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High Altitude Adaptation in Livestock and Poultry: Exploring Morphological, Physiological, Biochemical and Omic Insights: A Review

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ABSTRACT

High altitude environments pose unique challenges for both humans and animals, necessitating a range of adaptations for survival. Livestock species indigenous to mountainous regions, such as Yaks, Tibetan sheep, Ladakhi cattle and Himalayan goats, have evolved specialized physiological, morphological and biochemical mechanisms to cope with extreme conditions like hypobaric hypoxia, temperature fluctuations and limited forage availability. These adaptations are crucial for their survival and the livelihoods of mountain communities that depend on them for resources like milk, meat and wool. Omic studies have revolutionized our understanding of high altitude adaptation in livestock. Genomic analyses have revealed genetic signatures of adaptation, such as higher heterozygosity rates in Yaks and positive selection of genes related to energy metabolism and hypoxia response. Transcriptomics studies have uncovered gene expression patterns and pathways underlying high-altitude responses, including those related to oxygen transport, immune function and stress tolerance in sheep and goats, comparative RNA molecule analyses have identified key regulators of hypoxia adaptation and cellular metabolism. Skin transcriptomics studies have highlighted genes involved in coat color, UV protection and fiber quality adaptations. Overall, leveraging omics methods such as genomics, transcriptomics and comparative analyses provides valuable insights into the genetic, molecular and physiological basis of high altitude adaptation in livestock. These findings contribute to the development of targeted breeding strategies and sustainable management practices essential for livestock resilience and food security in mountainous regions amidst climate change challenges.

Key words: Adaptation, Genomics, High altitude, Livestock, Transcriptomics.

High altitude environments pose unique challenges requiring livestock to undergo various adaptations at physiological, morphological, biochemical, genetic and molecular levels (Witt and Huerta-Sánchez, 2019; Sharma *et al*., 2022). Adaptability refers to the capacity of a system or organism to adjust its behaviors, traits and responses to thrive and survive in changing environments or conditions (Ayalew *et al*., 2021). Different characteristics such as physical attributes and structural features of an organism play a pivotal role in its adaptation to its environment. Livestock adaptation to high altitude hypoxic environments is critical, as these animals play a major role in maintaining the socioeconomic conditions of local populations in such places. High altitude adaptation is recognized as an evolutionary process in mammals, involving significant changes that enable them to not only survive but also perform optimally in extreme environmental conditions. These adaptations encompass a wide range of morphological, physiological and biochemical traits.

Livestock species such as Yaks, Tibetan sheep, Ladakhi cattle and Himalayan goats are crucial for the livelihoods and economies of mountain communities (Fig 1; Henry *et al*., 2018). These animals have evolved unique physiological and metabolic traits to overcome the challenges of high altitude environments, including low oxygen levels, extreme temperature variations and limited forage availability (Qiu *et al*., 2012; Wang *et al*., 2021). The mountainous regions in India, have a dominance of sheep with a population of 4.18 million, closely trailed by 3.12 million goats and a modest count of 58,000 Yaks. They exhibit remarkable adaptability to thrive amidst the challenging conditions of high altitudes, providing vital resources like wool, meat and sustenance to mountain communities (https://dahd.nic.in/sites/default/filess/VolumeII.pdf). The double-hump camel is distributed in the

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Nubra valley of the Ladakh region, India (Lamo *et al*., 2020). Physiological changes include cardiovascular adjustments, respiratory efficiency and hematological adaptations enhancing oxygen utilization (Storz, 2021).

At the molecular level, omics research has become invaluable for unraveling the complex mechanisms behind adaptation in animals to diverse environments. By examining the collective molecular components of organisms at various levels - genomics, transcriptomics, proteomics, metabolomics and beyond - researchers gain unique insights into how animals respond and adapt to environmental challenges. Omics approaches, particularly transcriptomics, reveal gene expression patterns and regulatory networks crucial for high altitude adaptation (Zhao *et al*., 2022). Omics studies have significantly advanced our understanding of the genetic mechanisms underpinning adaptability in high altitude species. These studies highlight genes and pathways associated with hypoxia response, metabolic regulation, immune adaptation and stress tolerance (Ayalew *et al*., 2021; Henry *et al*., 2018). Understanding these adaptive strategies can aid in improving livestock management and food security in mountainous regions (Rojas-Downing *et al*., 2017; Friedrich and Wiener, 2020). The rationale behind this review is to synthesize current knowledge and research findings on high altitude adaptation in livestock. By examining the physiological, morphological, biochemical, genetic and molecular changes associated with high altitude environments, we aim to elucidate the adaptive strategies employed by livestock populations to thrive in extreme conditions. The specific adaptations of various livestock species are detailed below.

Yaks

Yaks, scientifically referred to as *Bos grunniens*, are sturdy bovines native to the Himalayas in Asia (Jing *et al*., 2022). Known for their robust build, long shaggy hair and curved horns, Yaks are specially adapted to the extreme conditions of their mountainous home - where oxygen levels are low, temperatures are freezing and the terrain is rugged (Qiu *et al*., 2012). The states in India where Yak rearing is practiced are Himachal Pradesh, Jammu and Kashmir, Arunachal Pradesh, Uttar Pradesh and Sikkim (Fig 1). They are found at a height of 4000-5000 meter above the sea level (Yak Husbandry in India, https://www.fao.org/3/ad347e/ad347e0q.htm#fn9).

They exhibit distinct physiological responses to temperature changes, such as an increase in heart rate from 51 beats/min to 78 beats/min and elevated breathing rates, along with seeking shade to avoid heat stress.These adaptations enable them to thrive in temperatures below 5°C annually and avoid temperatures exceeding 13°C (Haynes *et al*., 2014). Morphologically, Yaks differ from other cattle in several ways. They have larger lungs and hearts, an enlarged thoracic cavity and unique pulmonary artery characteristics that help them cope with low-oxygen environments at high elevations (Fig 2; Jing *et al*., 2022). Their coat, composed of coarse fibers, down fibers and mid-type hairs, aids in maintaining stable body temperatures crucial for thermoregulation in extreme weather conditions (Wiener *et al*., 2003). Yaks' feeding behavior is adapted to minimize exposure to the cold environment. Their short tongues and prominent lingual features improve food processing efficiency, allowing them to consume low herbages effectively (Jing *et al*., 2022). Moreover, their reduced number of taste buds allows them to eat a wider range of fodder species, reducing dependence on limited pasture resources (Ayalew *et al*., 2021). Biochemically, Yaks have unique adaptations for energy metabolism and nitrogen utilization. Yaks maintain a high level of fetal hemoglobin throughout their lives (7.45% in adult hill cattle) whereas in most mammals, it is typically present for only 6 to 7 months after birth. This adaptation enhances oxygen affinity and delivery in oxygen-

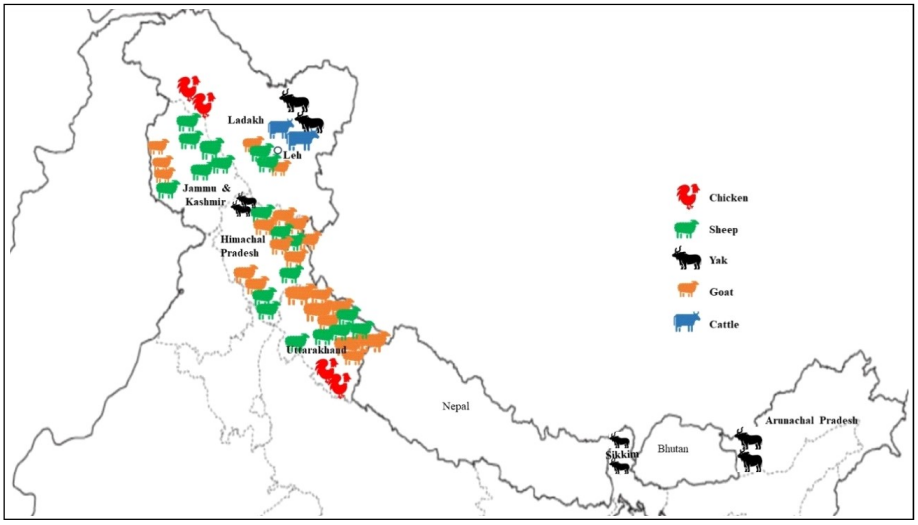


Fig 1: Distribution of livestock and poultry adapted to high altitude in India.

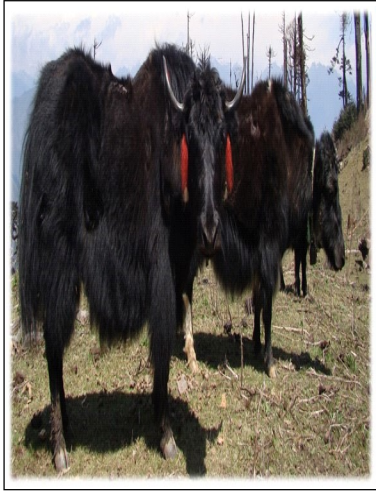
deprived environments (Jing *et al*., 2022). Additionally, their gastrointestinal microbiome diversity aids in efficient breakdown of fibrous plant materials in their diet, resulting in lower methane production compared to other ruminants (Ma *et al*., 2019; Jing *et al*., 2022).

Genomic studies on Yaks unveil their unique adaptation mechanisms, with a 1.5 times higher heterozygosity rate than bovines. Yak gene families are enriched in immune response, host defense and olfactory perception. Comparative analyses with cattle highlight higher expression of HIF-1α and HIF-2α in Yak tissues, especially the heart, showcasing distinct adaptation strategies (Qiu *et al*., 2012; Wang *et al*., 2021). Positive selection in genes related to hypoxia and energy metabolism underlines Yak's high altitude adaptations, including mitochondrial DNA modifications (Wang *et al*., 2011). The Tianzhu white Yak's genome revealed candidate genes linked to metabolic pathways and environmental processing, offering insights into coat color adaptations (Guangxin *et al*., 2019). Recent studies on Himachali, Ladakhi and Arunachali Yak populations identified SNPs impacting biological pathways crucial for high altitude adaptation, stress response and immune regulation (Kumar *et al*., 2024). Functional assessments highlight key enzymes like glutamine synthetase in nitrogen metabolism, emphasizing the genetic complexity of Yak physiology (Ahmad *et al*., 2024).

Cattle and buffaloes

Cattle and buffaloes play vital roles in the agricultural economies of numerous developing countries, supplying necessary resources like milk, meat and draught power. The harsh environment at high altitudes has a negative impact on agricultural techniques, resulting in low fodder output (Bharti *et al*., 2017). Ladakh and Leh, popularly known as the "land of high passes" in India, are located at elevations ranging from 3,500 to 5,500 meters. The local cattle of the Ladakh region are an excellent example of native populations that have evolved naturally throughout time to cope to the severe high altitude hypoxic environment of the Himalayan topography. These cattle have evolved distinct physiological adaptations, including a 25-30% increase in red blood cell count compared to lowland cattle, hemoglobin concentrations frequently exceeding 15-17 g/dL and a 25-30 mmHg elevation in pulmonary arterial pressure. These adaptations enable them to thrive in the harsh conditions of high-altitude environments (Bharti *et al*., 2017).

In cattle and buffaloes, cold stress causes a variety of physiological and behavioral reactions that help them maintain a consistent body temperature. One of the most common behavioral reactions is increased feeding behavior, as cooler temperatures require more maintenance energy. According to Wang *et al.* (2023), there can be a considerable increase in the energy needed for upkeep of beef cattle for every 1°C drop in ambient temperature. High altitude buffaloes show enhanced oxygen transport abilities and adaptations in various proteins, aiding in oxygen supply and stress tolerance (Wang *et al*., 2023). The 1865.0 m high altitude buffalo in Yunnan province, China, have been shown to exhibit elevated amounts of many hemoglobin subunits, including foetal subunit beta, alpha-I/II and beta, alpha-1, alpha-2 and subunit beta-A. This shows that high altitude buffalo have an improved ability to transfer oxygen to meet their physiological needs at high altitudes. Statistical analysis of MS2 peak area of proteins, which quantifies protein abundance based on mass spectrometry results, using the ANOVA test revealed significant increases in lactoferrin, serotransferrin, hemopexin and hemogen levels in high altitude buffalo compared to low altitude buffalo ($p<0.05$). Specifically, lactoferrin increased from 44,437,656.0 at low altitude to 62,055,141.0 at high altitude, serotransferrin from 78,140,829.8 to 104,291,760.7, hemopexin from 17,375,065.6 to 22,307,675.4 and hemogen from 153,398.1 to 210,144.2.



Physiological Adaptation	Biochemical Adaptation	Morphological Adaptation	Omic Adaptation
Larger Lungs & Heart	Elevated Levels Of Fetal Hemoglobin	Shorter Tongue with Fewer Taste Buds	Higher Levels of Hypoxia-inducible Factor-1a (Hif-1a)
Larger Diameter of Heart Capillaries	Less Urinary Nitrogen & Recycle Urea More	Graze by Labia Orris, Less Tongue Exposure to Cold Temperature	Mitochondrial DNA (Mtdna) Modifications
Lower Heart Rates & Metabolic Rates	Higher Lactate Dehydrogenase (LDH)	Larger, Thicker Keratinized Lenticular Papillae	Genes Related to HIF-1 & AMPK Signaling Pathway
Diminished Hypoxia Pulmonary Vasoconstriction	Diverse Gastrointestinal Tract Microbial Community	Low Dietary Nitrogen Intake	

Fig 2: Physiological, biochemical, morphological and genomic adaptive features of Yak *(Bos grunniens)* in comparison to cattle.

These findings probably result in higher blood oxygen levels, which help fulfill the oxygen demands at high altitudes (Lan *et al*., 2022). Prolonged cold exposure also affects rumen VFA levels and metabolic processes, influencing energy metabolism and hormone regulation in cattle (Kim *et al*., 2023). Apart from increased feed intake, cold stress impairs digestive function, reducing feed utilization efficiency and growth performance in cattle and buffaloes (Tengfei *et al*., 2022).

Understanding genomic selection signatures is crucial for studying adaptation in these populations. Genetic heterogeneity in Ethiopian mountain cattle revealed selection signatures in genes like *MB, ARNT* and *ITPR2*, suggesting convergent selection with humans (Terefe *et al*., 2022). Studies comparing taurine and indicine cattle breeds identified genes related to production traits and environmental adaptation including heat stress resilience (Saravanan *et al*., 2021). Transcriptome analyses in high altitude settings highlighted gene expression variations in cattle, Yak and gayal, particularly in immune system regulation, metabolism and hypoxia response pathways, shedding light on adaptation processes like oxygen transport, immune modulation and energy metabolism (Ma *et al*., 2022).

Sheep and goats

Sheep and goats are raised in environments that range from the high, steep Himalayas to the wetlands of Eastern India's Sunderbans to the plains of Northern and Central India. In India, there are 37 recognized goat breeds and 44 recognized sheep breeds as a result of domestication in a variety of agroclimatic zones and selection for various goals (Kumar *et al*., 2021; Arora *et al*., 2019). There are 1.8 million goats and 2.54 million sheep living in the northern temperate region of India comprising Jammu and Kashmir, Himachal Pradesh and hilly regions of Uttar. These include the well-known goat varieties that produce pashmina, including Chegu and Changthangi, as well as a wide variety of sheep breeds, including Gaddi, Gurez, Rampur Bushair, Bhakarwal, Karnah, Poonchi, Changthangi and Kashmir Merino. The local economy benefits greatly from these breeds, which flourish in difficult terrain (https://www.fao.org/3/X6532E/X6532E06.htm).

In cold environments, goats exhibit adaptive behavioral responses aimed at minimizing heat loss and maintaining body temperature within a comfortable range. When exposed to cold conditions, goats may increase their feed intake to provide the necessary energy for thermogenesis (Fig 3). Changes in posture, such as huddling together or curling up to conserve body heat, are common behaviors observed in goats during cold weather (Gouri, 1998). Larger body sizes in colder regions help them maintain optimal temperatures (Silanikove, 2000; Mili and Chutia, 2021). Ewes in high altitude areas have smaller litter sizes but carry heavier litters, indicating efficient placental exchange mechanisms under stress (Dwyer and Lawrence, 2005). Sheep at high-altitudes show adaptations in respiration rates, immune response and biochemical parameters like glycolysis and hematological indicators (Zhao *et al*., 2022; Sha *et al*., 2022; Barsila *et al*., 2020). Colostrum composition in goats varies with altitude, with higher levels of antioxidants and minerals in high altitude breeds' colostrum (Agradi *et al*., 2023).

Whole genome analyses in Tibetan sheep have identified the *SOCS2* gene under positive selection, crucial in the HIF-1 pathway regulating erythrocyte differentiation and energy metabolism (Yang *et al*., 2016). Comparative RNA studies, including lncRNAs, miRNAs and mRNAs, have unveiled mechanisms of hypoxia adaptation (Pokharel *et al*., 2018). Lung tissue transcriptomes revealed adaptive genes like *FNDC1*, *HPSE and E2F8* (angiogenesis), *GJA4*, *FAP*, *COL1A1*, *COL1A2*, *COL3A1* and *COL14A1* (vasomotion and fibrogenesis) and *HBB*, *HBA1*, *APOLD1 and CHL1* (gas transport) (Zhao *et al*., 2022). Heart tissue analysis highlighted pathways like Wnt and PPAR, boosting metabolism and ATP production (Wen *et al*., 2022). Kidney

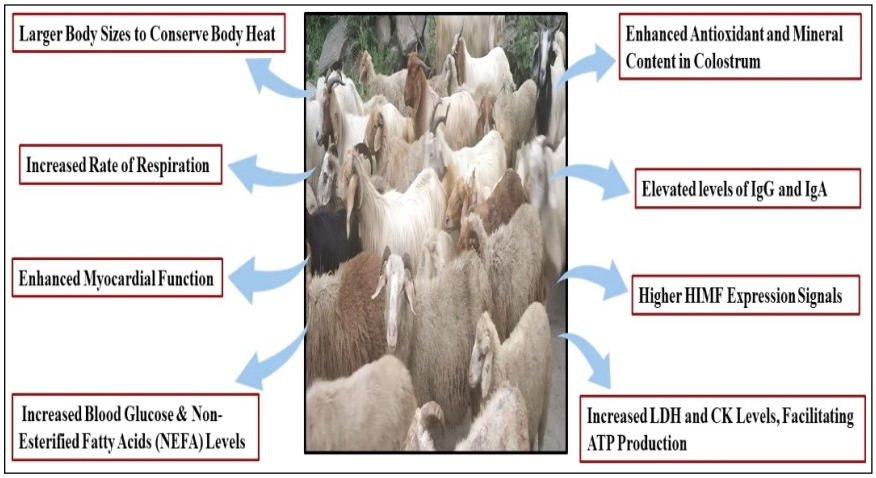


Fig 3: Adaptive strategies in sheep and goats in response to high-altitude environment.

Table 1: Physiological adaptations of chickens in response to high altitude environments.

Parameter	Response to high altitude
Cardiovascular system	Increased organ weights (liver, heart muscle)
Hematological parameters	Elevated levels of WBC, RBC, hematocrit (HCT) and hemoglobin (HGB)
Egg quality characteristics	Yolk weight, Reduced albumin height and Haugh unit; decreased shell thickness and shell weight
Gut microbiota	Decreased microbial richness and evenness in gut microbiota; variations in substrate utilization profiles
Biochemical	Elevated levels of endothelin (ET), aspartate aminotransferase (AST), glucose (GLU) and low-density lipoprotein (LDL)

comparisons showed higher expression of VEGF and HIF-1á in Tibetan sheep (Talks *et al*., 2000; Yang *et al*., 2020). MicroRNA-gene networks elucidated sheep muscling and meat quality (Kaur *et al*., 2020). Skin transcriptomics displayed melanogenesis genes in Changthangi sheep, suggesting adaptations for coat color and UV protection (Ahlawat *et al*., 2020; 2024; Vasu *et al*., 2024).

Chicken

Chicken are the most popular poultry worldwide and are now used for both meat and egg production. In India alone, there are a total of 20 indigenous breeds of chicken, reflecting the rich diversity of poultry resources available in the country. The poultry industry is one of India's most dynamic and rapidly growing sectors (Basic Animal Husbandry Statistics 2022, Ministry of Fisheries Animal Husbandry and Dairying Government of India). Analyzing the adaptive pressures that shape the genome of commercial chickens provides invaluable insights into the complex interactions among production, disease resistance and genetic variables.

Exposure to low temperatures prompts cardiovascular adjustments to meet increased energy demands resulting in organ weight increases like the liver and heart muscle in chicken (Wideman and Tackett, 2000). Moreover, cold exposure negatively impacts egg characteristics and shell properties (Li *et al*., 2020; Chuskit and Swati, 2023). Altitude affects gut microbiota functionality and diversity in broilers, with distinct substrate utilization profiles between low-altitude and high altitude chickens (Bhagat *et al*., 2023). High altitude chicken exhibit elevated white and red blood cell counts in cold conditions due to hypobaric hypoxia (Table 1; Su *et al*., 2018).

Genomic studies in Chantecler chickens identified key genes like *ZNF536* and *ME3* related to fat metabolism and neurological functions, enabling adaptation to cold climates (Xu *et al*., 2021). Transcriptomic analyses of Tibetan chickens revealed miRNAs like miR-499-5p and miR-144-3p crucial for high altitude adjustments, with pathways like I-kappa B kinase/NF-kappa B signaling implicated (Chen *et al*., 2022). Studies on chicken tissues highlighted genes linked to vasculature development, inflammation and immune responses, such as *ASH2L* and *FGFR1*, crucial for high altitude adaptation (Zhao *et al*., 2022a). Metabolomic-transcriptomic investigations in Tibetan chickens underscored pathways like arginine metabolism vital for energy regulation in hypoxic environments, showcasing their adaptation mechanisms (Xue *et al*., 2024).

Other livestock species

Apart from mainstream livestock, research on species such as pigs and camels at high altitudes has also gathered increasing attention due to its significance in understanding ecological dynamics, conservation strategies and adaptation mechanisms. Investigating their behavior, physiology and adaptation strategies not only sheds light on the intricacies of these ecosystems but also holds implications for conservation efforts, climate change resilience, biomedical research and comparative biology (Gebreyohanes and Assen, 2017; Gan *et al*., 2019).

Newborn piglets face challenges in cold stress but develop adaptive mechanisms over time, including increased metabolic heat production and fat mobilization for thermal insulation (Saturno *et al*., 2018). Tibetan pigs exhibit unique meat qualities at high altitudes, with variations in amino and fatty acid composition (Gan *et al*., 2019). Highlander camels demonstrate higher physiological activity and adaptive erythrocyte morphology for oxygen-carrying capacity at high altitudes (Lamo *et al*., 2020). Bactrian camels exhibit metabolic adaptations and differences in immune response compared to Dromedarian camels, indicating diverse adaptations across camel species (Gahlawat *et al*., 2021).

Genomic and transcriptomic studies in pigs from China revealed crucial genetic variants related to local adaptation, particularly in thermostatic regulation, vital for coping with diverse temperature conditions. The identification of gene loci, especially on the X chromosome, indicated adaptations to cold and hot climates (Ai *et al*., 2015). Additionally, research on Enshi black pigs highlighted skeletal muscle lncRNAs enriched in pathways linked to immune response, signal transduction and metabolism during cold exposure (Zhang *et al*., 2023). Contrary to common belief, cold resistance in certain pig breeds involves UCP3 and WAT browning, not shivering and showcasing unique mechanisms for cold adaptation (Lin *et al*., 2017). Existing research on camel genome are involved in identification of selection signatures for domestication based on re-sequencing (Fitak *et al*., 2020). Recently an SNP array for Indian Bactrian and dromedary camel has been developed that will aid in understanding the camel genome (Vijh *et al*., 2024).

CONCLUSION

As climate change poses increasing challenges to livestock farming, there is a pressing need to develop sustainable adaptation strategies. This means using advances in biotechnology and breeding techniques to find and use genetic markers linked to beneficial traits. Collaboration between different fields is essential to turn scientific discoveries into practical solutions for farmers and global food security. Combining genetic data with morphological, physiological or biochemical analyses provides valuable insights into the functional implications of genetic variations. It enables researchers to elucidate how genetic changes manifest at the phenotypic or biochemical level, shedding light on the biological pathways involved in adaptation. Looking ahead, future research should focus on understanding the genetic and molecular reasons behind animal adaptations. Leveraging omics methods such as genomics and transcriptomics offers a comprehensive insight into the intricate interactions among genes, proteins and the environment. Through comparative analysis of various breeds or populations, we can unveil distinctive traits and genetic variances, aiding in the formulation of targeted breeding strategies to enhance the resilience and productivity of livestock species.

Conflict of interest

The authors declare no conflict of interest.

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