



Review Article

The adaptive strategies of yaks to live in the Asian highlands

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ABSTRACT

The yak (*Bos grunniens*), an indigenous herbivore raised at altitudes between 3,000 and 5,000 m above sea level, is closely linked to more than 40 ethnic communities and plays a vital role in the ecological stability, livelihood security, socio-economic development, and ethnic cultural traditions in the Asian highlands. They provide the highlanders with meat, milk, fibres, leather and dung (fuel). They are also used as pack animals to transport goods, for travel and ploughing, and are important in many religious and traditional ceremonies. The Asian highlands are known for an extremely, harsh environment, namely low air temperature and oxygen content and high ultraviolet light and winds. Pasture availability fluctuates greatly, with sparse pasture of poor quality over the long seven-month cold winter. After long-term natural and artificial selections, yaks have adapted excellently to the harsh conditions: 1) by genomics, with positively selected genes involved in hypoxia response and energy metabolism; 2) anatomically, including a short tongue with a weak sense of taste, and large lung and heart; 3) physiologically, by insensitivity to hypoxic pulmonary vasoconstriction, maintaining foetal haemoglobin throughout life, and low heart rate and heat production in the cold season; 4) behaviourally, by efficient grazing and selecting forbs with high nutritional contents; 5) by low nitrogen and energy requirements for maintenance and low methane emission and nitrogen excretion, namely, 'Low-Carbon' and 'Nitrogen-Saving' traits; 6) by harboring unique rumen microbiota with a distinct maturation pattern, that has co-evolved with host metabolism. This review aims to provide an overview of the comprehensive adaptive strategies of the yak to the severe conditions of the highlands. A better understanding of these strategies that yaks employ to adapt to the harsh environment could be used in improving their production, breeding and management, and gaining benefits in ecosystem service and a more resilient livelihood to climate change in the Asian highlands.

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1. Introduction

The Asian highlands, also known as 'The Third Pole' and 'Asian Water Tower', are the largest and highest mountain region on earth, with an average elevation of over 4,000 m above sea level. The highlands, which cover the Qinghai-Tibetan Plateau (QTP) and regions of the Himalaya, Hindu-Kush, Karakoram, and Pamir ranges, are the source of the major rivers in Asia and are rich in biological and cultural diversities. They provide pivotal ecosystem services for more than 10 countries, including Afghanistan, Bangladesh, Bhutan, China, India, Kazakhstan, Kyrgyzstan, Myanmar, Nepal,

Pakistan, Tajikistan and Uzbekistan and upwards of 1.5 billion people; however, they are sensitive to global climate change and to the impact of human activities (Qiu, 2008; Xu, 2008; Yao et al., 2012; Xu and Grumbine, 2014). This region is characterized by an extremely harsh environment, namely, low air temperature and oxygen content and high ultraviolet light and winds, as well as severe snowstorms. The mean annual temperature for the Asian highlands region is 2.5 °C (below 0 °C in the QTP) and the mean annual precipitation is 440 mm (Niu et al., 2004; Yao et al., 2012, 2019; Zomer et al., 2016). There are no frost-free days and a short growing season of 90 to 120 days. Pasture availability fluctuates greatly, with sparse vegetation of poor quality over the long, cold winter. For instance, on a dry matter basis, biomass during winter on the QTP averages about 750 kg/ha, with a crude protein content of 6.2% and neutral detergent fibre 66% (Long et al., 1999a; Guo et al., 2021).

The yak (*Bos grunniens*), an indigenous herbivore raised at altitudes between 3,000 and 5,000 m above sea level across the Asian highlands (Wiener et al., 2003; Joshi et al., 2020), is the main livestock grazing on the highlands, particularly the vast rangelands of the QTP and regions around the Himalayan Mountain range. At present, there are approximately 16 million domestic yaks and 15 to 20 thousand wild yaks in the world, with more than 30 local dominant groups, of which 21 are in China as well as 2 artificially cultivated breeds (Wang et al., 2019; Joshi et al., 2020). More than 95% of yaks are raised in China, but yaks are also found in Nepal, Bhutan, India, Pakistan, Mongolia, Russia, Afghanistan, Tajikistan and Kyrgyzstan. Yaks are closely linked to more than 40 ethnic communities and play a vital role in the ecosystem stability, livelihood security, socio-economic development, and ethnic cultural traditions. They provide meat, milk, blood for some ethnic groups, dung and wool, are used as pack animals to transport goods, for travel and ploughing, and are important in many religious and traditional ceremonies (Wiener et al., 2003; Long et al., 2008; Wiener, 2013; Joshi et al., 2020). Yaks enabled large-scale population expansions and permanent human occupation of the QTP (Chen et al., 2015; Qiu et al., 2015).

Due to the extreme harsh environment in the Asian highlands, yaks and their production systems are facing greater challenges and risks than lowland livestock. However, after long-term natural and artificial selections, yaks have adapted well to the harsh conditions. Understanding how yaks thrive under these harsh conditions is important for improving their production, breeding and management. This review aims to provide an overview of yak grazing systems and the adaptive strategies of yaks to the harsh Asian highlands. The findings could benefit environmental conservation, livestock production and ecosystem management in the Asian highlands and could also enhance ecosystem and livelihood resilience to climate change.

2. The vital role of yaks in the Asian highlands

The yak is the only bovine species and one of the few large herbivores that can thrive in the harsh environment of Asian highlands. Phylogenetic analysis showed that the yak is a sister group of cattle/zebu, and has the closest genetic relationship to American bison (Hassanin and Ropiquet, 2004; Gu et al., 2007; Xie et al., 2010). From archaeological research, domestic and wild yaks originated from a primitive wild yak in the Pleistocene era, about 2.5 million years ago (Olsen, 1990; Hou, 1991; Wiener et al., 2003). The exact time and location for the domestication of the yak are still not clear. Based on ancient Chinese documents and archaeological evidence, researchers estimated that the wild yak was domesticated approximately 5,000 to 10,000 years ago by the ancient Qiang people (a collective name for ancient nomadic people in Western

China) in the northern QTP (Hassanin and Ropiquet, 2004; Gu et al., 2007; Xie et al., 2010; Qiu et al., 2012). This estimation was supported by mitochondrial DNA (mtDNA) analysis, indicating that the domestic yak started to expand its distribution at this same time period, with the eastern QTP as a centre of domestication (Bailey et al., 2002; Wiener et al., 2003; Qi et al., 2008). Based on whole-genome resequencing, yaks were domesticated 7,300 years ago, and the estimated population increased by six-fold 3,600 years ago. This increase was concomitant with a second human population expansion on the QTP (Chen et al., 2015; Qiu et al., 2015), suggesting that yaks enabled the early human occupation of the high-altitude QTP, and played vital roles in rangeland ecosystem, livelihoods and ethnic cultures in the Asian highlands.

Yak production follows a transhumance system, which is integrated into the local culture, and contains a wealth of traditional knowledge and experience in rangeland ecosystem management. Consequently, yaks and their grazing systems are important for the stability of the rangeland ecosystem in the Asian highlands (Degen et al., 2007; Long et al., 2008; Namgay et al., 2013; Joshi et al., 2020). This ruminant is vital for the livelihoods, social life, ethnic traditions and religious ceremonies for pastoralists, as well as for the ecology of the highlands (Fig. 1A) (Wiener et al., 2003; Rhode et al., 2007; Wiener, 2013; Joshi et al., 2020). Yaks provide more than 90% of the milk and milk products and 50% of the meat for local people, as well as hides, transport, and dung fuel (Long et al., 1999b; Wiener et al., 2003). The milk and meat provide all essential amino acids, fatty acids, vitamins and minerals required by the highlands people (Guo et al., 2014; Cui et al., 2016; Cao et al., 2018; Gu et al., 2021). Yaks account for more than 50% of the total output of animal husbandry in the Tibet Autonomous Region of China (Statistics Bureau of Tibet Autonomous Region of China, Fig. 1B).

Yaks are raised by more than 40 ethnic communities and are closely linked to their culture and religion in the Asian highlands (Joshi et al., 2020). They play an important role in cultural diversity of Asian highlands, and appear in cliff paintings and are mentioned in traditional ballads, legends and mythology. They are also used for recreational activities, such as yak racing, buzkashi and yak polo, unique traditional sports played in the Asian highlands. In addition, yaks are important to Buddhists, as horns often appear in religious activities and butter lamps using yak butter are commonly seen in Tibetan Buddhist temples and monasteries throughout the Himalayas. Yak horns are still common over the doors of houses, and yak head masks are an important part of the costume of some religious dancers in Tibet (Olsen, 1990).

Yaks play vital roles in the rangeland ecosystem, livelihoods, and ethnic cultures in the Asian highlands, and optimal production and management are vital. A better understanding of the adaptive strategies of yaks to the harsh environment would be important in improving their production and management. This review will discuss the genomic, anatomical, physiological, nutritional and behavioural adaptations and the unique gastrointestinal microbiota that enable yaks to thrive in the extremely harsh environment of the Asian highlands.

3. Genomic, anatomical, and physiological adaptations of yaks to highlands

3.1. Genomic traits

Comparative studies between yak and cattle (*Bos taurus*) provide valuable information in understanding the adaptations of yaks to the extremely harsh condition of highlands. Genomic comparisons revealed that the heterozygosity rate of yaks was approximately 1.5 time greater than that for cattle, and the yak specific gene families were over-represented in olfactory sensation, host

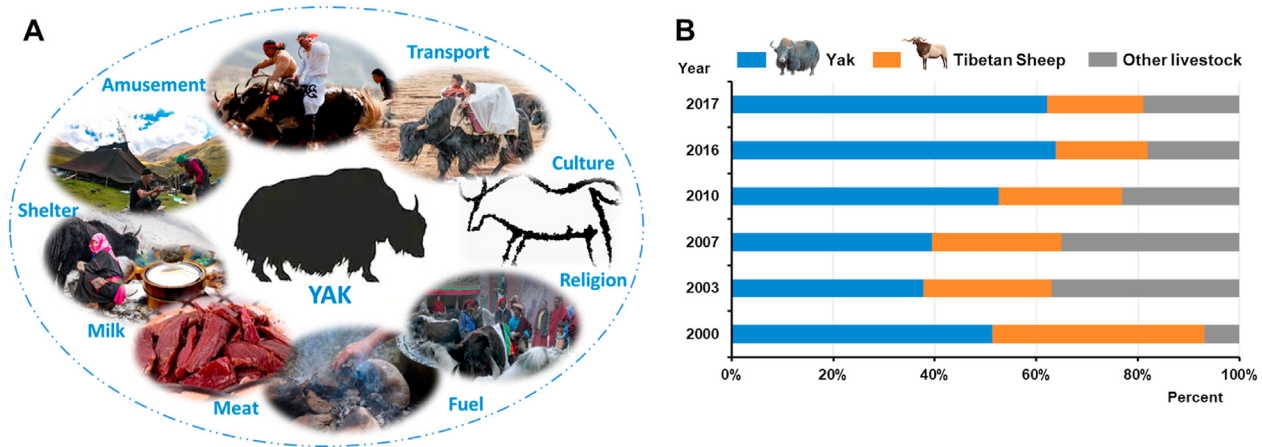


Fig. 1. The yak is crucial for livelihoods, social life, socio-economic standings and ethnic traditions for pastoralists. (A) Yaks provide milk, meat, hides, transport, and dung fuel for pastoralists, and are also important in traditional sports and ethnic culture. (B) Yaks have an impact on the socio-economic development, as yak production accounts for more than 50% of the total output of animal husbandry in the Tibet Autonomous Region of China.

defence and immunity categories (Qiu et al., 2012). In comparison with other mammals, 596 gene families were identified that were expanded substantially in yaks, and these were enriched mainly in functional categories related to sensory perception and energy metabolism, and in expansion of protein domains involved in sensing the environment and hypoxic stress (Qiu et al., 2012). Moreover, genes involved with hypoxia and energy metabolism were selected positively in yaks compared with cattle (Qiu et al., 2012). In comparison with wild yaks, the mtDNA of domestic yaks has been modified, as mitochondria are the vital producers of energy in cells and are sensitive to energy-related selective pressures (Wang et al., 2011b). In domestic yaks, the ratio of non-synonymous to synonymous substitutions in mitochondrial protein-coding genes is greater than in wild yaks, which results in a reduction in the respiratory-chain activity and, consequently, a lesser energy expenditure in skeletal muscle and in other organs (Lebon et al., 2003; Taylor and Turnbull, 2005; Wang et al., 2011b).

3.2. Anatomical traits

The body of the yak is compact (no dewlap, small ears and short limbs) with a small surface area to body mass ratio, which reduces heat loss (Hu et al., 1994; Wiener et al., 2003). The organs of yaks have evolved distinct morphological and structural characteristics to cope with the harsh environment. To cope with the extremely low air temperature, yaks have developed a thick, long outer layer of coarse wool (70 to 90 microns), an inner layer of finer wool (20 to 50 microns), and, in winter, they produce a layer of fine down wool (16 to 20 microns) that is shed in late spring/early summer. Yaks have fewer sweat glands than cattle and the reduction in sweat glands and growth of down wool enhance heat conservation in winter (Lu et al., 2013; Das et al., 2017). Yaks have a shorter tongue (4 cm, on average) than cattle, and graze forage using the *labia oris*, which minimizes exposure of the tongue to the cold environment, as well as enabling them to consume low herbage, as do sheep (Shao et al., 2010). In addition, the tongue of yaks has greater lingual prominence, and the surface has larger, more numerous and thicker keratinized lenticular papillae than cattle. The papillae enhance the mechanical function of the lingual surface and improve the efficiency of grinding food between the tongue and the upper palate, and, ultimately, increase digestibility. Moreover, yaks have less taste buds than cattle in the vallate papillae, which suggests a weaker sense of taste in yaks

than in cattle (Shao et al., 2010). This would allow yaks to consume a wider variety of plant species and, therefore, be less affected by sparse pasture than cattle.

To cope with low air oxygen content, the lung and heart of yaks have evolved distinct morphological and structural characteristics to enable a high, efficient oxygen uptake. The size of the heart and lungs of yaks are substantially larger than cattle. Yaks have 15 thoracic vertebrae, one more than cattle, which increases the volume of the thoracic cavity and provides ample space for the large heart and lungs (Wang et al., 2020). Heart weight in yaks is 1.18% of body weight as opposed to 0.39% in cattle (Hoppeler et al., 1984; He et al., 2016). The diameter of capillaries of the heart is substantially greater in yaks than in cattle (6.57 μm vs. 2.39 μm), which allows more blood flow to the heart (He et al., 2010; Noci et al., 2012). The pulmonary artery of yaks are thin-walled, with little smooth muscle and larger endothelial cells than cattle, which makes yaks less sensitive to hypoxic pulmonary vasoconstriction and allows them to withstand the low oxygen environment of high altitude (Heath et al., 1984; Durmowicz et al., 1993).

3.3. Physiological traits

Physiologically, yaks have a greatly diminished hypoxic pulmonary vasoconstrictive response, which cattle do not have, when exposed to low air oxygen content (Heath et al., 1984; Anand et al., 1986; Durmowicz et al., 1993). In addition, yaks maintain a high level of foetal haemoglobin throughout life; whereas, it is generally present in other mammals for only 6 to 7 months after the birth (Sarkar et al., 1999a, 1999b). Foetal haemoglobin has a greater affinity for oxygen, and can bind and release more oxygen than other forms of haemoglobin (Walker and Turnbull, 1955; Reece et al., 2015). Moreover, there is no right ventricular hypertrophy with aging yaks, as occurs in cattle when exposed to low oxygen. Yaks have a higher expression of hypoxia-inducible factor-1 α (HIF-1 α) than cattle in both the cytosol and nucleus of heart cells, HIF-1 α enables the heart to cope with hypobaric hypoxia (Heath et al., 1984; He et al., 2010), as it regulates physiological adaptations to hypoxia in mammalian cells by mediating the expression of vascular endothelial growth factor and vascular changes (Sogawa et al., 1998; Chávez et al., 2000; Koh et al., 2008). Furthermore, unlike other ruminants, yaks have a lower heart rate (51 vs. 78 beats/min) and metabolic rate during the cold season than the warm season (Han et al., 2002; Ding et al., 2014), while mammals

display an opposite pattern. These responses allow yaks to reduce their energy requirements at a time when available energy is low.

4. Grazing behavioural strategies of yaks adapting to highlands

4.1. Grazing behaviour

Yak pastoralists employ a grazing system that utilizes the pasture effectively and sustainably. It is a traditional transhumance system, with seasonal migrations between summer and winter pasture (Degen et al., 2007; Long et al., 2008; Namgay et al., 2013). Traditionally, the herdsman used to migrate yaks to higher altitude pastures in summer, and then move back to lower altitude winter pastures. Yaks graze rangeland all year-round, and generally, do not receive supplementary feed. As a result, their energy and nutrient intakes fluctuate greatly with seasonal forage availability and, are often below maintenance requirements for extended periods in winter. During the short growing season, there is sufficient forage for yaks, and body weight increases; however, during the subsequent cold winter, forage is sparse and there is insufficient energy and nutrients intake, and yaks can lose 25% to 30%, or even more, of body weight (Long et al., 1999b; Xue et al., 2005).

An understanding of the dynamics of feeding behaviour of grazing livestock is helpful for grazing management decisions and, ultimately, for rangeland sustainability. Ding et al. (2007) reported that forage quality and sward conditions are the main factors affecting the grazing and ruminating behaviour of yaks. To optimize nutrients intake and grazing efficiency, yaks alter their foraging behaviour with seasonal sward conditions. In winter, yaks forage mainly during the day from 06:00 to 19:00, and ruminate at night. They tend to gather in groups to reduce body heat loss and potentially defend against predator attack. In summer, with the growth of new green herbage, the grazing time increases and even extends to midnight (Ding et al., 2008). The yaks spend more time idling in winter and early spring (March and April) due to less herbage availability, and spend more time searching or lying down to avoid the cold and strong winds (Ding et al., 2008). Moreover, yaks have a higher number of bites/min (66 bites/min) in late spring when new shoots appear than in other seasons because of the reduced intake rate of dry matter (Ding et al., 2008).

Liu et al. (2019) reported that meteorological variables, such as air temperature, wind velocity and precipitation, are important in mediating the grazing behaviour of yaks. Reduced grazing activity of yaks in winter could be a strategy to lower energy expenditure for foraging and thermoregulation. In rangeland, late spring, which is an important period for sward growth, is the time of germination. During this time, yaks graze more intensively, which could lead to rangeland degradation. Proper pasture management, in particular appropriate stocking density, is essential during this period. Of interest is the soil ingestion by grazing yaks, as this allows them to meet their requirements in mineral elements. The amount of soil ingested is greater during the long, cold season than the warm season, and this greater intake coincided with the lower mineral contents in forage during winter than summer (Xin, 2010; Yuan, 2013).

4.2. Dietary selection

Identifying the dietary selection of grazing livestock can improve rangeland management, and can help in understanding the mechanisms of animals' survival and adaptation when forage is sparse. Yaks graze in three main ecosystems, alpine meadow, alpine steppe, and alpine desert, in which the composition of the herbage differs substantially (Long et al., 1999a, 2008). The

complex and diverse available herbage makes dietary selection of grazing yaks difficult to determine. Ding and Long (2010) used herbage N-alkanes to identify the main dietary components of grazing yaks in a transhumance grazing system, and the results indicated that forage consumed by yaks varied with season. Yaks consumed forbs throughout the year, but especially during the winter. For example, of the total dry matter intake in yaks, *Potentilla anserina* amounted to 26% in autumn, with *Heteropappus bowerii* to 32% and *Saussurea semifasciata* to 16% in winter. Generally, these forbs are not selected by grazing livestock due to the strong, unpleasant odor and high contents of anti-nutritional compounds. However, the crude protein levels of these plants are relatively high, which could be the reason why yaks consume these forbs, particularly during the cold season when there is limited herbage of low protein content. However, this could not explain why yaks consume forbs during the warm season, referred to as 'active choice' as opposed to 'forced choice', when forbs are consumed during the cold season. A recent study determined dietary composition of grazing yaks using DNA metabarcoding analysis, a method more accurate than N-alkanes. There were 41 plant families and 83 genera in the dietary intake of grazing yaks, and the composition was more diverse in winter than in summer (Guo et al., 2021). The yaks frequently selected and consumed forbs throughout the year, with the highest forage intakes consisting of *Polygonaceae*, *Rosaceae*, and *Gramineae* in spring and summer, *Gramineae*, *Rosaceae* and *Salicaceae* in autumn, and *Gramineae*, *Rosaceae*, and *Compositae* in winter (Guo et al., 2021). This confirms that yaks consume forbs actively, most likely for the high protein content, and suggests that the dietary selection of grazing yak could be explained by the plant's nutritive value. These findings provided important information in understanding the adaptational strategies of yak to the harsh highlands' environment, and for both herd and rangeland management.

5. Metabolic strategies of yak adapting to highlands

Efficient conversion and utilization of nutrients is the foundation for optimal livestock production, particularly under limited feed availability. After long-term adaptation, yaks have demonstrated a higher utilization of nutrients than cattle, which is characterized by 'nitrogen-saving' and 'low-carbon' traits. These responses allow yaks to cope with the fluctuating seasonal forage availability, especially with the extremely low energy and nutrient intakes during the long winter.

5.1. Nitrogen metabolism

Yaks require less nitrogen for maintenance and excrete less urinary nitrogen than cattle. In addition, yaks digest and retain nitrogen to a greater extent than cattle, especially at low dietary nitrogen intake (Long et al., 2004; Guo et al., 2012; Zhang et al., 2012; Zhou et al., 2017). For ruminants, urea is an important nitrogen source, and urea recycling plays an important role in nitrogen metabolism and homeostasis. Urea kinetics of yaks and cattle were determined by using intravenous infusion of $^{15}\text{N}^{15}\text{N}$ urea. More urea synthesized in the liver and more urea recycled to the gut in yaks than in cattle when consuming the same diets and nitrogen intakes. In addition, more recycled urea nitrogen was used by ruminal bacteria, more ruminal microbial protein synthesized and the efficiency of microbial protein synthesis was generally greater in yaks than in cattle, particularly with low dietary nitrogen intake (Guo et al., 2012; Zhou et al., 2017; Shi et al., 2020). Moreover, yaks had a lower glomerular filtration rate than cattle, which could explain the lesser urinary nitrogen excretion and greater urea recycling than in cattle (Wang et al., 2009, 2011a; Zhou et al., 2017). Nitrogen metabolism of yaks

indicated that they have a ‘nitrogen-saving’ strategy to cope with extremely low nitrogen intake during the long cold season (Fig. 2). These characteristics of nitrogen metabolism and conservation in yaks are similar to those displayed by Tibetan sheep, another indigenous livestock raised on the QTP. The similarities suggest convergent nitrogen metabolism evolved as both ruminants co-graze the rangelands of the extremely harsh Asian highlands.

5.2. Energy metabolism

Fasting heat production is lower in yaks than cattle, and, unlike most mammals, the heat production of yaks scales to $BW^{0.52}$ rather than $BW^{0.75}$ (Hu, 1992; Hu et al., 1994; Han et al., 2002). In contrast to other mammals, which increase their metabolic rate with a decrease in air temperature to maintain body temperature, yaks reduce their metabolic rate with a decrease in air temperature to conserve energy (Han et al., 2002; Ding et al., 2014). In addition, gross energy digestibility and the ratio of metabolizable energy to digestible energy are greater in yaks than cattle when consuming the same diet, particularly at low energy intake (Liu and Long, unpublished data). The low metabolic rate of yaks, especially at low air temperature, and high digestibility of forages, especially of low energy content, are adaptations to the low available forage of poor quality during the long, cold winter.

For ruminants, short chain fatty acids (SCFAs) produced by rumen fermentation are the main energy source (Bergman, 1990). Rumen fermentation of yaks produced more total SCFAs than cattle on the same diet in in vivo studies (Zhou et al., 2018) and on the same substrate in in vitro studies (Zhang et al., 2016). Yaks also emit less enteric methane than cattle under both grazing (Ding et al., 2010) and indoor feeding conditions (Bai et al., 2021; Shi and Long, unpublished data), and in in vitro measurements (Zhang et al., 2016). This reduces the amount of energy lost due to enteric methane emission and increases the metabolic energy available to yaks. Energy metabolism of yaks indicated that they have a ‘low-carbon’ strategy with low maintenance energy requirements and high efficiency of energy utilization to cope with the limited available forage and low energy intake in the winter (Fig. 3).

6. Gastrointestinal microbiome strategies of yaks adapted to highlands

The microbial community in the gastrointestinal tract plays a vital role in nutrient digestion and provision, especially for fibre digestion and microbial protein synthesis, and in the adaptation of the host to the environment (Sun et al., 2016; Zeng et al., 2017; Bang et al., 2018). Yaks possess rumen microbiome with distinct development and maturation patterns, composition, and functions, and that display unique interactions with the host.

6.1. The development and maturation of rumen microbiota in yaks

A distinct maturation strategy emerged in the rumen bacteria, archaea, fungi and protozoa in grazing yaks (Guo et al., 2020). Rumen microbiota varied with the growth stages in yaks from neonates to adults. Bacteria and archaea colonize earlier than protozoa and fungi (<7 days vs. 1 month of age), the alpha diversity of rumen microbiota increases with age but remains stable after 2 years, and bacteria and archaea are more sensitive than fungi and protozoa to changes in growth stages (Guo et al., 2020). The maturation age of rumen microbial groups in yaks were assessed using a random forest mode; bacteria, fungi and protozoa matured between 5 and 8 years and archaea at 5 years (Guo et al., 2020). This unique maturation pattern appears to be at a later age than in lowland cattle; however, it matched well with the late maturity and high-performance period of yaks, and could be a unique strategy of yaks to adapt to the limited forage availability under the harsh environment of highlands.

6.2. Composition and variation of gastrointestinal microbiome in yaks

Firmicutes and Bacteroidetes are the dominant phyla in the ruminal, intestinal and faecal microbiota of yaks, as was reported for other ruminant species (Ma et al., 2019; Xin et al., 2019; Zhang et al., 2020; Guo et al., 2021; Liu et al., 2021). Moreover, it was found that fibrolytic bacteria, such as *Ruminococcus* and *Butyrivibrio* at the genus level (Ma et al., 2019), and Ruminococcaceae at the family

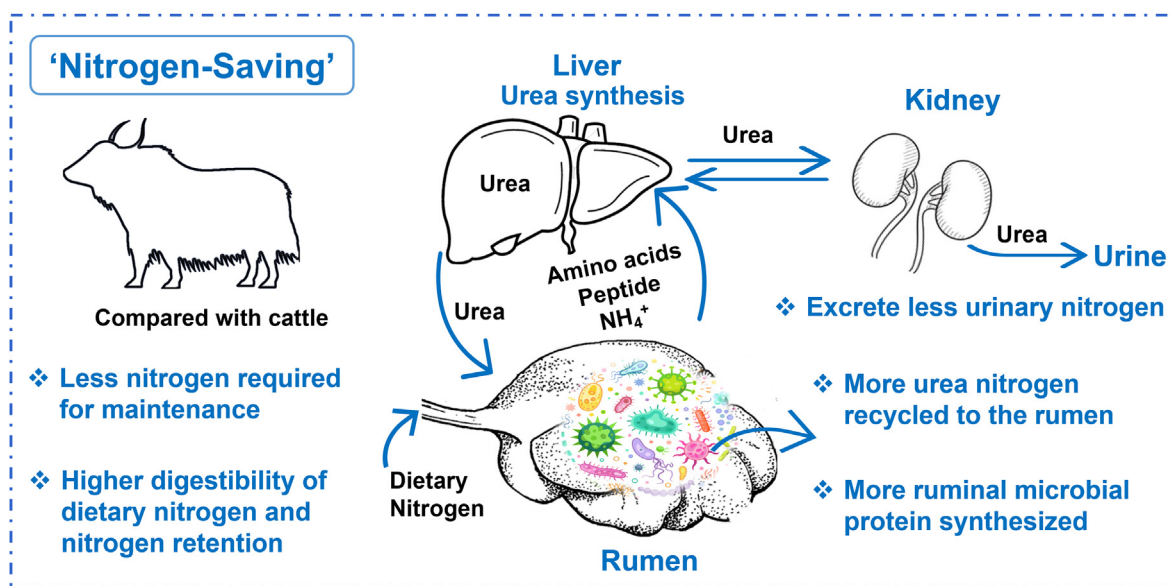


Fig. 2. The ‘Nitrogen-Saving’ strategy of yaks to cope with the harsh conditions of the Asian highlands. Compared with cattle, yaks require less nitrogen for maintenance and excrete less urinary nitrogen, digest and retain nitrogen to a greater extent, synthesize more urea by the liver and recycle more urea nitrogen to the rumen, use more recycled urea nitrogen by ruminal bacteria and synthesize more ruminal microbial protein when consuming the same diet and nitrogen intake, especially at low nitrogen intake.

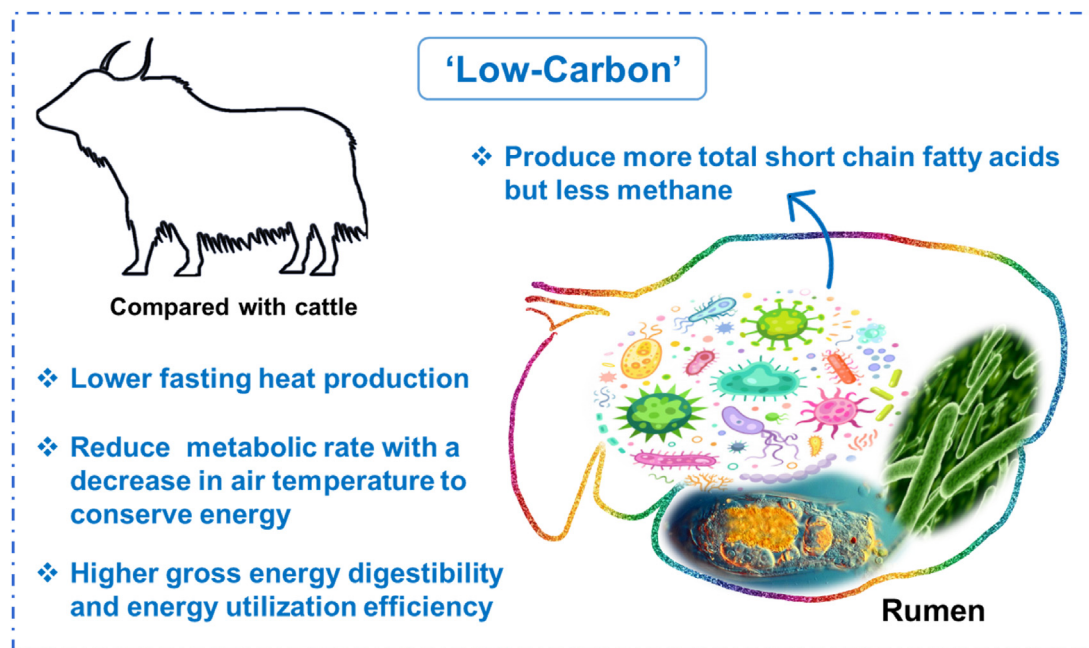


Fig. 3. The ‘Low-Carbon’ strategy of yaks to cope with the harsh conditions of the Asian highlands. Compared with cattle, yaks have a lower fasting heat production, produce more ruminal total short chain fatty acids, emit less enteric methane, digest gross energy to a greater extent, use energy more efficiently and reduce metabolic rate with a decrease in air temperature to conserve energy.

level (Guo et al., 2021; Liu et al., 2021), were the most abundant bacteria in the gastrointestinal tract of grazing yaks. This could explain, at least in part, the greater neutral detergent fiber (NDF) and acid detergent fiber (ADF) digestibilities in yaks than in cattle when both species had ad libitum access to oat hay during the cold season (Shi and Long, unpublished data). In addition, Verrucomicrobia, was identified as another dominant phylum in the gastrointestinal microbiota of grazing yaks (Han et al., 2021). Verrucomicrobia plays a vital role in plant fibre degradation, as these bacteria contain a wide array of glycoside hydrolyse enzymes (Sichert et al., 2020), and could help explain the better ability of yaks to consume low quality, high fibre forage than cattle.

Zhang et al. (2016) reported that the rumen microbial community of yaks differs consistently with cattle and other herbivores, and yaks have a higher relative abundance of *Prevotella* spp. The genus *Prevotella* is known for high SCFAs production, which could explain the higher concentrations of ruminal SCFAs in yaks than in cattle when consuming the same feed (Zhang et al., 2016). Functional analysis demonstrated that the rumen microbiome of yaks has an enrichment in enzymes for SCFAs production on the carbon fixation pathways of prokaryotes, which also explains the high SCFAs production in yaks (Zhang et al., 2016). Furthermore, the ABC transporters is the most abundant metabolism pathway in which the functional genes are enriched in the gastrointestinal microbiota of yaks, and they protect the host when consuming poisonous plants (Guo et al., 2018; Ma et al., 2019; Han et al., 2021). This enables yaks to consume forbs, which contain high concentrations of secondary compounds, such as tannin and phenols. Yaks exhibit a higher diversity and different composition of methanogen bacteria than cattle (Huang et al., 2012, 2016; Xue et al., 2016). In particular, yaks possess a high relative abundance of methylotrophic methanogens, belonging to the class Thermoplasmata. These bacteria are associated with a reduction in methane production, which contributes to the low enteric methane emission in yaks (Huang et al., 2016; Xue et al., 2016; Zhang et al., 2016). The gastrointestinal microbial composition and functions in yaks support their ‘low-carbon’ usage in energy metabolism, and provide valuable

information for ‘low-carbon’ livestock husbandry, which is being advocated worldwide to counter climate change.

Ma et al. (2019) reported that the relative abundance of rumen microbiota of yaks varied with the seasonal fluctuation of forage nutritional composition. For example, the relative abundance of *Prevotella* and some taxa associated with fibre degradation increased during the withered grass growth stage (Guo and Long, unpublished data). This increase in fibre degrading bacteria is concomitant with an increase in fibre content in forage and indicates that the rumen microbiota of yaks adapted to the seasonal fluctuation of dietary composition. The relative abundance of *Thauera* increases in the rumen microbiota in under-nourished yaks. *Thauera* provides nitrogen from fermenting nitrogen oxides and supports the yaks during a shortage of energy and nutrients (Zou et al., 2019). Furthermore, Guo et al. (2021) reported that at the genus level, the composition of faecal microbiota of grazing yaks varied with the seasonal change of dietary composition. However, the microbiota composition appeared to be more stable than changes in dietary composition, which suggests that yaks evolved a relatively stable composition of gut microbiota across seasons. Moreover, the relative abundances of *Clostridia* and *Lentisphaeria* increased in the gut with growing of yaks (from 0.5 to 2.5 years old), and these microorganisms contain a large number of genes that code enzymes related to the digestion of cellulose and hemicellulose (Nie et al., 2017). This indicates that the digestibility of plant fibre improved as yaks grew, concomitant with the increase of fibre intake after weaning.

These findings revealed distinct composition and seasonal shifts of gastrointestinal microbiota, indicating that yaks have co-evolved a unique gastrointestinal microbial ecosystem that is tightly matched with the highly fluctuating seasonal forage availability in both quality and quantity under the harsh environment.

6.3. Host-microbiome interactions

A better understanding of host–microbiome interactions can be beneficial for improving the management and production of yaks.

Different interaction patterns among rumen microbial groups have been identified throughout the lifetime of grazing yaks. A positive correlation was found between rumen fungi and bacteria, which inferred a synergistic relationship in degradation of plant fibre (Guo et al., 2020). Interestingly, a weak correlation emerged between bacteria and archaea, although, bacteria provide hydrogen and methyl compounds to archaea for growth (Guo et al., 2020). This could explain, at least in part, the low methane emission in yaks. Zhang et al. (2016) reported that the rumen microbiome and host genome showed co-evolution in yaks. The rapidly evolved genes of rumen microbiome in yaks exhibited an enrichment in carbon fixation pathways in prokaryotes, which included 9 enzymes involved in SCFAs production, while genes involved in SCFAs transport and absorption were upregulated in the ruminal epithelium in yaks when compared to cattle. In addition, gut microbiota plays an important role in the regulation of nutritional homeostasis of yaks, especially during the long, cold season, through its interaction with nutrients metabolism of the host. Guo et al. (2021) divided the gut microbiota of grazing yaks into three enterotypes according to functions, and observed that the dominant type changes among seasons. Enterotype 1 is distributed predominantly in the cold season, is dominated by *Akkermansia* and uncultured *Eubacterium WCHB1-41*, and is enriched with enzymes involved in arginine and fatty acid biosynthesis of the host. There are 12 enzymes involved in arginine biosynthesis and 6 enzymes involved in fatty acid biosynthesis; however, there is no enzyme involved in urea synthesis, resulting in a reduction in nitrogen loss through urine (Guo et al., 2021). Enterotype 2 is distributed predominantly in the warm season, is represented by *Ruminococcaceae_UCG-005* and is associated with the utilization of forage containing high protein and low fibre contents, while Enterotype 3 is distributed throughout the year and is represented by *Ruminococcaceae_UCG-010*. These findings indicate that the gut microbiota aid the host to utilize dietary nitrogen and energy more efficiently, which allows

the host to cope better with low-quality forage of low protein and high fibre contents during the long, cold season. A tight relationship emerged between yaks and their gastrointestinal microbiome, which advanced our understanding of the adaptive strategies of yaks to the harsh environment. Potentially, the information could be used to improve the productive performance of yaks by manipulating the gastrointestinal microbiome.

7. Challenges of yak to survive in the Asian highlands

7.1. Germplasm degradation

In recent decades, degradation of yak germplasm has occurred extensively, due to inbreeding and malnutrition. Body weight of adult yaks today is only about 70% of the body weights reported in the 1980s (Zhou, 2010). In 1978, the Household Contract Responsibility System (HCRS) was implemented in China, and yaks and rangeland were distributed to individual herdsmen on the QTP (Wang et al., 2010). The number of yaks in each household is relatively small, with few bulls, and this has led to increasingly serious inbreeding of yaks. In addition, the evolving geopolitics affect the transboundary of yaks between countries, which prevents the exchange of yak germplasm (Wu et al., 2016). Furthermore, seasonal malnutrition is another major factor in the degradation of yak performance. Access to germplasm is the foundation of animal husbandry production. Thus, it is urgent to make germplasm available to yak herders and to promote the exchange of yak germplasm in different regions. The exchange of germplasm between neighbours, areas and countries are fundamental to improve animal performance in addition to winter feed supplements. Technically, the genetic improvement of domestic yaks with frozen semen from wild yaks is used widely in the QTP, which has played a vital role in the improvement of yak germplasm. Today, cooperatives with large yak herds are increasing rapidly in

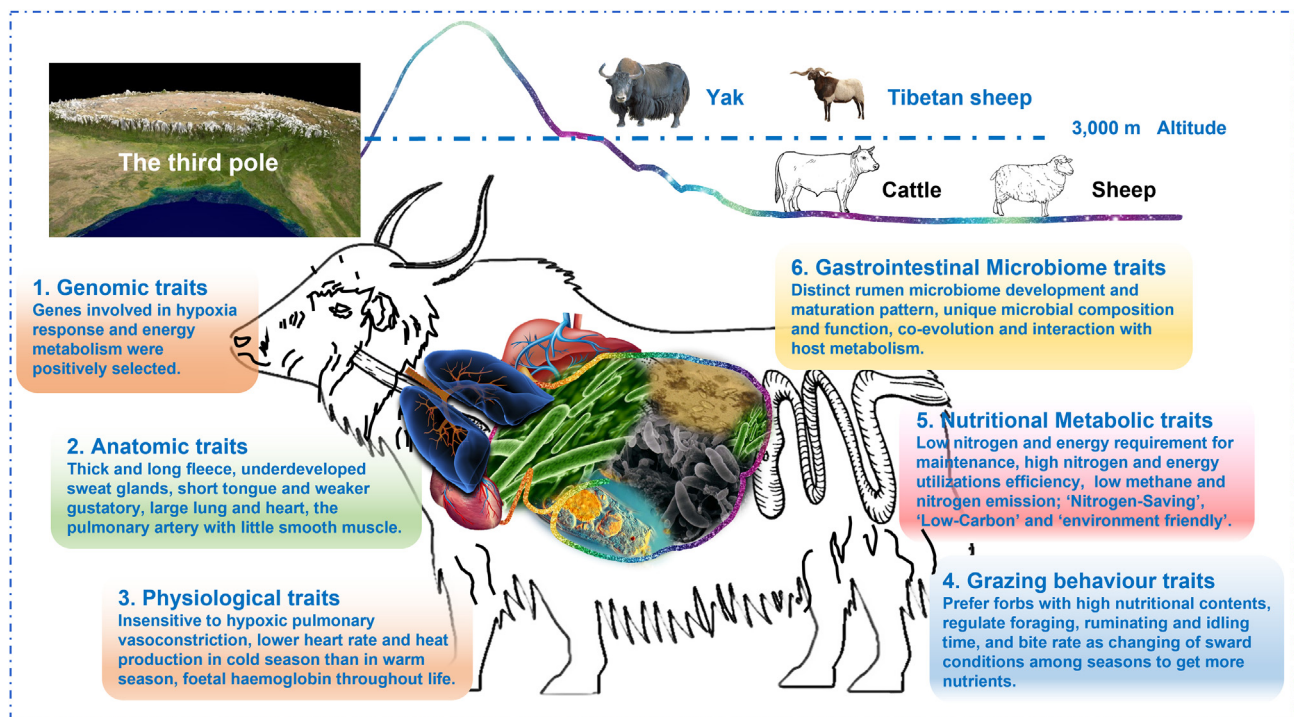


Fig. 4. The strategies of yaks that allow them to inhabit the Asian highlands. Yaks are raised at altitudes between 3000 and 5000 m above sea level across the Asian highlands. They have adapted well to the extremely harsh environment by evolving distinct genomic, anatomical, physiological, nutritional metabolic and grazing behavioural traits and by possessing unique gastrointestinal microbiota to cope with the sparse vegetation of low quality and the severe environmental conditions.

pastoral regions. Bulls from different small herds are managed together, and artificial insemination with frozen semen, is used widely. These have facilitated the gene exchange of yaks and helped prevent further germplasm degradation.

7.2. Rangeland degradation and forage shortages in winter

After HCRS policy, the number of yaks increased, resulting in higher stocking rates that the alpine rangelands could not support. Consequently, over-grazing has become a severe ecological problem for the sustainability of yak production system on the QTP. Thus, the diversity of plant species and ecosystem services have been declining as rangeland degradation (Mysterud, 2006; Long et al., 2008; Miao et al., 2015). Besides, climate change is altering rainfall patterns and is causing extreme weather events, such as droughts in summer and snowstorms in winter (Rosenzweig et al., 2001; Trenberth, 2011). These events are not only enhancing rangeland degradation but are also causing the death of a large number of animals (Long and Ma, 1996; Long et al., 1999b; Shang et al., 2012). Moreover, the ability of natural rangelands to provide forage for yaks is reduced, which is threatening the health of animals and sustainable development of the yak industry.

Therefore, restoration of the service function of the rangeland ecosystem and improvement in forage supply capacity are crucial for improving yak production (Long et al., 1999a, 2008). Controlling livestock grazing, excluding grazing, breeding local forage varieties to restore degraded rangelands, establishing artificial pastures and expanding forage sources from other areas, are being practiced. Moreover, a comprehensive and sustainable strategy should be implemented to integrate the management of rangeland-yak ecosystem. By improving the performance of individual yaks and yak products-adding value, then the number of yaks could be reduced without harming the livelihood of the pastoralists, and degraded lands could recover.

7.3. Climate change

It was reported that climate warming affected the air temperature and water distribution of the Plateau ecosystem and the animal habitat, as well as the temporal and spatial changes of transhumance on yaks (Moore, 2011; Wu et al., 2016). It is likely that the continuous or frequent high temperature in summer will affect the metabolism and grazing behaviour of yaks because of heat stress, as the yaks have a low thermoneutral zone of 8 to 14 °C (Wiener et al., 2003). Moreover, there are few studies on the strategies of yak production in response to climate change and more research is needed to address this issue.

8. Conclusions

Yaks play a vital role in the livelihood of highland inhabitants, ethnic culture and in the stability of the ecosystem. They have adapted well to the extremely harsh environment by evolving distinct genomic, anatomical, physiological, nutritional and behavioural traits, and by possessing unique gastrointestinal microbiota to cope with the sparse vegetation of low quality and the severe environmental conditions (Fig. 4). Yak industry faces considerable challenges due to rangeland degradation, the shortage of forage and germplasm degradation, and climate warming. However, the adaptive strategies of yaks to the harsh environment provide vital information for improving performance and management, especially in 'nitrogen saving' and in 'low carbon' use, and the unique gastrointestinal microbiota resources. Actions in breeding, feed supply, herd and rangeland management, improvement in value of yak products, marketing strategies, and

herdsmen education are needed in further development of the yak husbandry.

Credit author statement

Xiaoping Jing: Writing-Original draft, Investigation, Writing - Review and Editing. **Luming Ding:** Writing - Review. **Jianwei Zhou:** Writing - Review. **Xiaodan Huang:** Writing - Review. **Allan Degen,** Writing-Review and Editing. **Ruijun Long:** Conceptualization, Supervision, Writing - Review and Editing, Project administration.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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