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A review on the evaluation of horse coat color

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SUMMARY

The coat color diversity of horses represents a classic example of the genetic and evolutionary effects of domestication. While wild equids exhibited limited pigmentation patterns, human-mediated selection has dramatically expanded phenotypic and genetic variation among domestic horses. This variation is influenced by multiple interacting loci, with some genes exerting pleiotropic effects on physiological and morphological traits. Modern molecular genetics has identified key loci controlling base colors (Agouti, Extension), dilution (D locus), greying (G locus), and patterned phenotypes including Tobiano and Overo, while also highlighting the increasing importance of additional white patterning mechanisms such as MITF and PAX3-associated Splashed White phenotypes and KIT gene complex variants (e.g., Sabino 1 and W1–W30 alleles). Furthermore, some coat color–associated mutations illustrate the fitness costs of selection, as seen in Overo Lethal White Syndrome (OLWS) and the association between the Silver dapple mutation and Multiple Congenital Ocular Anomalies (MCOA), emphasizing the pleiotropic and sometimes deleterious effects of pigmentation genes). Quantitative assessment using Lab color metrics allows objective evaluation of coat pigmentation and facilitates comparisons across breeds, ages, and sexes. Phenotypic studies show that coat color does not directly correlate with performance or temperament but may affect thermoregulation, predator avoidance, disease susceptibility, and market value. Comparative research on other livestock species confirms that coat color is largely polygenic, heritable, and influenced by human selection. Integrating molecular and phenotypic analyses enhances our understanding of the evolutionary, genetic, and practical implications of coat color variation in horses. These insights support breeding decisions, breed identification, and the conservation of genetic diversity. Overall, the study of equine coat pigmentation provides a valuable model for investigating domestication, human-driven selection, and the genetic architecture of complex traits in livestock species.*

Keywords: *coat color; Equus caballus; genetic inheritance; Melanogenesis*

INTRODUCTION

Darwin (1859) demonstrated that domestication has significantly increased the phenotypic diversity of animal populations. This effect arises as a consequence of human activity, which diminishes the influence of natural selection while simultaneously increasing population size (Lauvergne, 1989). The process of domestication not only involved the selection of traits advantageous for economic purposes, but mainly based on behavior and locomotion (Librado et al., 2021). Futhermore it also contributed to the emergence of new mutations and the maintenance of existing genetic variation (Price, 1999; Diamond, 2002; Zeder, 2012). Consequently, phenotypic diversity among domesticated animals exhibits markedly greater variation than that observed in wild populations (Andersson & Georges, 2004). The association between coat color variation and behavioral traits in domesticated animals can be also explained by the Neural Crest Theory, which attributes these correlated changes to alterations in neural crest cell development, affecting both melanocyte formation and neuroendocrine systems. Selection for tameness may therefore indirectly influence pigmentation, providing a mechanistic basis for the co-occurrence of morphological and behavioral traits in domesticated species (Wilkins et al., 2014).

Globally, the horse population exceeds 58 million individuals (FAOSTAT, 2025), encompassing over 600 distinct breeds. This genetic diversity provides opportunities in animal breeding to enhance desirable traits, eliminate undesirable characteristics, and preserve both phenotypic and genetic variation within populations (Bowling & Ruvinsky, 1995). The elimination of “undesirable characteristics” in horse breeding should be also understood in the context of deleterious pleiotropy, where genes influencing coat color may also have harmful physiological effects. For instance, selection for specific color patterns has been linked to conditions such as Lethal White Foal Syndrome, highlighting that breeding for aesthetic traits can inadvertently increase the prevalence of genetic disorders. The variation in coat color and pattern among horses serves as a classical example illustrating the genetic and evolutionary impacts of domestication.

WILD HORSES AND DOMESTICATION

Based on current knowledge, wild horses exhibited diverse coat colors. Historical records indicate that the Tarpan (*Equus ferus ferus*) displayed a blue dun coloration (Pruski, 1959). The Przewalski horse (*Equus ferus przewalskii*), the last extant wild representative of the species, exhibits a yellowish dun coat with a wild-type pattern (Stasiewicz & Borkowska, 2007).

The presence of white markings on the face and limbs likely emerged during domestication. Domestication, followed by selective breeding, greatly increased coat color variation among horse breeds

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compared to the more limited diversity observed in pre-domestication populations. Some breeds are fixed at a locus andcharacterized by a single predominant color, whereas others exhibit a broad range of phenotypic variation (Klungland & Våge, 2000). However, no coat color is exclusive to a single breed, suggesting that the mutations responsible for the various color variants arose early in the domestication process, long before the formation of contemporary breeds (Bowling, 1996).

Coat color also functions as a protective trait, aiding wild horses in camouflaging from predators (Stachurska et al., 2004). For example, Thurner & Morrison (2001) reported that in the California–Nevada region, pumas (*Felis concolor*) predominantly prey on yellow/light dun foals, as this coloration closely resembles that of local mule deer (*Odocoileus hemionus*).

Moreover, coat color contributes to thermoregulation. Darker colors absorb solar radiation more rapidly and release heat more efficiently, while lighter colors retain heat for longer periods, providing an advantage in colder environments (Cena et al., 1957).

Genetic Basis of Coat Color

Certain genes exert pleiotropic effects, influencing not only coat color but also other traits that affect the organism as a whole (Falconer, 1981). Coat color is a qualitative trait determined by the combined action of multiple loci (Sponenberg, 2003; Stachurska, 2002; Ussing, 2000). Earlier studies often identified loci through linkage to polymorphic plasma proteins (Andersson & Sandberg, 1982); however, modern genomics focuses on identifying causative mutations within genes and distinguishing between linkage and pleiotropy. For example, genes such as the KIT gene exhibit pleiotropic effects, influencing both hematopoiesis and pigmentation.

The development of performance traits is influenced by the activity of additive polygenes as well as major quantitative trait loci (QTLs) (Edwards et al., 1987). However, to date, QTLs directly determining equine performance have not been fully identified. Performance traits are highly complex, difficult to quantify, and strongly influenced by factors such as rider skill, training methods, nutrition, and other environmental conditions (Saastamoinen & Barrey, 2000). The polygenic inheritance of performance further complicates investigations into possible associations with coat color. Opinions regarding such associations are widespread in the literature (Keeler, 1947; Sponenberg, 2003; Stachurska et al., 2001) and continue to be a subject of scientific study.

Estesworth (1948) found no significant differences in temperament among horses of different coat colors. Similarly, studies on warmblood horses by Blesa et al. (1999) and Dring et al. (1981) concluded that there is no correlation between mare coat color and gestation length.

In mammals, coloration is almost entirely determined by the melanin present in the skin and hair (Searle, 1968; Moellmann et al., 1988; Sponenberg, 1997). The overall body color, as well as the distribution and patterning of color, are considered qualitative traits (Horn, 1971). The mechanisms underlying pigmentation may vary across the body surface, leading to the formation of spots. Postnatal changes in coloration can also occur. Abnormal functioning of hair follicles can impede the transfer of melanosomes from melanocytes to the hair shaft (Jones, 1982).

Genetic studies have identified numerous coat color loci and characterized their inheritance. Research on coat color inheritance initially emerged as a descriptive science, with multiple animal species studied to elucidate the genetic basis of pigmentation (Searle, 1968; Adalsteinsson, 1970, 1978; Templeton et al., 1977; Adalsteinsson et al., 1987).

INHERITANCE OF COAT COLOR AND CLASSICAL GENETIC MODELS AND THEIR LIMITATIONS

Differences exist between the pigmentation of the main coat and peripheral areas, as described based on genetic knowledge of equine coat color (Lehmann, 1975).

Walther (1912) published the first study on the inheritance of horse coat color using Mendelian genetics, outlining the fundamental principles governing color determination. The inheritance of coat color has remained a central topic in genetic research, as it provides a model system that contributes to understanding biological phenomena and informs research in related fields (Silvers, 1979). Meregalli (1980) developed a coat color classification system, following terminology established by Lanzillotti & Buonsanti (1893). For several decades, it was commonly believed that coat color was determined by genes arranged in a simple epistatic series at a single locus, with the dominance hierarchy as follows: gray, bay, black, and chestnut. These representations served as useful heuristic models, but do not fully capture the complexity of the underlying genetic architecture. Over time, however, it was discovered that inhibitory factors also play a role in coat color expression. According to Ócsag (1990), inhibitory or partially inhibitory factors are responsible for the development of specific colors and their varying intensities. In this model, the epistatic hierarchy of horse coat color is: spotted, dun, gray, bay, black, and chestnut. Accordingly, the classical epistatic framework should be understood as a simplification of more complex locus–locus interactions.

The theoretical framework for equine coat color inheritance was primarily developed by American geneticists (Tóth et al., 2004). Several breeds, both established and emerging, have been created based on distinctive coat colors, including the Appaloosa, Palomino, Pinto, and Colorado Ranger. For this reason, the American system is considered the most developed and widely accepted approach to classifying equine coat color (Hyland, 1999).

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MODERN GENETIC INVESTIGATIONS

According to Dohy (1999), the rapid advancement of molecular genetics and the development of gene maps have provided access to numerous new and comprehensive insights. Extensive research on the inheritance of coat color is currently being conducted in several countries, including the United States, France, and the United Kingdom. In addition, computational tools have been developed that allow for simulated breeding predictions of coat color inheritance, highlighting the often complex nature of this trait (Animal Genetics, 2025).

These tools enable the quantification of coat color as a qualitative trait, providing a foundation for objective phenotypic analyses. By comparing registry-based color designations, researchers can identify measurable differences between shades. SNP studies have revealed the genetic background of multiple coat colors and patterns (Neogen, 2025). Certain color variants and genotypes can be accurately determined solely based on phenotype; however, genetic testing may be necessary for visually ambiguous phenotypes, aiding in the prediction of potential offspring colors (Sponenberg & Bellone, 2017).

From an inheritance perspective, these phenotypically ambiguous individuals are particularly valuable, as they can pass on colors that may be hidden in other horses (Zöldág, 2003). Fang et al. (2009) concluded from their genetic analyses that the increase in coat color variability is a direct result of human selection rather than reduced natural selection pressure.

Hair pigmentation is determined by seven loci controlling color and three loci influencing hair length (Brandsch & Gerber, 1987). Microsatellite marker studies have enabled the identification of the entire equine genome, as well as gene interactions and linkages associated with specific traits (Swinburne et al., 2000).

The Agouti (A) Locus

Horn (1976) described that black and bay horses differ in that black pigmentation covers the entire body in black horses, whereas in bay horses, an inhibitory factor restricts black pigment to the mane, tail, and lower limbs. The dominant allele (A) limits black pigmentation to specific body regions, while the recessive allele (a) allows uniform black pigmentation across the body (Equine Genetics, 2025). Molecular studies by Rieder et al. (2001) linked the recessive black phenotype to the ASIP (Agouti Signaling Protein) gene. Reismann et al. (1998, 2000) demonstrated that crossing two yellow horses produces only yellow offspring. Henner (2000) also studied the chesnut color gene using molecular genetic methods.

The C (Coloration/Albino) Locus

One allele of the C gene regulates tyrosinase activity and pigment production in animals (Odriozola, 1951). This allele produces diluted colors, including palomino, buckskin, smoky black, cremello, perlino, and smoky cream (Equine Genetics, 2025). In horses with the C gene, normal pigment production occurs, although certain mutations can cause partial albinism (Singleton & Bond, 1966). No color dilution occurs in CC horses, as their coat remains pigmented. Distinguishing between the C^crC^cr and Ww phenotypes can be difficult (Bowling, 2000; Overton, 2001; Zöldág et al., 2003). Alleles of TYR (tyrosinase) and PED (pink-eye dilution) genes influence pigmentation processes, as demonstrated in humans and mice, and likely correspond to the equine C gene (Jackson, 1994; Sponenberg & Bowling, 1996). The dilution gene in horses is located on chromosome 21, while TYR resides on chromosome 7 (Locke et al., 2001; Lindgren et al., 1998; Mariat et al., 2003).

The D (Dilution) Locus

Genes at the D locus have a similar effect to the C locus, lightening coat color. The D locus dilutes both eumelanin and pheomelanin (Gremmel, 1939; Van Vleck & Davitt, 1977). In yellow horses, the body appears pinkish or reddish, while the mane, tail, and extremities remain dark (Adalsteinsson, 1978). In bays, the body develops a reddish-yellow color with black markings (Craig & Van Vleck, 1985). In black horses, the D gene produces a mouse-gray coloration (Stachurska & Brodacky, 2003; Stachurska et al., 2004). Bay, black, and yellow horses with the dd genotype show no phenotypic effect, as the d allele is inactive. The D gene affects only the body coat, not the extremities, mane, or tail (Zöldág, 2004).

The E (Extension) Locus

The E locus contains alleles E, e, and E^D, with individuals possessing only two alleles (Marklund et al., 1996). Sponenberg and Weise (1997) described that in bay and black horses, the E locus, in combination with the A locus, determines black pigmentation in hair and skin, whereas its absence results in yellow coloration. Some black foals are born with mouse-gray or brownish coats, which can turn reddish-brown or summer black under sunlight (Salisbury, 1941). Other black horses retain their black coat regardless of sun exposure. In the first case, the genotype is recessive, and in the latter, it is dominant black (Castle, 1953).

The G (Grey) Locus

The G locus controls the expression of grey coat color via a dominantly inherited G allele. The foal's birth coat color is determined by alleles at other color loci (Nürnberg, 1993). Horses carrying the G allele exhibit white hairs interspersed among their darker coat from an early age (Locke et al., 2002). The greying process often begins around 10–15 days of age near the eyes and head (Mihók, 1994), and pigment gradually disappears at a genetically determined rate (Sponenberg & Beaver, 1983; Curik et al., 2002, 2004). Multiple studies have confirmed that the grey gene is located on chromosome 25 (Swinburne et al., 2002; Henner et al., 2002; Locke et al., 2002).

The TO (Tobiano) and O (Overo) Loci

The TO locus involves a large inversion on equine chromosome 3 (ECA3), likely disrupting regulation of the KIT gene (Brooks et al., 2007). It is dominantly inherited, and both heterozygotes (TO/n) and homozygotes (TO/TO) display the spotted pattern, with size and placement of markings determined randomly (Etalon, 2026). Genes at the O locus interact with other loci to produce overo spotting patterns. Heterozygotes exhibit the "frame overo" pattern, while homozygotes display severe defects, including a completely white coat and *Ileocolonic Aganglionosis*, leading to neonatal mortality (Equine Genetics, 2025). From an evolutionary perspective, this represents a classic case of a lethal recessive allele maintained through heterozygote advantage driven not by natural selection but by human aesthetic preference, thereby increasing genetic load within managed populations. A white spotting QTL associated with the KIT variant rs1140732842 and modified by the presence of the MC1R loss-of-function pheomelanin genotype in the horse, as well as the observed linkage of KIT W19 to this variant was reported by Patterson Rosa et al. (2022).

MEASURABLE CHARACTERISTICS OF COAT COLOR

Today, it is possible to approach color quantitatively due to significant advances in optical instrumentation. Modern methods allow the determination of color saturation and lightness. Light of different wavelengths evokes distinct color perceptions in human consciousness. The goal of color measurement is to assign numerical values to color sensations. This is achieved using additive color mixing. The primary instrument for such measurements is the chromameter. In Hungary, the CIE Lab* (Commission Internationale de l'Éclairage) color measurement system has been standardized (typically using a defined illuminant such as D65 and a standard observer angle, e.g., 10°, depending on the instrument configuration), ensuring comparability across measurements. Using the CIE Lab* system, both color intensity and saturation can be quantified.

The L* value represents lightness on a scale from 0 to 100, indicating the intensity of reflected light and correlating with the amount of light perceived by the human eye. The a* value represents the red–green component on a scale from -60 to +60, where positive values indicate stronger red intensity. The b* value represents the yellow–blue component on the same scale, with positive values indicating stronger yellow intensity (Curik et al., 2002; Curik et al., 2004). Chromameters are widely used across industry, healthcare, and agriculture due to their versatility. Since its development by the CIE in 1976, the Lab* system has been broadly applied for measuring various pigmentation levels (Ha et al., 2003; Wagner et al., 2002).

According to Horn (1976), in animal breeding, the evaluation of body conformation, coat color, and other traits is valuable as long as it provides insights into biological and physiological relationships relevant to economical production. Certain color variants are particularly suitable for distinguishing species, breeds, or individuals, as well as for studying gene function and receptor binding. Bodó & Hecker (1998) noted that the coat color of horses, even in ancient wild populations such as the Przewalski horse, was grey-brown or pale grey. During domestication, these colors diversified due to mutations. Although coat color is not associated with performance, it remains important for breeders and horse users for multiple reasons. Kuli (1988) emphasized that coat color can influence susceptibility to disease, resistance, market value, aesthetic perception, individual preference, and even uniqueness.

GENETIC STUDIES ON THE QUANTIFICATION OF COAT COLOR

In Tóth's (2005) study, horse coat color was quantified using L*, a*, and b* values. Among grey populations, Lipizzaner horses exhibited the lightest coat color. Age significantly influenced the L* value, particularly in grey horses, reflecting the progression of greying. Significant differences were also observed in the interaction between breed, sex, and color. Correlation analyses demonstrated a strong relationship between the L* value and total melanin and eumelanin content, indicating that L* is a reliable objective measure for assessing pigmentation. Stepwise discriminant analysis based on color measurements of different body regions effectively classified horses into color categories, supporting the reliability of visual classification.

The L* value of horse coat color shows a strong negative correlation with total melanin content, with the relationship being more pronounced in non-grey than in grey horses. Changes in L*, a*, b*, and chroma values with age reflect color intensity, where the faster increase of L* in grey horses indicates age-related greying. Genetic analyses suggest that polygenic effects are significant in grey horses, whereas main gene effects (color class) predominate in non-grey horses, with high heritability of color parameters. These results are not only of aesthetic significance but also shed light on the physiological role of melanin and the morphological, behavioral, and physiological traits associated with coat color in horse breeding (Tóth et al., 2005).

Druml et al. (2018) reported, based on coat color measurements using the CIE L*a*b* color system, that the combination of the genotypes A/a with E/E resulted in a statistically confirmed distinct phenotype cluster, represented by bay horses with the lowest mean L* value and the lowest chromacity indicating less production of phaeomelanin (red, yellow pigment). There were 32 Shagya Arabian and 25 Noriker horses included in their study.

Hofmanová et al. (2019) characterized the coat color in the black variety of the Old Kladruber Horse breed, estimated the coat color genetic parameters and identified factors influencing coat color intensity. They

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found that sex of the horse, season and housing system could have an effect on L*a*b* parameters of black color. The L* parameter showed stability in relation to age whereas a* and b* color components of the spectrum, were higher in young horses up to the age of three years compared to adult individuals.

Grilz-Seger et al. (2021) concluded that CIE L*a*b color spectrophotometry could be an effective tool to characterize and quantify coat color in horses and could be used for further analysis of chestnut coat color. They reported breed-specific differences in L*a*b measurements for Posavje, Noriker and Shagya-Arabian horses.

Coat color in alpacas is a quantitative, polygenic trait, primarily described by L* (lightness) and b* (yellow–blue axis) values, with a* playing a secondary role. Colors do not segregate sharply, and intermediate shades often overlap. Heritability of color traits is low to moderate, but L* and b* values may serve as potential selection criteria. White and black colors can be classified more reliably than intermediate shades (Cruz et al., 2021).

Coat color in Slovak Pinzgau cattle can be effectively described using CIE Lab parameters. Lightness (L*) shows low to moderate heritability, hue (H) is low, while chroma (C*) exhibits moderately high heritability. Chroma is the most stable color trait, being minimally affected by environmental and breeding factors, whereas lightness and hue are more influenced by the breeder and paternal lineage. These results suggest that C* and H parameters may serve as a basis for further genetic and molecular studies (Kasarda et al., 2016).

Hungarian grey calves are born red (piroque), with three distinguishable shades: light, medium, and dark. In adults, the coat color develops into “darus” (reddish-grey), grey, and light grey variations. Measurements using a Minolta Chromameter indicate that lightness (L*) provides the most reliable information for distinguishing color differences, whereas the red–green (a*) and yellow–blue (b*) axes contribute less. These findings highlight the breed-specific variability of the coat, observable across age groups and sexes (Radácsi et al., 2007).

A limitation of such evaluations the proper analysis of “so-called” patterned horses/animals. Their evaluation could be performed using pixel-based evaluation based on photos instead of the above-mentioned quantitative measurement. Such a pixel-based analysis might be able to quantify the percentage of white versus pigmented skin.

CONCLUSIONS

The diversity of horse coat color has primarily arisen due to domestication and human-driven selection, rather than solely as a consequence of relaxed natural selection. Phenotypic and genetic variation among domesticated horses is considerably greater than that it was observed in wild populations. Coat color is determined by the interaction of multiple genes and is inherited polygenically, which explains the wide spectrum of colors observed across breeds. Certain genes exhibit pleiotropic effects, influencing not only pigmentation but also other biological traits.

Modern molecular genetic techniques allow for the precise mapping of coat color inheritance and enable the identification of individuals with ambiguous phenotypes. Quantitative traits of coat color can be reliably measured and compared, thereby supporting breeding decisions. Specific colors and patterns play important roles in breed identification, individual preferences, and aesthetic evaluation. While coat color is generally not directly correlated with performance or temperament, an important exception to this rule is the presence of documented pleiotropic associations between certain pigmentation loci and sensory or developmental traits. For example, exception to the rule, mutations such as the Silver dapple-associated variants and their reported links to ocular abnormalities (MCOA), as well as Splashed White patterns associated with congenital deafness in some cases, illustrate that pigmentation genes may occasionally have clinically relevant side effects. These pleiotropic risks should therefore be considered in modern breeding strategies.

The combination of genetic research and phenotypic assessment provides insight into the evolutionary and breeding background of coat color. Overall, the study of equine coat coloration remains relevant for breeding strategies, breed preservation, and the maintenance of genetic diversity, particularly when pleiotropic effects are taken into account in selection decisions.

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