

REVIEW

Roan coat color in livestock

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Abstract

Since domestication, a wide variety of phenotypes including coat color variation has developed in livestock. This variation is mostly based on selective breeding. During the beginning of selective breeding, potential negative consequences did not become immediately evident due to low frequencies of homozygous animals and have been occasionally neglected. However, numerous studies of coat color genetics have been carried out over more than a century and, meanwhile, pleiotropic effects for several coat color genes, including disorders of even lethal impact, were described. Similar coat color phenotypes can often be found across species, caused either by conserved genes or by different genes. Even in the same species, more than one gene could cause the same or similar coat color phenotype. The roan coat color in livestock species is characterized by a mixture of white and colored hair in cattle, pig, sheep, goat, alpaca, and horse. So far, the genetic background of this phenotype is not fully understood, but *KIT* and its ligand *KITLG* (*MGF*) are major candidate genes in livestock species. For some of these species, pleiotropic effects such as subfertility in homozygous roan cattle or homozygous embryonic lethality in certain horse breeds have been described. This review aims to point out the similarities and differences of the roan phenotype across the following livestock species: cattle, pig, sheep, goat, alpaca, and horse; and provides the current state of knowledge on genetic background and pleiotropic effects.

KEYWORDS

coat color genetics, embryonic lethality, *KIT*, pleiotropic effect, white heifer disease

INTRODUCTION

Prior to domestication, livestock ancestors had coat colors that provided camouflage against potential predators. Wild species mostly had a uniform phenotype with species-specific coat colors and patterns (Charon & Lipka, 2015; Neves et al., 2017). With domestication, a large variation of phenotypes arose driven by adaption to different habitats and climate conditions as well as

by different human preferences (Bellone, 2010; Cieslak et al., 2011; Neves et al., 2017).

Numerous genes influencing pigmentation and coat color-associated loci have been identified (Cieslak et al., 2011). These genes often either influence production of the pigment melanin or its distribution by affecting the underlying pathways (Bellone, 2010; Hubbard et al., 2010). Two different types of melanin—eumelanin and pheomelanin—are synthesized and stored in

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melanosomes. The organelles of the melanocytes can be found in the skin's epidermis and tissues such as the ears, eyes, heart, brain, lungs, and adipose tissue (Bellone, 2010). Originating from the neural crest, the melanocyte precursors, the melanoblasts, migrate into skin, hair follicles, eye, inner ear, as well as further organs and tissues. Wherever the migration is interrupted, the concerned skin region lacks melanocytes leading to white hair in this area (Videira et al., 2013). The variation of pigmentation results from different size, shape, and transport of melanocytes to particular skin areas. Another contributing factor refers to the differences in the amount and the type of synthesized melanin (i.e. eumelanin or pheomelanin) (Hirobe, 2011). In addition to melanocytes, embryonic stem cells, which are essential for the rise of adipose tissue, cartilage, bones, endocrine cells, and different types of neurons as well as glia, also derive from the neural crest. As a consequence, genes that are involved in the development or migration of melanocytes may result in pleiotropic effects concerning sight, hearing, and neurologic functions (Bellone, 2010; Reissmann & Ludwig, 2013).

Due to these pleiotropic effects, knowledge and research on coat color genetics is necessary (Bellone, 2010; Charon & Lipka, 2015). Coat colors associated with hereditary diseases, which are often lethal, are not only the cause of nonviable or ailing animals, but also lead to economic losses (Charon & Lipka, 2015). Even though similar disorders and resembling coat color phenotypes may have different genetic backgrounds, it was observed that mutations in the same genes frequently produce identical coat colors and show comparable pleiotropic effects in different species (Reissmann & Ludwig, 2013).

The coat color roan is present in various species. Roan is described as a mixture of white and colored hair, while the particular phenotype and underlying genetic background differs across species. In this review, we aim to compare the roan phenotype in livestock including horses and show the similarities and differences in phenotype and genetic background. Furthermore, we outline the potential impact of roan coat color on health.

ROAN IN CATTLE

In cattle, roan is frequently present in the Shorthorn and Belgian Blue breeds, where roan is called 'blue'. Those breeds appear to share the same genetic mutation causing the coat color phenotype, as Shorthorns were crossed into the Belgian population during the 19th century (Charlier et al., 1996; Hanset, 1985). The popularity of roan differs between breeds: while roan in general is preferred over black in Belgian Blue (Hanset, 1985), the roan in Shorthorn is undesired in some countries (Seitz et al., 1999).

Following a co-dominant inheritance, there are several phenotypes present in both breeds: (i) spotted-black

in the Belgian Blue and solid red in Shorthorn, when the *r* allele is present in a homozygous state; (ii) a white phenotype, when the animals are homozygous for the alternative *R* allele; and (iii) roan, respectively blue, with white hair intermingling colored hair for the *Rr* genotype (Charlier et al., 1996; Laughlin, 1911; Wright, 1917). The amount of white hair can vary enormously between individuals from only a few white hairs to a nearly solid white coat (Jones, 1947; Laughlin, 1911). Therefore, identification of the correct coat color phenotype might be challenging and the presence of additional modifiers cannot be excluded (Jones, 1947). The proportion of incorrect phenotypic coat color records of roan Shorthorn and Belgian Blue was reported to lie between 3.7% (Seitz et al., 1999) and approximately 9% (Charlier et al., 1996).

Charlier et al. (1996) mapped the roan locus to the bovine chromosome 5 (BTA5) and identified the mast cell growth factor (*MGF* alias *KITLG* = tryrosine-protein kinase ligand), also named *Steel* locus, as a candidate gene. Additionally, the *Steel* locus was shown to cause reduced pigmentation, speckling or single white hairs among the coat in mice (Green, 1990; Jackson, 1994). The bovine *KITLG* is localized on the telomeric end of BTA5 (Aasland et al., 2000). Seitz et al. (1999) described a missense mutation (c.654C>A) within the *KITLG* as the causative mutation for roan in Belgian Blue and Shorthorn. This mutation located in exon 7 of the gene leads to an amino acid substitution (alanine to asparagine) in the protein sequence, which potentially changes the hydrophobicity and modifies the α -helix structure of this protein region.

Roan is associated with the White Heifer Disease (WHD) comprising a range of anomalies of the female genital tract (Charlier et al., 1996; Rendel, 1952). The disorder includes a missing or underdeveloped vagina, cervix, or uterus as well as one or even both uterine horns, abnormal development of the Müllerian ducts, and posterior vaginal occlusion. The different lesions can occur separately or in combination. Based on current understanding, the ovaries are unaffected (Charlier et al., 1996). The majority of the affected heifers suffering from WHD carry the alternative homozygous genotype (*RR*; >90%), the other WHD heifers (<10%) are heterozygous (*Rr*) (Charon & Lipka, 2015).

In the 1950s, the incidence of WHD in Belgian Blue was as high as 5–10%. Due to systematic selection, exclusion of affected females and progeny testing of the sires, the incidence decreased to 1.5% at the end of the 1960s (Charlier et al., 1996).

Even though the bovine roan locus and the murine *Steel* locus show some phenotypic similarities, the sterility induced by *Steel* (synonym for *KITLG* in mice), where mutations cause various phenotypes with reduced pigment, differs fundamentally. The sterility in mice, caused mainly by homozygous *Steel* mutations, is characterized by the lack of primordial germ cells in the gonads and these animals often suffer from severe anemia.

However, this disorder is not reported for roan cattle (Charlier et al., 1996).

The association of the roan phenotype and *KITLG* can only be shown in Belgian Blue and Shorthorn cattle, so it is likely that in other breeds, one or more different genes are causative for roan coat color (Seitz et al., 1999).

ROAN IN PIG

In addition to the predominant white coat color, pigs also show solid red or black pigmented phenotypes, as well as colored spots or patches, belts, and roan (Cho et al., 2011; Giuffra et al., 1999; Johansson et al., 1992). Roan is characterized by intermingled white and colored hair and is mostly observed in crossings with the Landrace breed (Cho et al., 2011; Hetzer, 1948).

Based on the remarkable similarity of the roan phenotype in cattle and horses, *KIT* and its ligand (*KITLG*) were proposed as major candidate genes for roan in pig. This hypothesis is supported by a strong linkage between the *KIT* locus on chromosome 8 and the roan pattern in an intercrossed population of Landrace and Korean Native pigs, even though none of the single-nucleotide polymorphisms (SNPs) in the *KIT* coding region was perfectly associated (Cho et al., 2011).

KIT has a large allelic diversity in commercial pig populations (Johansson et al., 2005; Rubin et al., 2012). Among those are the recessive wild type allele (*i*) resulting in colored phenotypes, patches caused by *I^P*, *Dominant White* (*I*) (Johansson et al., 1992; Johansson Moller et al., 1996; Marklund et al., 1998), the *Belt* allele *I^B* and *I^{Rn}* (former *I^D*, 'D' for dilution, Hetzer, 1948) causing the roan coat color (Pielberg et al., 2002). The *Dominant White* allele (*I*) is dominant over the roan allele (*I^{Rn}*), thus animals with a *Dominant White* allele and a roan allele are completely white, while *I^{Rn}* is dominant over the wild type allele (*i*) and causes a roan phenotype (Lim et al., 2011).

The genetic variant resulting in the belted or the roan phenotype was hypothesized to be similar or even caused by the same gene in different breeds showing either roan coat color or a belted pattern (white belt across the shoulders and front legs against a solid black or red background) (Pielberg et al., 2002; Giuffra et al., 1999). It is also plausible that belt and roan phenotypes are caused by divergent alleles, because the phenotypic expression of *KIT* alleles displays an epistatic interaction with the *Extension* locus (*MC1R*) (Cho et al., 2011; Johansson et al., 2005; Pielberg et al., 2002). This interaction is possibly associated with the variation of phenotypes from mild roan with only a few intermingled white hairs to deep roan with a larger amount of white hair (Lim et al., 2011). Rubin et al. (2012) described four duplications (DUP 1–4) within or close to *KIT* in a sample of pigs with *Dominant White* (DUP 1–4), *Patch* (DUP 1),

and *Belt* (DUP 2, DUP 4, low frequency of DUP 3 as well) phenotypes. Wu et al. (2019) suggested a new *i* allele (*i^N*) carrying DUP 2 and DUP 3 in addition to a splice site mutation, also present in *Dominant White*, which was observed in roan pigs.

A 4-bp deletion of *KIT* intron 18 is associated with the roan phenotype in an Italian breed (Fontanesi et al., 2010). This association is also confirmed for Landrace intercrosses (Cho et al., 2011; Lim et al., 2011). Although Lim et al. (2011) could not identify a coding SNP or another polymorphism in complete association and linked to the roan phenotype, the authors reported an exon-skipping event only present in roan pigs. A *KIT* protein with truncated trans-membrane and intracellular domains is produced by skipping 169 bp of exon 5 and shifted reading frame of the *KIT* gene. In the investigated Landrace cross-breed carrying the *I^{Rn}* allele, both the truncated and the wild-type *KIT* mRNA are expressed. The *I^{Rn}* allele might have a hypomorphic effect over the wild-type *i* allele, which could explain the intermingling of white and colored hair. Furthermore, the exon 5 skipping was only identified in the skin and the large intestine, so that tissue-specific expression might exist. The skipped exon could be responsible for roan coat color in pigs, however, the causative variant seems to be part of a wide-ranging haplotype; hence, other yet unknown variants cannot be excluded.

Although the *Dominant White* (*I*) allele at the *KIT* gene shows not only an impact on the coat color, but also on hematological parameters (Johansson et al., 2005), no other pleiotropic effect of roan is described. Additionally, the effect of the *I* allele on *KIT* expression in developing melanocytes might be quite mild, as white pigs are known for good growth and vitality (Johansson Moller et al., 1996).

ROAN IN SHEEP

It is unclear if the coat color in sheep described by Nel (1966) and Schoeman (1998) could be classified as roan. However, the authors describe the fleece's color as black-roan (gray) or brown-roan (grayish brown) (Schoeman, 1998), due to a mixture of colored and white fibers (Nel, 1966). The coat color is mainly present in breeds used to produce gray fleece and is most frequent in Karakul sheep.

The quantity of white fibers can vary tremendously between animals (Lundie, 2011; Schoeman, 1998) and even on the individuals themselves: the shoulders, face, ears, tail tip, and the lower legs often appear lighter. Homozygous roan sheep are mainly lighter in color (Lundie, 2011).

The causative mutation is unknown. It is not clear whether roan in sheep is a variant of the *White* locus ($W \rightarrow W^R$) (Schoeman, 1998) or if there is a roan locus with the wild type allele Rn^+ responsible for solid coloration

and the (lethal) roan allele Rn^{Rn} producing a phenotype with reduced pigmentation (Lundie, 2011). It is also unknown if the *White* locus might be part of the *KIT* gene or the *KITLG* (Charon & Lipka, 2015).

Roan fleece color is inherited in a dominant manner. Under homozygous condition, the color roan is sub-lethal in sheep. These animals often die relatively young, suffering of a dysfunctional innervation of the digestive system causing problems in the rumen, abomasum, and intestine. The defects are congenital and the affected lambs are often weak, suffer from anemia, and lose weight. Life expectancy of the affected animals ranges from a few days to 2.5 years (Lundie, 2011; Nel & Louw, 1953; Schoeman, 1998). Unfortunately, some affected sheep reach maturity and breed; therefore, it is advised that the mating of two gray animals should be avoided. Additionally, it is important to identify homozygous lambs (Lundie, 2011). They regularly have a lighter fleece, an unpigmented tongue, no black hair on the chin and white spots in their ears (Nel, 1966).

Homozygous white Karakul sheep (*WW*) show similar symptoms as gray sheep, which are caused by reduced size of abomasum and rumen. The abomasum walls are much thinner as the musculature is poorly developed. Nevertheless, these lambs often survive longer than the homozygous roan lambs (Schoeman, 1998).

In the Damara sheep, a similar roan phenotype exists, even though it is rare. As roan Damara sheep do not appear to have a shortened life span, a different genetic background was hypothesized. It is now known that Karakul sheep were crossed into the Damara and the Persian sheep as well. The lack of homozygous diseased animals could also be explained by the low allele frequency of the defect allele (Lundie, 2011) making a mating of two heterozygous gray sheep unlikely.

Analogies to roan in cattle exist. Both homozygous roan cattle and sheep are lighter in color and might suffer from a disease, but the symptoms of the defects are tremendously different.

ROAN IN ALPACA

Like sheep, alpaca have been bred for their fiber and meat. Alongside the fiber diameter and length, color is a quality determining trait (Frank et al., 2006). Although several colors are described in the literature, there is no standardized nomenclature for the fiber color in alpaca. Among those colors, roan is characterized by a mixture of white and colored fiber in black skinned alpacas (Feeley, 2015). The extent of white fibers varies between animals. Similar to roan in horses, the body displays the most mixed fibers while fibers on the head, neck and distal legs are darker (Munyard, 2013). The proportion of white fibers increases over time in contrast to the classic gray phenotype, which might lead to misclassifications of

coat color phenotypes (Feeley, 2015; Jones et al., 2019). The roan fiber appears to be very fine, whereas darker fleece has a higher fiber diameter with greater coarseness (McGregor & Butler, 2004; Wuliji et al., 2000).

Roan is hypothesized to be dominantly inherited and epistatic to both types of melanin without an effect of zygosity on the extent of fiber mixture (Munyard, 2013). In contrast, Cransberg (2017) suggested an incomplete dominant inheritance. However, the causative mutation for roan in alpaca is still unknown. Additionally, there is no evidence of a pleiotropic effect of the roan coat color in alpaca and so far no associated disorders are described (Munyard, 2013). Regardless, the fiber color is an important trait for the textile industry, which prefers fine fibers and various colors. With further knowledge of the genetic background, breeding for fiber quality and color could be improved (Fan et al., 2010; Mendoza et al., 2019).

ROAN IN GOAT

In comparison to other species, coat color and its inheritance in goats have been so far sparsely studied (Sponenberg & LaMarsh, 1996). Even though similarities to fleece color in sheep are present, coat color genetics in goats differ significantly (Sponenberg, 2004). White wool in sheep is of economic importance, thus knowledge about its genetic background is relevant (Sponenberg & LaMarsh, 1996). With growing interest in the production of cashmere fibers, especially completely white fibers, due to their higher market prices, attention has been driven towards coat color genetics in goats (Adalsteinsson et al., 1994). Until recently, only a couple of genetic regions and a small number of SNPs within and near genes possibly affecting coat color have been reported (Becker et al., 2015; Henkel et al., 2019; Henkel et al., 2021; Nicoloso et al., 2012).

Comparable to other livestock species, roan in goat describes white hair intermingling with colored hair. The amount of white hair can vary enormously between animals (Asdell & Buchanan Smith, 1928; Sponenberg, 2004). Most noticeable is the intermixture over the goat's body and neck, while the head and legs usually remain colored (Sponenberg, 2004). A clear identification of roan is hampered, as the phenotype can be confused with ticking patterns, characterized by colored spots on white background (Talenti et al., 2018). Roan could equally be confused with gray, as there is no clear distinction between these coat colors and the terms are often used synonymously (Adalsteinsson et al., 1994).

Asdell and Buchanan Smith (1928) suggested that roan is dominant over 'the black series', while it is recessive to brown. Despite lack of segregation studies, Sponenberg (2004) observed a couple of matings and proposed roan to be a dominant allele, as there are similarities to other species.

A study on the Bari and Beetal Muki Cheni Pakistani breeds identified a 1.7-Mbp region including the *KITLG* on caprine chromosome 5 with a loss of variability. In particular, an SNP, which is located within that gene appears monomorphic among the roan group in comparison to a wide range of other breeds. With goats belonging to the Bovidae family, a similarity to cattle in terms of roan coat color genetics is plausible; therefore, *KITLG* is a potential candidate gene for roan in goats (Talenti et al., 2018). A pleiotropic effect of roan coat color has not yet been described.

ROAN IN HORSE

The coat color roan in horses is characterized by an intermixture of white and colored hair over the body, while the head and distal legs are not affected (Castle, 1948; Sturtevant, 1910; Wilson, 1910). Roan horses mostly appear lighter in summer and turn darker in winter (Bailey & Brooks, 2013). This seasonal change in coat color is produced by the white and colored hair belonging to different hair types. The white undercoat can be seen clearly while molting the colored covering hair in spring and fall (Voß et al., 2020). In general, this coat color is rare in many horse breeds (Hintz & van Vleck, 1979; Sturtevant, 1910) such as draught horses, British pony breeds including the Shetland pony, some breeds with Spanish origin (Sponenberg & Bellone, 2017; Thiruvankadan et al., 2008), and Quarter horses (Hintz & van Vleck, 1979). Especially in breeds known for mainly uniform coat color, e.g. Friesians and Norwegian Fjord Horse, roan does not occur (Sponenberg & Bellone, 2017).

As gray also shows a mixture of white and colored hair at a certain age, the coat colors might be confused with each other (Gremmel, 1939; Wilson, 1910). In the past, it was hypothesized that roan and gray have a common genetic background (Wentworth, 1914). In contrast to gray, foals are born roan and the number of white hairs remains unchanged with age (Castle, 1954; Gremmel, 1939; Salisbury, 1941). Even though a roan foal might appear solid colored at birth, with their first shedding at the latest the roan coat color becomes visible (Anderson, 1914). Gray horses are born solid and get lighter with age as the number of white hairs increases until the coat turns almost solid white (Castle, 1954; Gremmel, 1939). This incidence might lead to misclassification and wrong studbook registration (Sturtevant, 1912).

In addition to gray, other ambiguous coat patterns exist. To differentiate roan from 'roaned', a pattern with sparse white hair within the base color on the entire horse and unknown genetic cause, the phenotype is sometimes called 'true' or 'classic roan'. The coat color rabicano also displays varying amounts of white hair along the ribs, on the flanks and on the tail base. Frost characterizes another roaning pattern that scatters

white hairs over the whole body (Neves et al., 2017). The leopard spotting pattern (*Lp*) may also cause roaning effects on the horse's rump (Bailey & Brooks, 2013; Castle, 1954). The estimated error for coat color classification is 2% (Castle, 1948). Additionally, a unified nomenclature for all languages, countries, and breeds is missing (Sponenberg & Bellone, 2017).

Roan is dominantly inherited (Heizer, 1932; Wentworth, 1914) and epistatic to other coat colors (Anderson, 1914; Castle, 1948; Sturtevant, 1912). The causative mutation is so far unidentified (Rieder, 2009); however, roan was assigned to the equine linkage group II located on chromosome 3 (Lear & Bailey, 1997) consisting of two further coat color loci (*Tobiano* and *Extension* locus) and three genes coding for serum proteins (albumin, esterase, vitamin D binding protein) (Andersson & Sandberg, 1982; Sponenberg et al., 1984). Furthermore, no recombination between the roan phenotype and the *KIT* gene suggested a linkage between both loci. Particularly, a synonymous substitution in *KIT* exon 19 showed an association to roan in most of the investigated breeds (Marklund et al., 1999). As roan in Shetland and Gotland ponies does not appear to be associated with this substitution, a heterogeneous genetic cause is plausible (Bailey & Brooks, 2013; Marklund et al., 1999) and supported by recent studies (Grilz-Seger et al., 2020).

Castle (1954) proposed roan coat color to be homozygous lethal. He based the hypothesis on a personal communication that reported matings of two roan horses resulting in a ratio closer to 2:1 roan to non-roan foals, than 3:1 and the absence of roan stallions siring only roan offspring. Hintz and van Vleck (1979) analyzed the registered offspring of roan Belgian draught horses and observed a nearly 2:1 roan to non-roan ratio out of roan × roan matings, which strengthened the embryonic lethality hypothesis. Additionally, the hypothesis is supported by similarities to the White mutation in the murine *KIT* (Marklund et al., 1999) and lethal variants of *White Spotting* in horses, which is also caused by various *KIT* mutations (Thiruvankadan et al., 2008).

Meanwhile, there is evidence of Quarter Horse and Spanish Mustang stallions with 100% roan progeny (Sponenberg & Bellone, 2017). Some of these Quarter horses have been genetically tested, which indirectly confirmed homozygosity for a region that probably carries the roan mutation (Veterinary Genetics Laboratory, UC Davis). In the Hokkaido Native Horse, roan is frequent, therefore, the probability that homozygous roan horses exist is very high. Statistical analyses of roan × roan matings contradicted the lethality hypothesis (Yokohama et al., 2002; Yokohama & Nozawa, 2004). Furthermore, statistical mating analyses for the Icelandic breed showed no evidence of lethality (Voß et al., 2020).

An overview over roan in the above reviewed species is given in Table S1 in the supporting information. In

addition to the breeds where roan coat or fleece color is present, the description of phenotype and genetic background as well as the pleiotropic effect can be found. Further, the OMIA (Online Mendelian Inheritance in Animal) link, if available, is given. This platform provides a compendium of inherited disorders and phenotypes in over 300 animal species.

CONCLUSION

In all reviewed livestock species, roan is characterized by white hair intermingling with colored hair and differences in phenotype and genetic background are present. In the ruminant species cattle and goat, roan is associated with *KITLG*, whereby only in cattle was a pleiotropic effect shown. Whether the coat color roan in sheep actually exists and which is the causative mutation is still unclear. While sheep are also ruminants, an association to the *KIT* ligand was not reported, although the phenotype described as roan is associated with health disorders similar to cattle. In alpaca, the genetic background of the coat color roan is rudimentarily investigated. Both monogastric species, pigs and horses, show a linkage of the roan phenotype to the *KIT* gene. For porcine roan, a potential causative polymorphism within *KIT* was identified and, if there is a health impact, it is non-severe. In horses, no candidate polymorphism has been reported so far, while its lethality is under discussion. A heterogenic genetic background for roan in different breeds might be a possibility.




Regardless of species, the phenotypic recording requires improvement. A fundamental prerequisite to coat color research is a precise, species-specific definition, which includes a clear distinction to similar coat color or patterns.

Knowledge about pleiotropic effects on health is imperative to arrange matings without the risk of diseased progeny; therefore, further research is needed. Using genomics and other omics technologies would be useful to understand the phenotypes, e.g. the distribution of melanocytes to restricted areas of the animal's body, and the pleiotropic effect.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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