i>100 %</i>	<i>(450)</i>	<i>20806</i>
(unknown= Stripe)							
No dorsal stripe	95,5	(16868)	59,1	(1585)	24,2	(111)	18564
Dorsal stripe	4,5	(799)	40,9	(1095)	75,8	(348)	2242
<i>Total</i>	<i>100 %</i>	<i>(17667)</i>	<i>100 %</i>	<i>(2680)</i>	<i>100 %</i>	<i>(459)</i>	<i>20806</i>