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Northernmost autochthonous Yakutian horses: A radically adapted genome for a uniquely sustainable production system

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Abstract

Yakutia is one of the coldest inhabited regions on Earth, with extreme annual temperature fluctuations ranging from 30 °C in summer to −70 °C in winter. In this environment, autochthonous Yakutian horses exhibit remarkable physiological, reproductive, metabolic and behavioral adaptations that allow year-round free-range grazing, even under deep snow cover and severe cold conditions. This breed underpins a traditional livestock system central to Yakut culture, where horse meat forms a major dietary component. It also supports food security, providing meat rich in polyunsaturated fatty acids (PUFAs) with an optimal omega n-6/n-3 ratio. Yakutian mares produce nutrient-rich milk with a biochemical profile similar to that of human milk, allowing foals to achieve exceptional growth rates, up to 1.5 kg/day. This breed is an example of rapid adaptation (~100 generations; 600–800 years) to Arctic extremes through such mechanisms as changes in coat, fat metabolism, thermogenesis, and energy efficiency, as supported by genes within the positive selection signatures in its genome. This narrative review integrates a comprehensive evidence base on the origin, adaptation, year-round free-grazing management and sustainable production system of Yakutian horses. We also provide an overview of the more advanced functional genomics of Yakut cattle to propose a roadmap for future genomic studies of the Yakutian horse. We hypothesize that recent migration followed by rapid natural selection-driven adaptation explains the survival, productivity and cultural importance of Yakutian horses in one of the harshest environments in the world.

Keywords

Adaptation to Arctic region; Autochthonous Yakutian horse; Horse meat and milk; Sustainable free-grazing system; Reproduction; Selection signatures; Conservation

1. Introduction

The Republic of Sakha (Yakutia) is globally recognized as one of the coldest inhabited regions on Earth. A source of diamonds and fossil reserves (Vasiliev and Danilova, 2020), it is a vast territory (3,103.2 thousand km²), located in the Siberian part of the Russian Federation (55°29'–76°46' N, 105°32'– 162°55' E). It comprises approximately 20% of the total land mass of Russia, constituting the largest subnational entity in the country (Petrov et al., 2020). The region experiences extremely harsh cold climatic conditions, with temperatures dropping below –70 °C (–94 °F) in winter (Scherf, 1995). Winters are long (220–250 days of snow cover), and the frost-free period is only 67–76 days. Annual precipitation is low (250–300 mm, varying by terrain) and unevenly distributed throughout the year, with only 30 to 50% occurring during the active plant vegetation period (>10 °C) (Buslaev et al., 1987; Liu et al., 2017; Vladimirov, 2021). Only 6.3% of the region is agricultural land, with the rest consisting of permafrost soils that are largely unsuitable for agricultural production (Vladimirov, 2021). Like many other places on Earth, the meteorological conditions of the region have been significantly impacted by global climate change. That is, the average annual air temperature in Yakutia has increased by 1.1–3.3 °C between 1966 and 2015 (Skachkov, 2016).

Agriculture in Yakutia is a traditional integrated system, combining pasture-based livestock farming, reindeer herding, and crop cultivation; the region, however, faces several unique challenges. These include the preservation of traditional farming systems, significant differentiation of the agro-climatic zone, a low proportion of arable land (<1.3%), limited land accessibility, remoteness/isolation of rural settlements, fragmented low-yield farmland, transportation infrastructure constraints, and rural unemployment rates that exceed urban levels (Vasiliev and Danilova, 2020; Vladimirov, 2021). Furthermore, long, severe winters and extremely unfavorable soil properties (Stepanov et al., 2018) make crop cultivation very challenging in the region.

Given these constraints, the agricultural sector in Yakutia strongly depends on domestic animals uniquely adapted to the harsh climate, such as the autochthonous Yakutian horse (Figure 1), cattle, and laika (dog), as well as reindeer (Kolosov, 2014; Librado et al., 2015; Yurchenko et al., 2018a,b; Krutikova et al., 2024). Despite some recent growth in the agricultural sector, the Yakutia region relies heavily on external supplies, with critically low self-sufficiency rates for key staples such as meat (26.4%), milk (56.7%), potatoes (61%), vegetables (37.8%), and eggs (56.1%) (Vladimirov, 2021). These shortfalls highlight the ongoing challenges to achieving full food security

and agricultural self-sufficiency.

Addressed knowledge gap and objectives of the review: The Yakutian horse is one of the few domestic horse populations to sustain year-round, low-input production in an Arctic climate, and one of the few with a documented genomic basis for cold adaptation (Librado et al., 2015). It is thus both an important regional resource for food security in the Sakha Republic and a natural model of rapid adaptation among domesticated mammals. Much of the primary work has been published in Russian-language or regional sources, however, with no report linking the genome and physiology to the breed's production system. While climate change affects livestock systems worldwide, emerging omics tools can now connect molecular adaptation to phenotypes. Therefore, this narrative review aims to (i) describe the production system, geography and management of the Yakutian horse and summarize its meat and milk production; (ii) clarify its origin by ordering the historical, morphological, craniological and genomic evidence; (iii) integrate its genomic, physiological and phenotypic adaptations; and (iv) outline a roadmap for future work, including conservation and sustainable breeding.

Methods used: This is a narrative (non-systematic) review. Published papers and reports were searched using Google Scholar, Scopus, PubMed and eLibrary.ru databases, considering such keywords as “Sakha”, “Yakut”, “Yakutia”, “Yakutian”, “Siberia”, “Arctic”, “horse”, “Arctic livestock”, “cold adaptation”, “horse meat”, “horse milk” and “kumis/kumys”, covering the publication range 1941–2025. Sources in Russian and English were included, with priority given to peer-reviewed papers and regional/historical works. Duplicates were identified using Zotero software (Vanhecke, 2008), and the final check was performed manually. The publications were included if they addressed Yakutian horses in terms of origin, genetics, physiology, adaptation, management, or meat and milk production, or provided directly comparable evidence from other cold-adapted breeds or species. Regional or historical works were only considered where they provided primary data not available in the international literature.

2. Population changes and production system

Russia accounts for approximately 7% of global horse meat production (Belaunzaran et al., 2015). The Yakutia region ranks first in Russia in terms of horse number, which currently is 182.8 thousand animals, i.e., 13.7% of all horses nationally. The horse population in the region has experienced significant demographic fluctuations (Figure 2). The population declined by 42% from 1992 to 1999, levelling from 120,900 to 134,211 head in 1999–2007.

Subsequently, from 2007 onward, it experienced steady growth, reaching a peak in 2017 (184,182 head) and has thereafter remained stable (182,766 in 2020) at near-peak levels (Vasiliev and Danilova, 2020; Vladimirov, 2021). This indicates a growing horse population in recent years, which could reflect an increasing demand for horse meat products in the region.

Figure 3 shows significant shifts in Yakutia's equine management structure, with peasant farms increasing from 49,812 to 73,598 animals and household farms growing from 44,670 to 70,509 animals between 2010 and 2019, corresponding to increases in their proportions of the regional horse population from 30.46% to 40.21% and from 27.31% to 38.52%, respectively. This redistribution highlights the growing importance of small-scale production systems in Yakutia's equine sector.

Yakutian horses are currently reared mainly for meat production, an important component of the local diet, while simultaneously providing critical transportation services for local communities. In particular, during snow-free seasons when reindeer cannot pull sledges, horses facilitate the migration of people and the transport of goods across the region's challenging terrain (Maj, 2009; Stammeler, 2010).

The profitability of horse breeding relies heavily on year-round free-grazing systems (Grigorev et al., 2022), but the region faces two zootechnical challenges that are the main limiting factors for the development of this sector. These include (1) long and severe cold seasons cause extremely harsh conditions for outdoor herding, leading to metabolic exhaustion, seasonal reproduction, mortality and abortion; and (2) short growing seasons, coupled with summer heat stress (up to 30 °C) and insect harassment, reduce pasture productivity. Collectively, this results in a decrease in growth rate and overall weight gain, especially in young stock, during the summer.

These factors lead to inadequate feed availability that directly compromises productivity and immunity, even though the animals show high tolerance to cold.

3. Breed description and distribution

According to the Law of the Republic of Sakha (Yakutia) of 2003 (amended in 2021) “On Herd Horse Breeding”, three different horse breeds are reared in the Yakutia region, including the autochthonous Yakutian breed and two synthetic breeds Megezhekskaya, and Prilenskaya, both officially registered in 2011. The

characteristics of these three breeds and two intrabreed types of Yakutian horses are shown in Table 1. The Megezhekskaya breed was developed through crossbreeding of the Kuznetsk horse with the Russian Heavy Draft, while the Prilenskaya horse was developed by crossbreeding Yakutian horses with imported Orlov Trotter and Russian Heavy Draft horses.

Table 1. The characteristics of the breeds and types reared in Yakutia. Ref.: Filippova et al. (2020).

Parameter		Breed			Yakutian intrabreed type	
		Prilenskaya	Megezhekskaya	Yakutian	Kolyma	Yansky
Population ¹		32,062	25,729	116,086	3,349	14,874
%		17.5	13.9	66	2.9	8.1
Weight (kg)	stallion	450–560	470–610	430–490	440–530	–
	mare	450–530	450–580	415–470	430–520	–
Head	size	large	relatively large	medium	massive	medium
	shape/profile	slightly convex	straight/slightly concave	straight	straight	straight/slightly concave
Coat colors		mouse-colored, bay, roan, chestnut, piebald and gray in various shades	dun, roan, bay, gray and mouse-colored	gray in various shades, roan, mouse-gray, bay, chestnut, pinto	gray in various shades, up to white	shades of gray, mouse-gray, dun, and others

¹Population size is based on the 2020 head count.

The native Yakutian breed was officially recognized and registered as a separate breed in 1987 (Alekseev and Stepanov, 2006), although Yakutian horses have inhabited the region for the last 600–800 years (Liu et al., 2017). They are the world's most cold-resistant equine breed (Librado et al., 2015) and have maintained a sustainable genetic purity with almost no traces of crossbreeding (Atroshchenko et al., 2023). The Sakha people have preserved this unique breed through traditional year-round pasture grazing, including the 7 to 8 month snow season when vegetation is completely snow covered (Scherf, 1995). During winter grazing (called *tebenevka*; Figure 4), most domesticated equines cannot survive without supplementary feeding (Vasiliev and Danilova, 2020).

The Yakutian horse was initially used for transport in forested and swampy areas, with meat and milk production a secondary order of importance (Kalinkova et al., 2022). Today, the breed is primarily used for meat production, while also providing secondary products, including milk, kumis (or kumys, i.e., fermented mare's

milk), leather, and wool, along with continued roles in hunting, equestrian sports, and even agricultural work and transportation in remote regions and inaccessible places (Vasiliev and Danilova, 2020).

Morphologically, Yakutian horses have a compact and harmoniously built body conformation, extremely thick winter coats with long manes and tails, and predominantly light coat colors of gray and dun (Kalinkova et al., 2022). In summer, they resemble southern breeds in body type, but in autumn, after grazing and gaining weight, they become more massive and robust. Body measurements differ among types and between sexes. Withers height, oblique body length, chest girth, and cannon bone girth vary as follows: 135–141, 141–149, 163–182 and 18.4–19.7 cm in stallions and 132–137, 138–150, 158–176 and 17.2–18.4 cm in mares, respectively (Dmitriev and Ernst, 1989).

Conservation status: The breed and its intrabreed types are of conservation interest given their unique adaptation and genetic purity. The Yakutian horse is registered in FAO's Domestic Animal Diversity Information System (DAD-IS) as Yakutskaya (Russian Federation) and is classified as not at risk at the national level (Dmitriev and Ernst, 1989; Scherf, 1995). This classification is probably based on the last update data in 2003, with no counts of breeding females recorded, and risk status consequently returned as unknown at the global level. This absence of current data reflects incomplete reporting to DAD-IS rather than any decline in the breed, since regional statistics record a stable population of 182,766 head in 2020 (Figure 2).

4. The origin and current state of Yakutian horses

Conflicting hypotheses exist that either Yakutian horses arose from wild, northern ancient horses, or they appeared carrying the ancestors of the Yakutian people who originally claimed the territory. The timeline of the hypotheses proposed for the origin of Yakutian horses is shown in Figure 5. The autochthonous conjecture is the oldest, originating at the time of the first scientific expedition to study horse breeding in Yakutia (Rogalevich, 1941), when it was hypothesized that northern Yakutian horses have the blood of wild horses. Gabyshev (1957) reviewed earlier works that contained a hypothesis, without demonstrating supporting findings, that ancient wild horses were contemporaries of the woolly mammoth and lived within the Arctic Circle, downstream of the Yana River, and on the New Siberian Islands.

Morphological evidence supported this idea, though it remained suggestive rather than conclusive. Comparing

the skeletal anatomy of late Pleistocene horses with that of modern Yakutian horses, Lazarev (1980) reported that these were nearly identical and inferred local survival through the extinction events that eliminated the woolly mammoth and woolly rhino. Later, Ivanov (2021), on a similar basis, differentiated horses of the Kolyma type arising from their wild ancestors and the horses that arrived with the Yakutian people, probably explaining why the former are larger.

Craniological and immunogenetic characteristics refined the picture without resolving it. Comparing Yakutian and Kazakh horses of the Jabe type (described elsewhere, e.g., Kassymbekova et al., 2025) and Mongolian horses, Guryev (1990) identified genotypes unique to Yakutian horses linked to erythrocyte antigens and serum proteins, but also close similarities between Yakutian horses from central regions and southern steppe horses. This suggested a southern affinity, though the timing and direction of the breed's origin remained unsettled. Alekseev (2003), however, disagreed with all the above. He further claimed that the general physiological capabilities of horses in general and Yakutian horses specifically are not entirely explained by the response to environmental conditions. Exactly why Alekseev (2003) disagrees with the evidence of the former earlier studies is not entirely clear from our reading. Later, Alekseev (2005) concluded that *“the Yakut horse breed, thanks to the technology of keeping it developed for the conditions of the North, has survived to this day and its roots go back to the horses brought by the ancestors of the Yakuts from the Baikal region [south to Yakutia] and is its direct descendant.”*

With the advent of new genotyping technologies, whole-genome data have proved decisive and largely settled the debate in favor of the introduction hypothesis. Librado et al. (2015) sequenced the complete genomes of nine modern horses and two horses excavated from the Eveno-Bytantaysky National District. Comparative analysis with two late Pleistocene, 27 domesticated, and three wild Przewalski horses led to the conclusion that modern Yakutian horses are not descended from local horses inhabiting the region until the mid-Holocene. In the Eveno-Bytantaysky National District, they were crossbred by the ancestors of the Yakuts, who first settled these territories. This, most likely, occurred following their migration from the Altai-Sayan and/or Baikal regions between the 13th and 15th centuries. Comparative genomics of modern and ancient horses (~5,200-year-old) is consistent with this, finding no ancestry from the extinct wild populations that once inhabited the region (Kantanen, 2019). Together, these findings indicate a recent introduction followed by unique adaptation to Arctic conditions over an unusually short evolutionary interval (see also Section 5).

In its current state, the breed consists of two intrabreed types, Kolyma and Yansky (Table 1). The Kolyma type descended from the Native subtype through a long-term breeding program and is characterized by good grazing ability and excellent weight-gaining and fattening capacity. These horses are kept in covered shelters during summer, where smudge fires are used to protect them from swarms of mosquitoes.

The Yansky type was derived from native purebred Yakutian horses through selective breeding in the valleys of the Yana and Indigirka rivers. These horses resemble their ancestral predecessors but are larger and heavier. They are known for their robust constitution, high fattening capacity during the short summer, and exceptional winter hardiness.

5. Genomic, physiological and phenotypic adaptation

Yakutian horses are frequently described as “rapidly” or “fast” adapted. Adaptation over roughly 100 generations (c. 600–800 years) following introduction (Librado et al., 2015), as reported for Yakutian horses, is a short period relative to the timescales usually cited for major morphological and physiological change in large mammals. The proposed mechanism is natural selection acting on standing genetic variation within a domesticated population, rather than the long-term accumulation of new mutations. Unlike wild cold-adapted species such as reindeer (Krutikova et al., 2024) or snow sheep (Dotsev et al., 2026), the Yakutian horse breed was subject to human-mediated migration, management and selection, so its rapid adaptation reflects natural and artificial selection combined (Kantanen, 2019). These adaptations have occurred through integrated physiological, nutritional, and metabolic changes that maintain energy balance and homeostasis.

Genomic signatures of selection: Despite their long domestication history, the northernmost autochthonous Yakutian horses (Librado et al., 2015) and cattle (Buggiotti et al., 2021, 2022; Yudin and Larkin, 2023), likely have a short adaptation history compared to reindeer (Krutikova et al., 2024). Therefore, they can be regarded as “imported” animals that adapted very quickly to the Arctic environment (Kantanen, 2019). Comparative genomic analyses have identified positive selection in multiple genes involved in glucose metabolism, suggesting that sugar-related antifreeze properties and seasonal thermoregulation contribute significantly to Arctic survival (Librado et al., 2015). This is similar to genetic adaptations documented in woolly mammoths (Lynch et al., 2015), suggesting convergent evolution among Arctic-adapted mammals. Two particularly important candidate genes with strong

selection signatures map directly onto the breed's most prominent phenotypes, i.e., its dense winter coat and the capacity for rapid seasonal fat deposition. These are *BARX2* (BARX homeobox 2), involved in hair development and probably associated with the dense insulating winter coat, and *PHIP* (PHIP subunit of the CUL4-Ring ligase complex, or pleckstrin homology domain interacting protein), related to insulin metabolism (Librado et al., 2015, 2016). Moreover, a few kilobases variation upstream of translation start sites appear to be the main cause of fine-tuning the expression of cold-adaptation genes, representing a primary genetic mechanism for cold resistance in this breed (Librado et al., 2015). In addition, genomic studies using microsatellite markers (Sild et al., 2019), Y chromosome sequence data (Felkel et al., 2018), and autosomal whole-genome sequence data (Librado et al., 2015) indicated the uniqueness of the Yakutian horse genome, highlighting a distinct paternal lineage that is not found in other present-day domestic horse populations. This could be due to fast adaptation, geographical isolation, and cultural factors limiting interbreeding with other horse populations (Librado et al., 2015; Wutke et al., 2018; Li et al., 2025). In another study, fewer and shorter homozygosity segments were found in the Yakutian horse genome, suggesting ancestral inbreeding and selection signatures due to adaptation to natural exposures in this breed (Chen et al., 2023). Comparable runs-of-homozygosity (ROH) analyses of other ancient native breeds adapted to harsh conditions have similarly attributed reduced or structured homozygosity to historical demographic bottlenecks and adaptation rather than recent inbreeding. In the Icelandic horse and Exmoor pony, both of which underwent historic bottlenecks and remain adapted to cold environments, ROH patterns distinguish selection for performance from selection for environmental adaptation (Sigurðardóttir et al., 2024). Similarly, selection-signature studies of native Italian breeds interpret their genomes as shaped by natural adaptation to harsh climates (Asti et al., 2025).

Physiological, metabolic and biochemical adaptation: The physiological and metabolic adaptations of Yakutian horses are precisely synchronized with seasonal changes, which are principally directed toward the conservation of energy rather than the elevation of functional output. Over the short summer growing season, the horses rapidly accumulate abdominal and subcutaneous fat, distributing adipose tissue evenly across the body rather than concentrating it in specific regions, and develop the thick insulating coat required for wintering (Librado et al., 2015; Kalinkova et al., 2022). Their activity is then reduced during the cold months to conserve energy (Solomonov et al., 2009), and the cycle closes in spring, when increased carbohydrate metabolism supports higher energy demands of late gestation and fetal development (Grigor'eva and Koryakina, 2008).

Winter itself is characterized by pronounced metabolic depression. Respiratory volume, respiratory frequency,

and oxygen consumption all decline (Alekseev, 2003), and metabolic rate falls toward near-hibernation levels, an effect attributed to the production of bioactive substances (Solomonov et al., 2012). Circulatory adjustments are consistent with this strategy rather than opposed to it. Erythrocyte number and hemoglobin concentration increase by >33% and >20%, respectively, in January relative to March (Ignatiev et al., 2020), while, relative to summer values, winter increases of 71.6% in erythrocytes, 59% in minute blood circulation, 23% in circulating blood volume, and 19% in blood-flow rate have been reported (Alekseev, 2003); the magnitude of the reported response thus depends on the reference period used. Because oxygen-carrying capacity rises while oxygen consumption falls, we suggest that these changes maintain tissue oxygenation at a reduced ventilatory cost, therefore sustaining thermogenesis and perfusion under cold-induced vasoconstriction rather than supporting increased aerobic output.

Adipose tissue shows complementary biochemical specialized thermogenic properties through an uneven distribution of PUFAs. Linoleic acid is concentrated primarily in the liver for the biosynthesis of physiologically active compounds, while alpha-linolenic acid (ALA) predominates in adipose tissue (Petrov et al., 2020). The lower melting point of ALA enhances membrane fluidity and stimulates mitochondrial activity, increasing energy production and highlighting its crucial role in cold adaptation (Pisani and Ailhaud, 2019). Fat in this breed therefore functions not only as insulation and energy reserve but also as a thermogenically active tissue. These physiological adaptations likely reflect specific genetic modifications that emerged during the evolution of the breed.

Phenotypic outcomes through coat color and gait: Yakutian horses predominantly exhibit gray and dun (savrasovaya) coat colors, most likely as a result of natural selection (Alekseev and Stepanov, 2006). This gray phenotype is associated with an autosomal dominant trait characterized by progressive depigmentation of the coat hairs while maintaining pigmented skin (Sponenberg and Bellone, 2017). Light gray coloration provides effective camouflage in Arctic environments, reducing visibility to predators against snow-covered landscapes (Gabyshev, 1957). Similarly, savrasovaya coloration improves crypsis by blending with natural landscapes (Kalinkova et al., 2022). These interpretations remain hypotheses, however: no study has demonstrated a selective advantage through reduced predation, and the observed distribution may equally reflect founder effects or human preference in a breed maintained with high purity (almost no crossbreeding).

The breed has also developed a characteristic ambling gait, the tropota (broken or fox trot; Russian: тропота), in which diagonal limb movement produces a smooth four-beat rhythm: the forelimbs perform long, sweeping

motions with minimal carpal flexion, while the hindlimbs take shorter, spring-loaded steps with pronounced hock flexion (Vincelette, 2023). This pattern reduces ground reaction forces and is well suited to soft, deformable terrain such as snow, marshes and uneven ground. Lower heart and respiration rates and lower blood lactate relative to other gaits indicate greater energy efficiency (Wanderley et al., 2010; Filho et al., 2012; Vincelette, 2023), consistent with an adaptation to long-distance travel over snow and with the breed's continuing role in transport across Yakutia. The tropota is not, however, unique to Yakutian horses, occurring among several gaited breeds (Vincelette, 2023), and is therefore better regarded as a trait favored under Arctic conditions than as an adaptation exclusive to this population. Similar patterns are seen in the closely related Chinese Mongolian horses, which graze year-round at temperatures below -40°C , develop heavy winter coats shed by late spring, and carry a selection signature at the *DMRT3* (doublesex and mab-3 related transcription factor 3) gene in their gaited Wushen type (Han et al., 2023). This parallel reinforces the interpretation of the ambling gait as an adaptive trait.

Comparative insight from Yakut cattle: The northernmost Yakut (Yakutian) cattle, a native taurine breed from the same region, offer a closely matched comparator, because their history parallels that of the Yakutian horses. Their ancestors moved from the Lake Baikal area alongside the migrating Turkic-speaking Sakha people to Siberia roughly 500–800 years ago. They belong to the Turano-Mongolian lineage, clustering with East Asian rather than European taurines (Yurchenko et al., 2018a; Buggiotti et al., 2022). Like the horse, they are thus a recently arrived domestic animal that adapted to Arctic extremes over a short evolutionary interval, surviving year-round outdoors in the Yakutia region and foraging under deep snow with minimal supplementation (Yurchenko et al., 2018a; Weldenegodguad et al., 2019). Their genomes retain high SNP diversity and numerous private alleles relative to temperate breeds, indicating a large historical effective population size and limited intensive breeding rather than a severe bottleneck (Weldenegodguad et al., 2019). Whole-genome studies have revealed that all Yakut cattle individuals examined carry a nearly fixed missense variant (H100Q) in *NRAP* (nebulin-related-anchoring protein), a conserved cardiac muscle gene, which is unique to hibernating and cold-adapted mammals and absent from other cattle and bovines (Xia et al., 2023). Functional annotation suggests that the *NRAP* change may reduce basal metabolism while enhancing cardiac output during stress (Xia et al., 2023), supporting the hypothesis that Yakut cattle enter a mild hypometabolic state in deep winter (Buggiotti et al., 2021; Xia et al., 2023). Selection signatures also implicate *RETREG1/FAM134B* in temperature sensation, while copy-number variants (CNVs) spanning *CYP4A11* and enriched for thermogenesis and fatty-acid pathways suggest that structural variation contributes to

lipid-based heat production (Buggiotti et al., 2022; Xia et al., 2023). The resulting pattern (cardiac and metabolic depression, enhanced thermogenesis, and allocation of energy to heat production rather than rapid growth) closely mirrors the physiological profile described above for the Yakutian horse. A recent transcriptomic study reported that some genes upregulated in adipose tissue of Yakut cattle (e.g., *NR4A3*, *TEKT3*, *FGGY*) are linked to energy metabolism and response to cold temperatures (Ruvinskiy et al., 2024), illustrating the kind of functional-genomic analysis that could be extended to the Yakutian horse. Taken all together, these findings link specific genomic signatures to their physiological mechanisms and phenotypic outcomes, from BARX2 and coat development to PHIP and seasonal fat deposition (Figure 6). This integrated view distinguishes the inherited capacity for adaptation, encoded largely in regulatory variation, from its reversible seasonal deployment, and situates the Yakutian horse alongside the better-characterized NRAP-based adaptation of Yakut cattle.

A roadmap for Yakutian horse genomics research: The genetics of the Yakutian horse was studied before that of Yakut cattle, yet cattle functional genomics has since overtaken it, driven by the breed's commercial importance for milk and meat. The approaches applied to cattle can therefore be transferred to the horse. These include (1) genome-wide scans to identify further signatures of selection, (2) CNV analysis to test whether horses carry analogous duplications affecting lipid metabolism and protein turnover, and (3) targeted searches for equine orthologues of adaptation genes such as *NRAP*, whose convergent appearance in cold-adapted mammals illustrates how selection can favor rare beneficial mutations in harsh climates (Xia et al., 2023). Coupling these approaches with transcriptomic profiling of the seasonal traits described earlier would link genotype to the physiological and production phenotypes and would supply the gene networks required for conservation-oriented, genomics-informed breeding.

6. Herd management

The reproductive cycle and herd management of Yakutian horses are aligned with the seasonal weather conditions of the Yakut region (Figure 7). Mares remain fertile up to 15 years of age, but they are typically bred for only 10 years, since abortion rates and infertility increase at advanced ages. Stallions are similarly productive for about 10 years, with mare-to-stallion ratios of 10–15 mares for middle-aged stallions (5–18 years) and 7–10 mares for younger (<5 years) or older (>18 years) stallions. Stallions with poor fertility, weak herd leadership, or dangerous habits are culled. About 10% of the breeding and working horses are culled annually based on body

condition at the time of mass slaughter in late October to early November. Stallions are typically separated in April and provided with supplementary feed for 30–40 days before the peak of the breeding season (Khompodoeva et al., 2019).

Foaling takes place from mid-March through mid-May, and mares are isolated for intensive management practices and supplementary feeding about one month before the expected delivery. This period aligns well with the region's brief growing season. Early (pre-March) or late (post-May) foaling is discouraged due to undesired environmental conditions, because, in late-season foaling, both mares and their newborn foals require close monitoring and care.

Foals reach 180–200 kg by weaning at 6–7 months of age. The weaning period (late October to early November) coincides with breeding stock evaluation, selection, culling, vaccination and slaughtering. During weaning, foals experience significant stress, usually refusing to feed for 2–3 days; they are restless and run extensively, leading to excessive sweating. In extreme cold, this sweat freezes into an icy crust, causing weight loss. To prevent these effects, foals are initially housed in small sheltered pens before transitioning to larger areas protected from the wind.

Grazing begins in mid-May and continues through October, during which time the horses alternate between grazing and resting periods every 1–3 hours during both day and night. Traditional management practices employ shaded shelters and smoke barriers (smudges), which reduce insect harassment and thermal stress.

Fattening from late August to early November, allows horses to demonstrate exceptional metabolic efficiency, accumulating substantial subcutaneous and visceral fat reserves and gaining weight exceeding summer growth rates by 30–40% (Gabyshev, 1957; Andreev and Alekseev, 1982; Grigorev et al., 2022). After autumn fattening, fat deposits can reach 11 kg of visceral fat protecting the internal organs and up to 67 kg of total carcass fat (Andreev and Drugin, 1970). This high autumn lipid accumulation enables them to successfully withstand the harsh natural and climatic conditions (Prisyazhny, 2011; Petrov et al., 2016; Grigorev et al., 2022).

Yakutian working horses are trained for riding and pulling sleighs (Figure 8) at 3 to 4 years of age, with training typically initiated in late winter (February–March) when frozen ground conditions facilitate the use of the sleighs. Winter management of these animals requires specific interventions. These include (1) the provision of

supplementary feed with mineral salt licks to maintain electrolyte balance, (2) daily removal of accumulated snow and ice from legs to prevent injuries and frostbite lesions, and (3) application of insulated wraps to ice-crusting areas overnight (if any).

Abortion is the main reason for the relatively low annual foaling rate (~60%; range: 53–69%), arising from twin pregnancies, injuries from crowded conditions, cold stress, and severe exhaustion. Abortions mainly occur in early winter (October–November), when horses are driven to central bases for weaning, veterinary tasks and inventory. These tensions, along with galloping and sweating, coincide with the first strong cold fronts across Yakutia (–13 to –20 °C), thereby causing abortion in cold-sensitive mares, especially those that get pregnant late. The second peak occurs in December to January, when the temperature is at its minimum (–45 to –60 °C) (Alekseev, 2009).

Over Yakutia's long winter, poorly nourished mares deplete most of their subcutaneous and visceral abdominal fat, reducing the insulation during the final months of pregnancy (February–March). This disruption of the adaptive balance between heat loss and heat production leads to an increase in energy expenditure for thermoregulation (body temperature maintenance) and overall heat production, and consequently, increasing the risk of abortion. Therefore, supplementary emergency feeding for 25–30 days, typically in mid to late March, is essential to prevent pregnancy losses (Alekseev, 2009).

7. Meat and milk production

Yakutian foals grow rapidly (~1 kg/day), reaching approximately four times their birth weight by the end of the fourth month (Table 2). Meat production and quality in foals at 6 months of age depend significantly on maternal milk yield, as milk constitutes the main nutritional source during this period (Vladimirov, 2021). The Yakutian horse is distinguished by high slaughter and carcass meat yields, ranging from 49.1% to 55.8%, depending on slaughter age, with no statistically significant differences between sexes (Abramov et al., 2013; Pak et al., 2021) (Table 3). Meat from 6-month-old foals accounts for 80% of the horse meat sold regionally (Pak et al., 2021).

Table 2. Early body weight and average daily gain (kg) of Yakutian horses. Ref.: Vladimirov (2021).

BW	W3	W4	W6	ADG0-3	ADG0-4
40–42	133–136	155–157	188–196	1	0.95–0.97

BW, birth weight; W3, body weight at 3 months of age; W4, body weight at 4 months of age; W6, body weight at 6 months of age; ADG0-3, average daily gain from birth to 3 months of age; ADG0-4, average daily gain from birth to 4 months of age.

Table 3. Slaughter yield after fattening in autumn. Ref.: Abramov et al. (2013).

Trait	6 months	2.5 years	Mature
Carcass weight (kg)	102.3	165	228
Carcass (%)	55.8	49.1	55.5

Yakutian horse meat is unique due to its high energy content (1,922–2,724 kcal/kg), balanced amino acid profile, vitamin content, presence of bioactive substances, high digestibility, marbling (i.e., intramuscular fat layers rich in PUFAs) and low saturated fatty acid content (Petrov et al., 2016; Slobodchikova et al., 2018; Pak et al., 2021). It is valued for its high α -linolenic acid content and an optimal ratio of n-6 to n-3 PUFA ratio in both internal and abdominal fat (Petrov et al., 2016, 2020; Pak et al., 2024). The rich PUFA content supports immunity and liver repair and reduces the risk of thrombosis (Egorova, 2017). A recent study by Yakut scientists suggested that consumption of young horse meat may contribute to longevity (Suknyova et al., 2019). An unpolluted and ecologically safe environment in the region (Vasiliev and Danilova, 2020), coupled with the high resistance of horses to adverse conditions, eliminates the need for hormones, antibiotics, growth stimulants, and artificial feed additives. With year-round free grazing under stress-free conditions, Yakutian horse products are well suited for organic food certification, although they are not yet officially certified (Pak et al., 2024). The horse and foal slaughtering and meat processing are performed under Russian state standards (GOST 32225-2013, GOST 32785-2014, and GOST R 55335-2012 for infant food), and regional research institutes have developed technical specifications and patented processing methods for a range of national meat products (Makhatov et al., 2023).

Yakutian horse milk is distinguished by its high lactose content and richness in vitamin C (Ivanov et al., 2021). Ammosova (1971) reported an average daily yield of 9.9 L over a 6-month lactation, with total production averaging 1,750 L and ranging from 1,124 to 1,942 L. Peak yield occurred in the second to third month, and mares foaled in early spring can maintain a yield of 7.0 to 8.0 L/day even in the seventh to eighth month of lactation. Ivanov et al. (2021) reviewed the milk productivity of Yakutian horses and reported that daily milk production in

some mares can reach 10–12 L.

Yakutian horse milk has the lowest total solid content (9.7%) among farm animal species (Nurtazin et al., 2015; Ivanov et al., 2021). It supports a foal growth rate, approximately twice that of calves, even on nutrient-poor pastures, with an efficient conversion of 1 kg body weight per 10 L of milk (Nurtazin et al., 2015). Foals gain on average 1 kg/day between 3 and 6 months of age, reaching a maximum of 1.5 kg/day (Andreev and Alekseev, 1982).

Interestingly, winter and summer milk differ markedly in composition. Winter milk is lower in protein (by 14.4%), fat (by 33.1%), phosphorus (by 39.5%), calcium (by 53.7%) and vitamin C (by 37%), but is more acidic and contains 21.2% more sugars (Pavlova, 2004). With its high sugar content, easily digestible lipids, and balanced profile of essential amino acids and vitamins, mare milk closely resembles human breast milk in composition, making it valuable for the production of infant food formulas (Nurtazin et al., 2015). Therefore, to optimize growth in young Yakutian horses, there are two key factors to address: (1) winter mare's milk composition should be carefully considered when formulating starter feeds, and (2) maternal genetic effects should be incorporated into selective breeding programs to maximize genetic progress for growth traits in Yakutian horse populations.

Kumis, a traditional fermented dairy product with both lactic acid and alcoholic components, has been an important part of Central Asian culture since the Chalcolithic era (around 3500 BCE) (Nurtazin et al., 2015). Due to its unique restorative, laxative, and healing properties, kumis has traditionally been used to treat various conditions, including gastrointestinal disorders, bone diseases, pulmonary and cardiovascular conditions, nutritional deficiencies, beriberi, anemia, allergies, immunodeficiency, and tuberculosis (Nurtazin et al., 2015; Egorova, 2017).

The fermentation process in kumis production substantially alters milk composition, increasing several amino acids (cysteine + cystine, histidine, arginine, proline, and methionine + valine) more than 2.8-fold and reducing the sugar content from 6.25% to 0.98% (Nurtazin et al., 2015). Mare's milk is used almost exclusively for kumis rather than direct consumption, and kumis production is likewise governed by an industry standard, though in Yakutia it remains largely seasonal and farm-based. The domestic market absorbs essentially all horse and foal meat and dairy products, indicating a regionally consumed product rather than export commodity (Makhatov et al., 2023).

8. Conclusions

This review collated evidence on the critical role of the northernmost autochthonous Yakutian horse in the regional agro-ecological system of Yakutia, emphasizing its genetic distinctiveness and unique adaptive traits. Nutritious, high-quality meat and milk obtained from this breed under sustainable, antibiotic-free husbandry conditions play a critical role in the food security of the indigenous Sakha people. The Yakutian horse's evolutionary adaptations, shaped by approximately 100 generations of natural selection and traditional rearing practices, reflect an integrated energetic economy system, rather than only a set of traits. Enhanced fat storage, the ability to graze under snow, a seasonal insulating winter coat, and efficient energy metabolism together allow it to thrive year-round in harsh, cold environments without shelter or supplementary feed, a low-input system that distinguishes it from commercial livestock production. To ensure the long-term sustainability and benefits of this production system, efforts should focus on preserving traditional knowledge about breeding and pasture management, supporting product certification and branding to enhance market value, and monitoring the breed's conservation status regularly. Close monitoring of the impacts of climate change on grazing conditions and animal health, as well as expanding genomic research to identify key adaptation gene networks, are priorities, as are comparative studies in cattle, in which genomic research, in many ways, is more advanced. Implementing all of this knowledge in a genomic-based selective breeding program will ensure long-term survival of this horse breed and the communities it supports.

Abbreviations

PUFAs, polyunsaturated fatty acids; ALA, alpha-linolenic acid; SNP, single nucleotide polymorphism; NRAP, nebulin-related-anchoring protein; CNV, copy number variant; ROH, runs of homozygosity; DAD-IS, Domestic Animal Diversity Information System.

Authors' Contributions

HB, EUM and MNR conceptualized and designed the study. HB, MOI, LMK, LYG, EUM, DML, DKG and MNR were involved in original draft preparation and editing.

Funding

This work was supported by the Russian Science Foundation (RSF Grant No. 25-26-00395).

Availability of Data and Materials

There are no raw data to be made publicly available.

Ethics Approval and Consent to Participate

Since there are no human or animal participants in this work, ethical approval is not needed.

Conflict of Interest

The authors declare no conflict of interest.

Declaration of AI and AI-assisted Technologies in the Writing Process

We thank the Writefull tool (Thinqlab Ltd., London, UK; <https://www.writefull.com/terms>) for providing language-related feedback on this manuscript. We did not use this tool as a substitute for human critical thinking, expertise and evaluation. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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