

University of New England



**Genetic diversity, inbreeding and breeding strategies for
native goats in Central Laos**

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A thesis submitted for the degree of Doctor of Philosophy at the

University of New England in

November 2024

School of Environmental and Rural Science

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This research has been conducted with the support of the Australian Government Research Training
Program Scholarship.

Abstract

Goats are important livestock in smallholder production systems in Laos, contributing economically, nutritionally, and culturally. Most goats in Laos are native breeds, distributed throughout the country, with almost half of the population in central regions. This thesis aimed to evaluate 1) the genetic diversity and population structure 2) signatures of selection and identify the candidate genome regions and potential genes in Lao goats that are associated with production traits and adaptation 3) animal movement patterns and the degree of mixing between herds across villages and 4) village breeding strategies to improve genetic merit for Lao native goats while controlling inbreeding.

Maintaining genetic diversity in livestock is important for long-term genetic improvement in breeding programs. In Laos, concerns have arisen about the possible reduction of genetic diversity and increasing inbreeding for Lao goats in smallholder systems. In Chapter 3 the genetic diversity and population structure of Lao goats was explored using their genomic data and comparing them with 163 global goat breeds. The genomic analyses revealed a close genetic relationship between Lao goats and those from China, Mongolia and Pakistan. Results show Lao goats have moderate genetic diversity, low inbreeding and adequate effective population size, with some genetic differences reflective of geography and culture.

Domestication, selection, and breeding have produced indigenous goats well-adapted to local environments, making them valuable genetic resources. Understanding the genetic adaptations can guide the development of effective breeding strategies. In Chapter 4, the signature of selection for Lao goats was investigated, using the de-correlation composite multiple signals method. We identified 24 genomic regions harbouring 68 unique coding genes linked to adaptation to the tropical monsoon climate and economic traits such as growth and status, reproduction, milk production and carcass characteristics.

In pastoral agricultural systems, the movement and mixing of animal cohorts is important for the understanding of mating patterns in free-roaming herds or flocks, as it impacts the degree of genetic diversity and levels of inbreeding. In Chapter 5, spatial data was used to track animal movement and examine the home range and the overlap home range between different villages while genomic data was used to track animal relatedness and gene flow between herds. The results show village-specific differences in home ranges, with males covering larger areas than females, and larger ranges in the dry season. There was low to moderate gene flow between villages even with minimal home range overlap between them. Within each village, the degree of gene flow is consistent with the degree of home range overlap between herds.

Chapter 6 presents a simulation study to assess potential genetic improvement for Lao native goats and mating strategies that limit the rate of inbreeding. A mating strategy where bucks are rotated among herds or villages offered a significant body weight improvement and allowed an increasing but comparatively low level of inbreeding. The village rotational mating strategy could be implemented for isolated villages, while the district rotational strategy could benefit areas where there are accessible trade networks and minimal geographical boundaries. In contrast, traditional random mating at the herd level showed minimal body weight improvement and a significant increase in inbreeding over time.

Declaration/Certification by Author

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Publications included in this thesis

The following paper has been published:

Le S., de las Heras-Saldana S., Alexandri P., Olmo L., Walkden-Brown S.W. & van der Werf J.H.J. (2024). Genetic diversity, population structure and origin of the native goats in Central Laos. *Journal of Animal Breeding and Genetics* **141**(5): 531- 549. <https://doi.org/10.1111/jbg.12862>.

The following paper has been submitted for publication:

Le S., Alexandri P., van der Werf J.H.J., Olmo L., Walkden-Brown S.W. & de las Heras-Saldana S. (2024). Signature of selection analysis reveals candidate genes related to tropical monsoon climate adaptation and production traits in Lao native goats. Submitted for publication in the *Journal of Animal Breeding and Genetics*.

Other publications during candidature

Peer-reviewed papers

Le S., de las Heras-Saldana S., Alexandri P., Olmo L., Walkden-Brown S. & van der Werf J. (2023) Genetic diversity of domestic goats from Central Laos. In: *Proceedings of the Association for the Advancement of Animal Breeding and Genetics*, pp. 250-253, The University Club of Western Australia, Hackett Drive, Crawleg, WA 6009. <https://hdl.handle.net/1959.11/55804>

Le S. (2023). Selection index for Duroc pigs based on average daily gain, feed conversion ratio, and intramuscular fat content. *Vietnam Journal of Science, Technology and Engineering*, 65(1), 54 - 62. [https://doi.org/10.31276/VJSTE.65\(1\).54-62](https://doi.org/10.31276/VJSTE.65(1).54-62)

Le S. & Trinh H.S (2024). Genetic parameters and correlations for female reproductive performance and early growth performance of piglets in Landrace breed across various regions of Vietnam. *Canadian Journal of Animal Science*. e-First <https://doi.org/10.1139/cjas-2024-0003>

Published reports

Walkden-Brown S., Colvin A., Millar J., Hoang N., Phengsavan P., Phengvilaysouk A., Olmo L., Xaikhue T., Nguyen H.V., Nguyen X.B., Cuc N.T.K., Nga B.T., Nguyen D.V., **Le S.**, Jayasekara P., Liehr E., Nguyen C.V., van der Werf J., de las Heras-Saldana S., McNeill D., Kongmanila D. & Porsavathdy P. (2024) *Goat production systems and marketing in Lao PDR and Vietnam - Final Report*. ACIAR, Canberra ACT 2601, Australia. <https://www.aciar.gov.au/sites/default/files/2024-08/ls-2017-034-final-report.pdf>

Conference abstracts

Le S., de las Heras-Saldana S., Alexandri P., Olmo L., Walkden-Brown S.W. & van der Werf J.H.J. (2024). Selection signature analyses identify genomic footprints in Lao native goats. In Book of Abstract of 7th International Conference of Quantitative Genetics, pp. 128-9, University of Vienna, Universitätsring 1 1010 Vienna, Austria. <https://hdl.handle.net/1959.11/62029>

Le S., Moghaddar N. & van der Werf J.H.J. (2024). Genome-wide association study and its impact on the accuracy of genomic prediction for live body weights in Australian Merino sheep. In Book of Abstract of 7th International Conference of Quantitative Genetics, p. 128, University of Vienna, Universitätsring 1 1010 Vienna. <https://hdl.handle.net/1959.11/62038>

Le S., de Las Heras-Saldana S., Alexandri P., Olmo L., Walkden-Brown S.W., van de Werf J.H.J. (2023). 'Genetic diversity and inbreeding of Lao native goats revealed by genome-wide single nucleotide polymorphism markers. In Conference proceedings and program of International Conference on Sustainable Animal Agriculture in Developing Countries, pp. 52, Vientiane, Lao PDR, November 2023.

Le S. & Trinh S.H (2023). Genetic parameter for reproductive traits of genetic exchanged Landrace breed in Vietnam. International Conference on Sustainable Animal Agriculture in Developing Countries. In Conference proceedings and program of International Conference on Sustainable Animal Agriculture in Developing Countries, pp. 51, Vientiane, Lao PDR, November 2023.

Contributions by others to the thesis

Primary supervisor Prof. Julius van der Werf, co-supervisors Dr Sara de las Heras-Saldana, Dr Panoraia Alexandri, Dr Luisa Olmo and Prof. Walkden-Brown Stephen contributed to the concept and design of the project. All supervisors provided a critical review to this thesis, especially Prof. Julius van der Werf. Dr Doug Gray, Dr Ammaly Phengvilaysouk, and Dr Chay Bounphanouxay assisted in getting permission from local authorities to collect data in Savannakhet provinces and establish relationships with Lao farmers. Dr Phengvilaysouk and Mr Thaixiong Xaikhue contributed to data collection. Dr Watthana Theppangna assisted in paperwork and arranging shipments of samples from Laos to New Zealand. Prof John Mc Ewan assisted in the genotyping strategy. UNE and Crawford Fund funded scholarships and ACIAR funded the research project LS/2017/034.

Statement of parts of the thesis submitted to qualify for the award of another degree

No works submitted toward another degree have been included in this thesis.

Acknowledgements

I would like to thank my supervisors, Julius van der Werf, Sara de las Heras-Saldana, Panoraia Alexandri, Luisa Olmo and Walkden-Brown Stephen for their guidance, encouragement and support. Firstly, I would especially like to thank Prof. Julius for his wisdom, invaluable advice and patience. I deeply value our interesting conversations that ignite my curiosity and encourage my enthusiasm for genetics and statistics. Julius is not only a mentor but also like a father that I know whenever I have any sort of problem, he will be there to offer advice. Thank you, Julius, for continuously supporting and believing in me throughout my Master's and PhD studies.

Secondly, I would like to thank Sara for your unwavering support, suggestions and advice on all my chapters. You are always there, both as a mentor and as a friend, keeping me on track from day one of my journey. I also thank Rea for your support and guidance; I have learnt a lot about population genetic from you. Additionally, I am grateful to Luisa and Steven for giving me the opportunity to work on the ACIAR project in Laos and for your advice on my manuscripts, helping them reach a broader audience. To Luisa, thank you for assisting me with all the paperwork and for connecting me with an amazing team in Laos.

I would like to acknowledge the financial support provided by ACIAR, the Research and Training Program Scholarship and the Destination Australia Program Scholarship. I could not have completed this journey without those funds. I am grateful to all the farmers in Phin, Songkhone and Sepon districts who warmly welcomed me and provided the best conditions to collect the necessary data. I also thank Ammaly for his support during the data collection in Laos, and for teaching me the basic Lao during our time in the field. Ammaly - of course, I do like Lao spicy food with a cold Beerlao after work.

To my friends, Dom, Bank, Erin, Zhi, Hyoun, Mette, Viet, Chanh, Eoin and others, I owe thanks for random discussion in science, and general knowledge, and for all the colour of emotion that we have experienced together. The good moments we have shared have made this journey more enjoyable. I hope that our paths cross again in the foreseeable future. A special thanks to Dom for cheering me up during the tough times and for driving me to work for almost the past three years.

This thesis would not have been possible without the support of my family. Mom and Dad, thank you for all the emotional and spiritual support. Thanks, Mom, for your sacrificing and unconditional love. To Dad, thank you for never giving up on your cancer battles. You have shown me the true strength of a man. To my siblings, my big sister Sao and my little brother Quyet, thank for being there to take care of our family when I was away.

Most importantly, I would like to dedicate this thesis to my daughter, Le Khanh An, who passed away two years ago and could not see her dad finish the PhD. Khanh An, you are always in our hearts. This thesis is also for my grandma, who has recently passed away. Grandma, you saw me take the first walk of my life, watching me grow up, and now I have completed my PhD, but you are not here to see it. I hope you would be proud of me.

Finally, thank to my partner, Khanh Huyen. I am so grateful for your constant love, patience and understanding.

Research Details

Keywords: Genetic structure, signature of selection, mating patterns, breeding programs, Lao native goats

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Chapter One: Introduction

Livestock production in developing countries is important for farmers as a source of income and food, but it is constrained by many challenges, including low productivity, small herd sizes, land shortage, reliance on communal lands, low forage quality and availability, uncontrolled mating, and a lack of pedigree and performance recording (Gizaw et al. 2009; Gray et al. 2019). Small populations can often exhibit high inbreeding rates, which are associated with a reduction in fitness and productivity (Lynch & Walsh 1998). There is also a lack of effective, sustainable breeding programs for local breeds in low-input systems for those regions (Kosgey 2004; Kosgey & Okeyo 2007). These issues need to be studied and addressed, yet research on livestock in smallholder systems in developing countries is currently very limited (Gizaw et al. 2009; Mueller et al. 2015).

Goat production in the Lao People's Democratic Republic (Laos) makes important for livestock farming, contributing in various ways to farmer livelihoods. Goats provide meat, contributing up to 42% of total farmers' income, and also supplying manure for crop cultivation (Phengsavanh et al. 2017; Gray et al. 2019). Additionally, goats in Laos also contribute to sociocultural functions such as spiritual rituals, festivals and ceremonies (Liehr et al. 2024b; Walkden-Brown et al. 2024). However, the productive performance of Lao native goats is low compared to other local breeds, characterized by small body size, low growth rate and a high mortality rate (Gansberghe 2005; Colvin et al. 2022). Lao native goats are managed through traditional practices, where goats are typically housed at night and range freely during the day in unsegregated groups with overlapping grazing areas between herds and villages (Windsor et al. 2018). Breeding occurs throughout the year, driven by natural mating and the absence of castration or other human intervention (Olmo et al. 2022b). These practices raise concerns about the reduction in genetic diversity and an increase in inbreeding among Lao native goat populations (Gray et al., 2019). Therefore, there is a need to investigate the genetic resources of Lao native goats and prioritize strategies to increase goat production in smallholder systems in Laos.

To address these challenges, understanding the underlying genetic diversity of the current goat population is important. Previous studies have investigated the genetic diversity of goats in Asia (Chen et al. 2005; Tarekegn et al. 2019; Cai et al. 2020; Hermes et al. 2020), Africa (Tucho & Tesfaye 2004; Nguluma et al. 2018; Onzima et al. 2018; Nandolo et al. 2019; Tarekegn et al. 2019), Europe (Cañón et al. 2006; Danchin-Burge et al. 2012; Lenstra et al. 2017; Oget et al. 2019), and Oceania (Brito et al. 2017). These studies have demonstrated the characteristics of divergent goat breeds in different regions and have applied this information to design or update goat breeding or conservation programs. However, no studies have investigated the genetic variation, gene flow and genetic relatedness of the goat populations in Laos, which limits the development of informed breeding strategies or objectives.

To better understand the mating patterns between herds within a village and between villages, researchers can utilize genomic data analyses to detect the genetic relationship and gene flow or they can observe actual roaming behaviour. The rapid development of genotyping and sequencing technology has made it possible to generate genomic data which can be used to estimate genetic relatedness in animals and gene flow between populations. Analysis of genotype data can reveal genetic relatedness for individuals through the genomic relationship matrix (GRM) and the genetic distance between pairs of populations (fixation index, F_{ST}) (Lynch & Ritland 1999; Weir et al. 2006; Wang 2011). In pastoral agricultural systems, the movement and mixing of animal cohorts are important for the understanding mating patterns in free-roaming herds, as they impact the degree of genetic diversity and levels of inbreeding (van der Werf 2000). Animal movement and mixing between herds can be tracked using the global positioning system (GPS). GPS technology has been increasingly used to track animals' movement, home ranges and overlap in home ranges more effectively than routine monitoring (Urbano et al. 2010; Forin-Wiart et al. 2015; Justicia et al. 2018). An animal's home range refers to areas that the animal regularly travels to, searching for food, shelter, or mates (Burt 1943; Spencer 2012), while home range overlap indicates the degree of interaction among individuals within and between herds, which could explain disease transmission, genetic material exchanges and genetic structure between herds (Kitchen et al. 2005; Spencer 2012).

There is currently no documented breeding program for native goats in smallholder systems in Laos. Developing and implementing successful breeding programs for smallholder systems is a challenge. These programs must be tailored to low-input smallholders and they must balance high genetic gain in the short term and maintaining genetic diversity and avoiding inbreeding depression in the long term (van der Werf 2000). The village-based breeding program has been theoretically analysed and proven effective in smallholder systems (Nomura & Yonezawa 1996; Sölkner et al. 1998; Gizaw et al. 2009; Gizaw et al. 2014a). Nomura and Yonezawa (1996) provided the framework of rotational mating schemes in subpopulations and reported that this program could reduce the rate of increase in inbreeding level in the long term. The village-based breeding program was effective in selecting for body weight of Menz sheep in Ethiopia (Gizaw et al. 2014a).

This thesis aimed to assess the genetic diversity and population structure of Lao native goats, to evaluate the level of inbreeding of Lao native goats in smallholder systems, to identify candidate regions and potential genes in the Lao goat genome that help them adapt to the monsoon climate and associated with production traits, to examine animal movement patterns in different seasons and the degree of mixing between herds, and to design and implement an effective breeding program to enhance the genetic merit for Lao native goats while maintaining their genetic diversity.

Chapter Two is a review of literature that discusses 1) the characteristics of goat production and roles of native goats in smallholder systems in Laos, 2) the methods used to identify genetic diversity,

population structure, and inbreeding level by using genomic data, 3) the method and tools for detection of signature of selection, especially signature of selection in goats, 4) tracking animal movement and application of GPS in goats, and 5) methods and tools to improve genetic resources of local breeds.

Chapter Three examines the genetic diversity, population structure, and inbreeding levels of Lao native goats. It also examines the genetic relationship of Lao native goats with other goat breeds, especially goat breeds in Asia.

Chapter Four explores de-correlation composite multiple signal methods to assess the signature of selection for Lao native goats, to identify genomic regions and potential genes that allow Lao native goats to adapt to local climates and production traits.

Chapter Five examines the mating pattern of Lao native goats by using spatial and genomic data. We use GPS data to track animal movement and the overlap in the home range between herds within and between villages in dry and rainy seasons in Laos. The genomic data is used to evaluate the gene flow and genetic relatedness of animals from those herds.

Chapter Six evaluates the body weight gain and inbreeding rate in different breeding programs. We use a simulation study which reflects both traditional random mating strategies and alternative breeding programs to assess potential genetic improvement for Lao native goats. We also discuss the potential implementation of alternative breeding programs for Lao goats in smallholder systems.

Chapter Seven is the general discussion of this thesis. It covers the main findings of this study and discusses three main topics arising from this work. These are 1) sustainable improvement and conservation of local goat breeds, 2) the design and implementation of breeding programs for indigenous breeds, including alternative breeding strategies and the use of genetic evaluation tools, and 3) research limitation and future consideration.

Chapter Two: Literature review

2.1. Goat production

2.1.1. Global goat populations and products worldwide

After sheep, goats were one of the first animals that humans domesticated. Evidence shows that the initial goat domestication occurred in the Zagros mountains (modern-day Iran) around 10,000 years before the present (YBP) (Zeder & Hesse 2000; Zeder 2008; Amills et al. 2017). Goat domestication probably involved specific Near Eastern populations that survived the last glacial periods in local refugia (Colli et al., 2015). After domestication, goats spread across Europe and Africa through Neolithic farmers (Zeder, 2008). Goats are considered to have reached Asia through the Indian subcontinent using overland and maritime routes or through the Eurasian steppe belt connecting the Middle East with Northern China (Amills et al. 2017). Raising goats brought benefits for humans such as meat and milk (Aldridge et al. 2019). This has led to the world goat population steadily increasing during the last six decades. The global goat population, which was 348.73 million in 1961, increased to 1,145 million in 2022, resulting in a 328% increase over 63 years (Table 2.1). In 2022, more than 95% of the goat population in the world was from Asia (50.90%) and Africa (44.19%) (FAOSTAT 2024). The goat population in Asia has increased by 176.65% over the last six decades. This reflects that goats were in greater demand in developing countries of Asia and Africa. For many regions, goat development is related to religious practices impacting food consumption. For instance, in all Islamic countries, pork is not consumed, while beef is not traditionally consumed in India. Moreover, goats can be kept in a wide range of different environments and offer significant advantages to smallholder farmers in marginal communities. Because they can browse and digest low-quality pasture, trees and roughages, require a smaller upfront investment and provide greater financial security as they can assist with short-term cash flows (Mayberry et al. 2018). This may partly explain why a vast goat population is raised in these regions.

Table 2. 1. Goat population in five continents in 2022

Continent	The number of goats (million head)	Percentage	Countries number
Africa	506.16	44.19	54
America	23.86	2.08	17
Asia	583.12	50.90	49
Europe	27.95	2.44	57
Oceania	4.41	0.39	10
Total	1,145.50	100.00	187

Source: FAOSTAT (2024)

Raising goats has many advantages, for example, goats produce a variety of valuable products, including meat, milk, fibre, skins, and manure (Aldridge et al. 2019). Goats provide a staple resource of red meat for developing countries and goat meat has high nutritional values as it contains essential amino acids and is a good source of haem iron (Pellett & Young 1990). This contributes to the price of goat meat being consistently higher than other livestock products. Goat meat accounted for 2% of total global annual meat consumption, amounting to 4.9 million tons (Miller & Lu 2019). Developing countries produced approximately 97% of goat meat, reflecting its great importance in feeding these populations. Goat meat production is a key source of food and income for the majority of people in developing nations, particularly in rural regions (Barry & Godke 1991; Phengvichith & Preston 2011; Turner et al. 2014).

Goat milk is another nutritionally valuable goat product with dairy goats making up 20.8% of the global goat population (FAO 2018). Goat milk production was 18.7 million tons in 2017, accounting for 1.3% of the world's total milk production, while cattle produced 83.1% (FAO 2018). Jerop et al. (2014) reported that goat milk and its products reduce the risk of allergy and digestive side effects, making it preferred by some consumers, especially among children and elderly populations.

Goat milk production and consumption vary widely throughout Asia, with India, Bangladesh, Pakistan, and Turkey producing the highest volumes of goat milk (Skapetas & Bampidis 2016). India is the top producer of goat milk in the world, accounting for 32.9% (i.e. 6.16 million tons of the total global goat milk production) (Sepe & Argüello 2019). However, goat milk production tends to be limited and their goat milk is consumed raw by Southeast Asians, especially Vietnamese and Laotian people (Norton et al. 2009; Gray et al. 2019).

Guard hair and down hair are two types of fibre produced by goats and several other livestock species. Down hair (also called cashmere in goats) protects the goat from the chilly weather while guard hair shields the goat's body. The majority of cashmere production occurs in Central China (IGA 2014). Production of mohair is estimated to be around 5000 tons per year with most coming from South Africa (CFC & FAO 2008). Goat fibre production has not been reported in Laos probably because goat fibre production is not well-suited to tropical and subtropical regions with high rainfall.

Asia is the world's largest producer of skin, followed by Africa. China is the largest skin producer with a volume of 381 thousand tons per year and makes up 30% of total world production (Skapetas & Bampidis 2016). Along with these products goats also provide intangible benefits to the farmer such as savings, insurance (Herrero et al. 2012), contribution to cultural and ceremonial roles, and providing the owner some level of prestige and social status (Kosgey et al. 2006).

2.1.2. Goats in Laos

2.1.2.1. The role of goat production

In Laos, goats are one of the most significant livestock species, serving economic, nutritional, and cultural functions in smallholder production systems. They provide meat for local consumption, serve as savings and insurance by being sold for immediate cash when needed, and supply manure for crop cultivation (Gray et al. 2019). Sales from goats contributed 27 to 42% of annual household income in goat raising households in 2016 (Phengsavanh et al. 2017). Additionally, goats in Laos also contribute to sociocultural functions such as spiritual rituals, festivals and ceremonies (Liehr et al. 2024b; Walkden-Brown et al. 2024).

2.1.2.2. The increase of goat raising in Laos

The goat population in Laos has been increasing substantially over the last two decades. A 576.5% increase in the number of goats has been observed since 1999, resulting in 648 thousand goat heads by 2019 (MAF 2014, 2020). However, after the COVID-19 pandemic, the goat population in Laos was 537,860 in 2022 (FAOSTAT 2024). The annual growth of the Lao goat population was 26.83% (Table 2.2).

Table 2. 2. Population and distribution of goats by region in Lao PDR from 1999 to 2019 (1000 heads)

Region	1999	2003	2011	2017	2018	2019	Growth per annum (%)
Northern	60.1	63.3	68.9	240	252	265	10.3
Central	43.1	58.1	116	246	258	272	11.5
Southern	9.2	15.1	30.7	101	106	112	5.1
Total	112.4	136.5	215.6	587	616	649	26.9

Sources: MAF (2014), MAF (2020)

The rapid goat population growth has been attributed to increased demand for Lao goats from Vietnam (Gray et al. 2019). An estimated 90% of Lao goats are exported to Vietnam, where they receive an estimated price premium of 30% over Vietnamese cross-bred goats, due to their associated clean, green, mountain origin (Gray et al. 2019). Unlike India, Pakistan and Bangladesh, Laos and Vietnam seldom practice goat milk production, with goats being predominantly raised for meat production (Gray et al. 2019).

Goats can be found in any region in Laos, but their density varies between areas. In 2011, the goat population was concentrated in the central areas (54%), followed by Northern areas (32%) and Southern areas (14%) (MAF 2014). In 2019, the central areas hosted the largest goat population (42%), followed

by Northern areas (41%) and Southern areas (17%). The Savannakhet province, in Central Laos, has the largest proportion of Laos' goat population with 17% in 2019 (MAF 2020).

2.1.2.3. Goat production systems

Goats raised in Laos are mainly a native Lao breed with only a small proportion of goats being crossbreeds between native breeds and the Southeast Asian Mountain goat groups (Gray et al. 2019; Xayalath et al. 2021). The native Lao goat breed, *Kangbing-Katjang* (Wilson 2007), has diverse phenotypic coat colours, ranging from black, grey, brown and mixed among them (Figure 2.1). These goats have erected medium-sized ears with horns.

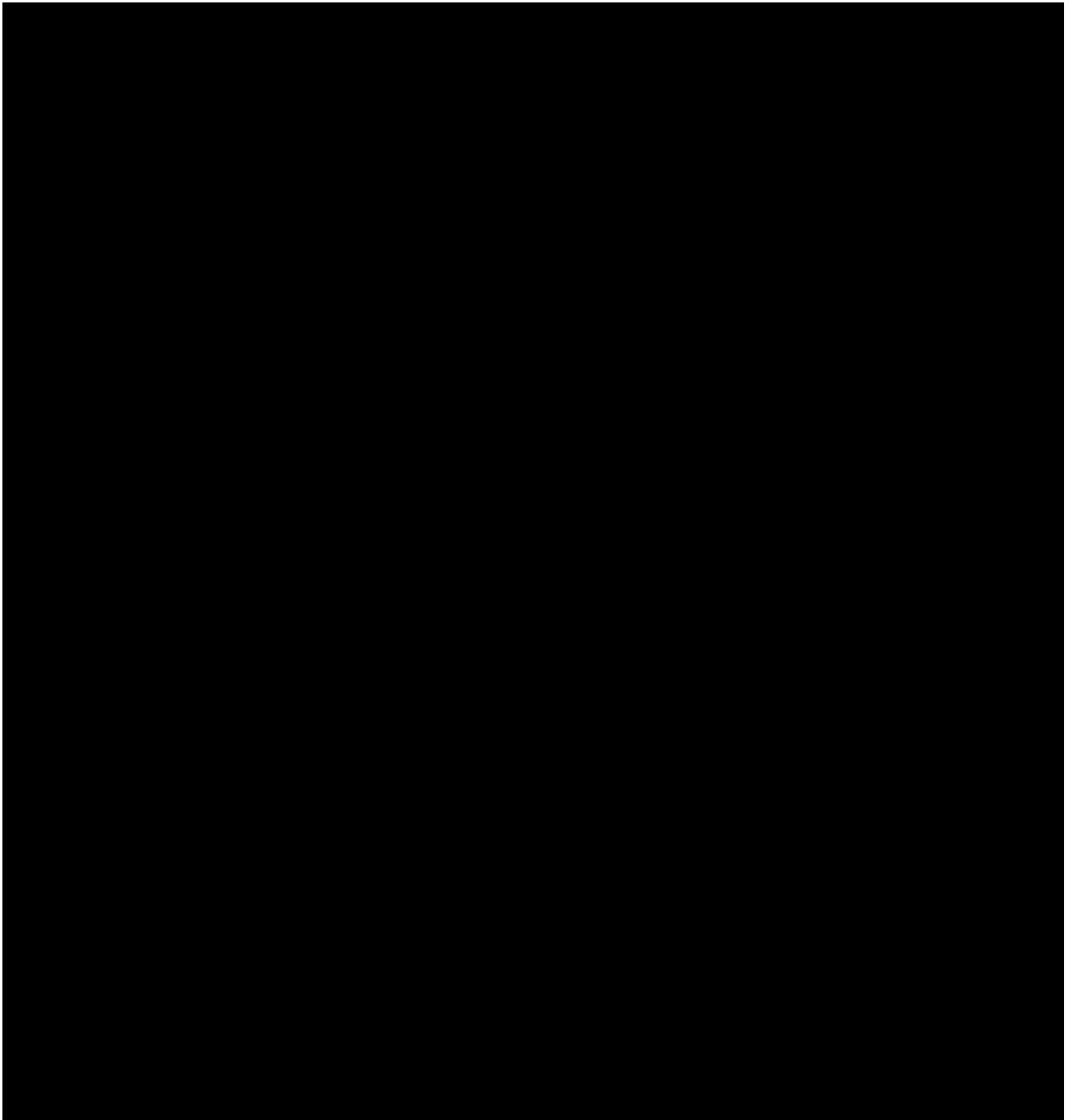


Figure 2. 1. Lao goats are phenotypically diverse

Lao native goats have a small body size. Mature weights can reach 40kg but the average adult weight is 26.8kg for females and 31.8kg for males (Phengsavanh 2003). Kids can weigh between 1.1 to 1.5kg at birth and reach 9.7kg at weaning. The kids can take 6 to 8 months to reach 15kg of body weight (Xayalath et al. 2021) and 13.4 months to reach 20 kg (Gray et al. 2019). The body size of the Lao native goat is smaller than that of other mountainous goat breeds in Southeast areas, with average mature body weight ranging from 28kg to 47.5kg (Wilson 2007; Trach & Phiovankham 2011).

Studies have reported that Lao native goats have a slow growth rate and a high rate of mortality. The average daily gain ranges between 27 to 71g/day (Phimphachanhvongsod 2001; Phengsavanh 2003). Walkden-Brown et al. (2024) reported an average daily gain for Lao goats in free grazing groups of 20.8g/d and 67.5g/d in the groups with extra-supplemented feed. Phengsavanh (2003) reported that the mortality rate of goats in Laos from birth to weaning was up to 50% in many smallholders' systems. In recent research, Colvin et al. (2022) reported a high mortality rate of 37.5% of Lao native goats in smallholder systems in Savannakhet province.

Lao native goats have a moderate reproductive performance, but data is limited to farmer recounts of productivity rather than measured data (Xaypha 2005). The age of first kidding is between 12 to 18 months (Xayalath et al. 2021). On average, does give birth to 1.4 litters per year and 1.5 kids per litter, ranging from 1.3 to 2.1 kids/litter (Windsor et al. 2018; Xayalath et al. 2021; Walkden-Brown et al. 2024). The does normally give single kids but could give birth to twins or triplets. Does can be kept in the household for up to eight years while males are generally sold at young ages (Liehr et al. 2024a; Walkden-Brown et al. 2024).

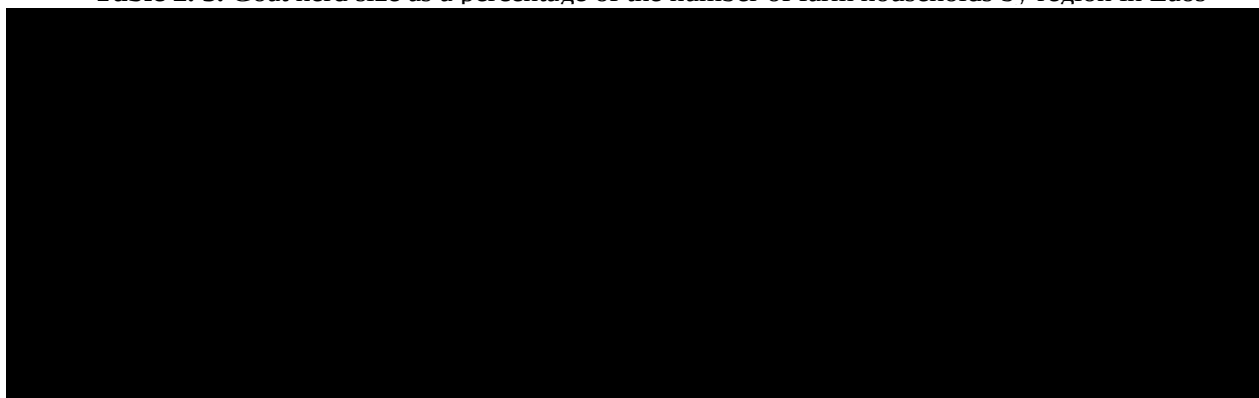
Although the majority of goats in Laos are native goats, there is a small proportion of Boer, and Bach-Thao goats and their crossbreds with local breeds in Laos. Bach-Thao, a dual Vietnamese goat breed, was introduced to Laos in 2005 and their crossbreds between Bach Thao and Lao native goats were heavier than the indigenous goats at every stage of growth (Trach & Phiovankham 2011). There is also Boer goat breed in the Northern areas which was imported from Thailand (Wilson 2007). Unfortunately, until today there are no further records that document those breeds and their development in Laos. Additionally, there are goat exchanges between Laos and Vietnam through the border but goat breeds have not been specified (Nga et al. 2021; Walkden-Brown et al. 2024).

The Lao goat production system is characterised by low input and low output (Gray et al. 2019). The industry is dominated by smallholders who generally manage small herd sizes, from 3 to 10 goats (Windsor et al. 2018). The number of goats in each household in Laos differs significantly depending on the area. The number of goats per household was from 2.2 to 3.4 goats in the Northern areas and from 12 to 16 goats in the Central areas (Gray 2004; Kounnavongsa et al. 2010). MAF (2014) noted that the average number of goats per household in the North, Central, and South regions of Laos were 4.6, 6.0, and 4.8 heads, respectively. In addition, the herd size of goat production in Laos was small.

The majority (59%) of goat raising households own less than 5 goats, 27% own from 5 to 9 goats, and 14% more than 9 goats (Table 2.3). There are concerns that these small herd sizes could lead to a high rate of inbreeding.

The number of commercial goat farms in Laos was limited (Phengvichith & Preston 2011). However, between 2017 and 2019, the number of commercial goat farms in Laos increased by 29.2%, rising from 72 to 93 farms (Xayalath et al. 2021). In 2019, there were 59 large goat farms in the Central, 18 large farms in the South and 16 large farms in the North. However, a total of 93 commercial farms only hosted 1.03% of the total goat population (Xayalath et al. 2021).

Table 2. 3. Goat herd size as a percentage of the number of farm households by region in Laos



Sources: MAF (2014)

Lao farmers typically raise goats in traditional production systems, where goats freely graze during the day and are sheltered at night (Gray et al. 2019). Lao goats are raised alongside crop enterprise, in mixed crop-livestock production systems (Xaypha 2005). Farmers use two-thirds of cultivated land to plant rice and it accounts for the major contribution to crop production in Laos (Xaypha 2005). As it is common in smallholder systems, goats in Laos are most commonly raised in free grazing, semi-rotational grazing, semi-free grazing, or permanent grazing systems (Xaypha 2005).

In free grazing systems, goats are freely grazing in communal lands or rice fields post-harvest. Goats are kept in enclosed areas during the wet season and fed native grasses through cut-and-carry methods to prevent them from damaging crops in the semi-free grazing systems. In semi-rotational grazing systems, goats are moved between fallow lands and communal pastures. In this system, while farmers own their goats individually, they often combine with goats from other herds to be managed. In the permanent grazing systems, which are rare, goats are kept fenced in the owner's property, and goats are provided salt and water. Of these systems, free-grazing is the most common in Laos and can be found in any region. Xayalath et al. (2021) noted that more than 85% of the goat production system in Laos was based on free-grazing. In these systems, goats have not been vaccinated. The goat owners lack disease treatment experience. Overall, goat management systems in Laos are traditional and have low profitability.

In this traditional management practice, goat breeding is uncontrolled and occurs via natural mating, potentially leading to inbreeding (Gray et al. 2019). Buck and does are co-reared together throughout the year without sex segregation and bucks are not castrated (Olmo et al. 2022b). Typically, Lao farmers keep 1 to 2 bucks (Gray et al. 2019) and use them to mate with other females in their herds (Liehr et al. 2024a). There was a small proportion (3.7%) of Lao farmers borrowing the buck from their friends and neighbours to mate with their goats and this practice stopped after their goats gave birth to a buck (Gray et al. 2019; Liehr et al. 2024a). These practices often result in high inbreeding which can be detrimental to animals' fitness traits (Gray 2005).

The absence of pedigree and phenotypic recording was typically observed in smallholder systems in Laos (Gray et al. 2019). No breeding programs have been recorded for Lao native goats (Xayalath et al. 2021). Therefore, it could limit the genetic improvement for Lao native goats as well as impede the management of genetic diversity and inbreeding. The farmers have practised a light selection on their goats by selecting the heavier kids at birth for the next generation (Liehr et al. 2024a).

2.2. Identification of genetic variation and inbreeding level using genomic data

2.2.1. Genetic diversity of goats

Goats were first domesticated in Southwest Asia from wild goat bezoar (*Capra aegagrus*) (Naderi et al. 2008). Like other livestock, goats followed humans on their travels after domestication and were distributed over many continents (Colli et al. 2018). Following colonisation, goats underwent evolution to adapt to environmental conditions and husbandry, including the mutation process, breeding selection by the owners, adaptability, reproductive isolation, and genetic drift. These factors have generated an immense diversity of the goat population. To date, there are nearly 600 goat breeds in the world (FAO 2018). These breeds are characterized by a variety of traits such as body size, hair (colour, type), horn (quantity, form, size), and traits related to production (meat, milk, fibre, skin).

The introduction of selection programs accelerated genetic progress for several goat breeds during the last few decades assisted through artificial insemination and embryo transfer. This results in a greater number of high-yielding exotic breeds introduced in local breeding programs which can threaten the survival of indigenous breeds through the decrease in population size and the depletion of genetic diversity (FAO 2010; Mekonnen et al. 2020). In favour of exotic breeds and their crosses, there has been a growing tendency to overlook the distinctive traits and variety given by indigenous breeds. This development has led to concerns about the dwindling of genetic resources, especially the indigenous breeds (Rischkowsky & Pilling 2007). Toro et al. (2009) highlighted the importance of indigenous breeds for future breeding programs, as their genetic variation can contribute to improve traits such as adaptability, disease resistance, or productivity, which may be valuable in current or future breeding efforts. Thus, it is increasingly acknowledged that it is critical to create conservation goals and methods to maintain genetic variation within and across breeds in order to minimize additional genetic resource

losses. Genetic variety is one of the most significant elements in determining whether a breed lives and thrives or eventually succumbs to depression and extinction.

Maintaining genetic diversity in livestock species is crucial for the genetic improvement of economically important traits and for providing the opportunity to adapt to potential changes in environmental conditions and breeding objectives. Assessing the genetic diversity and differentiation of livestock breeds can provide useful information about their evolution and develop strategies for their conservation (Bennewitz & Meuwissen 2005; Melka & Schenkel 2012). Genetic diversity information can be used to identify suitable breeding programs and strategies to achieve reachable goals for their herds and ensure sustainable genetic improvement (Lwin et al. 2018). Owners also use this information to adjust other management strategies such as diets and housing conditions for different growth stages within the breed and differences between breeds. Researchers can apply this information to control animal experiments and to investigate the interaction between breeds and the environment.

2.2.2. Measuring genetic diversity and genetic relatedness

There are two methods to estimate genetic diversity and breed composition in livestock, based on pedigree and phenotypic information (Saitbekova et al. 1999; Yang et al. 1999; Xiang-Long & Valentini 2004). These methods are comparatively cheap and simple but require accurate recording of the traits of interest and phenotypes. In developing countries, particularly in low-input smallholder systems, the infrastructure needed to consistently record phenotypes and pedigree of animals with precision is often lacking. Therefore, traditional methods to estimate the genetic diversity of the population are based on probabilistic estimates using pedigree records, and cannot be applied in developing countries (Ducrocq et al. 2018). An alternative is the use of molecular markers, especially microsatellites and Single-nucleotide polymorphism (SNPs) that have been widely applied to estimate the genetic variation within and across breeds in the last two decades. SNPs provide more advantages than microsatellite markers as they can be used in panels with increased density and their results are highly repeatable. Decreasing genotyping costs allowed SNPs to be the marker of choice for an increasingly large amount of genetic diversity studies both in domestic and wild animals.

In genomic best linear unbiased prediction (BLUP) of breeding values, information on relative performance can be incorporated through the genomic relationship matrix (GRM). The GRM can be constructed from different densities of SNP data, from low marker density to whole genome sequence and it explains the underlying covariance structure among individuals because it is based on estimations of actual relationships rather than expected relationships (Hayes et al. 2009b). In a GRM, higher estimates indicate closer genetic ties than average, while negative values suggest less relatedness. There are several methods to build the GRM, such as the Wang (2002) approach, the approach of Lynch (1988), and that of Queller and Goodnight (1989). The most popular methods for forming the GRM

were described by VanRaden (2008) and Yang et al. (2010). These methods construct the GRM using identity-by-state (IBS) data, scaled by allele frequencies.

Assessing the genetic diversity of a population most commonly involves the estimation of the F-statistic and Wright's fixation index. These parameters include the inbreeding coefficient (F_{IS}) of a population, pairwise fixation index (F_{ST}) between populations, and overall fixation index (F_{IT}). These indicators are proportional to the amount of heterozygous genotypes (heterozygosity) present at different levels of the population. F_{IS} measures the average decrease in an individual's heterozygosity caused by non-random mating within a subpopulation. F_{IS} can be calculated from the observed heterozygosity (H_0) and expected heterozygosity (H_E). The value of F_{IS} ranges from -1 (all individual heterozygous) to +1 (no observed heterozygotes) (Wright 1965). F_{IT} represents the correlation between gametes within an individual compared to the overall population, and F_{ST} is the correlation between gametes chosen randomly from within the same subpopulation overall population. F_{ST} values are classified into low genetic distance (0.00-0.05), moderate (0.05-0.15), high (0.15-0.25) and exceptional (>0.25) between populations (Wright 1978).

Additionally, the concepts of relatedness and gene flow are important in population genetics (Wright 1921) and have significant implications for quantitative genetics, conservation biology, evolution, and ecology (Weir et al. 2006). Genetic relatedness between individuals occurs because they share a common ancestor. Related animals have more similar genotypes at each locus because their alleles are more likely to be identical by descent than those of unrelated animals (Weir et al. 2006). Gene flow within and between herds or populations can contribute to genetic relatedness when animals or their genetic material are transferred from one group to another (Wright 1921).

The rapid development of genotyping and sequencing technology has made it possible to generate genomic data which can be used to estimate genetic relatedness in animals and gene flow between populations. Population genetic analysis based on genomic data has become widely applied in genetic studies of various plant and animal species (Lynch & Ritland 1999; Weir et al. 2006; Wang 2011). Genetic relatedness is measured using a genomic relationship matrix (GRM), where higher estimates indicate closer genetic ties than average, while negative values suggest less relatedness. Additionally, gene flow between herds or populations is quantified using the fixation index (F_{ST}), which ranges from 0 (indicating complete sharing of genetic material) to 1 (indicating no sharing of genetic material) (Wright 1984).

The availability of the Illumina Goat 50K SNP BeadChip, as a result of recent advances in genomic technologies, has provided an opportunity to look for genomic areas that may have undergone selection (Tosser-Klopp et al. 2014). Several studies to understand the genetic variation of local and international goat breeds were conducted in Asia (Chen et al. 2005; Tarekegn et al. 2019; Cai et al. 2020; Hermes et al. 2020), Africa (Tucho & Tesfaye 2004; Nguluma et al. 2018; Nandolo et al. 2019; Tarekegn et al.

2019), Europe (Cañón et al. 2006; Danchin-Burge et al. 2012; Lenstra et al. 2017; Oget et al. 2019), and Oceania (Brito et al. 2017). These studies have demonstrated the characteristics of divergent goat breeds in different regions and used that information to design and modify goat breeding and conservation programs. There have been no genetic studies on Lao native goats, therefore to implement the breeding program of goats in Central Laos, it is essential to first assess the genetic diversity of the current goat breeds as it provides essential information for establishing a suitable breeding program.

2.2.3. Inbreeding and runs of homozygosity

Inbreeding is technically defined as the mating of closely related animals in the population (Wright 1922). It results in the chance of two alleles in an animal being identical-by-descent (IBD), which is higher than in a base population where all alleles are believed to be unrelated. When an offspring is inbred, it is possible to observe IBD autozygous chromosomal regions inherited from both parents. Inbreeding usually results in a drop in overall performance manifested in a variety of ways. Poor reproductive efficiency, increased mortality rates, and reduced growth rates are the most visible repercussions of inbreeding (Bjelland et al. 2013; Gurgul et al. 2016). The amount of performance loss is proportional to the degree of inbreeding and its impact can be different depending on the species and traits.

The level of inbreeding is generally indicated by the inbreeding coefficient. Inbreeding coefficients derived from genomic data, such as F_{IS} (described above) and F_{ROH} , are important indicators of genetic diversity and the degree of inbreeding. F_{ROH} is based on estimates of the fraction of the total length of continuous homozygous segments (runs of homozygosity, ROHs), in the total length of autosomes, which is increased due to inbreeding (Purfield et al. 2012). The F_{IS} parameter estimates the average decrease in heterozygosity of individuals due to non-random mating within a population (Wright 1965; Peripolli et al. 2017). Keller et al. (2011) demonstrated that F_{ROH} is closer to true inbreeding than F_{IS} .

In recent years, ROH analyses have been extensively employed to study genetic diversity reporting recent and ancient inbreeding in various livestock species (Muir et al. 2008; Makina et al. 2014; Al-Mamun et al. 2015; Munoz et al. 2019). The frequency of ROH offers a deeper understanding of the population's demographic history and how it has been managed over time. ROH usually arise from the transmission of identical haplotypes from each parent to offspring (Purfield et al. 2012) and its accumulation in the genome can have significant impacts on overall biological fitness (Manunza et al. 2016). The length of ROH is significant, with long ROH illustrating recent inbreeding which can be caused by a decrease in population size, unbalanced paternal contribution, and selection. Short ROH is derived from older common ancestors. Because recombination events reduce the likelihood of an individual having two copies of the same long haplotype, the rate of local recombination is negatively associated with ROH frequency (Pemberton et al. 2012). Selection is another key factor that can

increase homozygosity. Intensive selection to increase interested traits can also reduce the difference in regions of the genome (Zavarez et al. 2015).

In domesticated animals, the first ROH research was conducted in cattle by Sölkner et al. (2010), and in swine by Bosse et al. (2012). The research of Bosse et al. (2012), and Saura et al. (2015) on ROH in pigs illustrated the population relationships and historical demographic events effects on inbreeding on homozygosity and inbreeding depression. In sheep, the study on population structure using ROH was presented by (Beynon et al. 2015). In goats, characterized ROH patterns and $F_{(ROH)}$ were presented in previous studies (Cardoso et al. 2018; Onzima et al. 2018; Nandolo et al. 2019; Deniskova et al. 2021).

2.3. Signature of selection

2.3.1. The goat dispersion and signature of selection

Animal domestication has played a crucial role in human demographic and cultural development. The important evolutionary forces acting along with domestication such as genetic drift, natural and artificial selection have produced an immense diversity of livestock populations observed today (Diamond, 2002). Goats were one of the first livestock species to be domesticated from wild goats (*Capra aegagrus*) in the Zagros mountains in modern-day Iran (Zeder & Hesse 2000). Following the initial domestication, goats were dispersed by humans to different parts of the world.

In addition to domestication, both natural and artificial selection played a crucial role in shaping the dominant goat breeds today. These selections tend to cause changes in specific genomic regions that control the particular breed characteristics such as morphology, body conformation, production performance, reproduction, behaviour, adaptation to different environments, and resistance to diseases (Saravanan et al. 2020). To date, there are nearly 600 goat breeds in the world (FAO 2018). These breeds are characterized by a variety of traits such as body size, hair (colour, type), horn (quantity, form, size), and production (meat, milk, fibre, skin) (Aldridge et al. 2019).

In the adaptation process, each breed is adapted to particular environmental and management conditions. These populations are gradually evolving with more animals with favourable alleles which transfer from one to another generation. Positive selection pressure leads to an increase in the frequency of advantageous alleles, resulting in unique signatures within the genome (Nielsen, 2005; Jensen et al., 2016). These alleles are left in the genomic regions which are subjected to selection.

A selection signature refers to unique patterns left behind in genomic regions subjected to natural or artificial selection (Nielsen, 2005; Jensen et al., 2016). The detection of selection signatures provides opportunities to find the selected genomic regions and genes related to economic traits, provide insights into functionally important genetic variants and understand the history of a particular goat population (Saravanan et al. 2020).

2.3.2. Methods and tools used to detect signature selection

The available genomic data that has been generated using SNP analyses and the comparison of genomic patterns of SNP variation between divergent breeds has successfully identified putative genomic regions and genes associated with differences in selection pressure in various livestock species (Ai et al. 2014; McRae et al. 2014; Stainton et al. 2015; Zhao et al. 2015). Various approaches have been proposed and applied to detect the signature of selection in livestock wild animals (Saravanan et al. 2020). These approaches can be classified into inter and intra-population statistics (Saravanan et al. 2020).

Intra-population statistics detect the selection footprint in genomic regions within the population while inter-population statistics search for candidate regions in genomic data by comparing the differentiation of specific loci allele frequency between the populations (Zhao et al. 2015). A comprehensive review of differential methods for inter- and intra-population statistics methods of detecting the signature of selection was published by Saravanan et al. (2020), who discussed the pros and cons of each method as well as the tools to detect them. Briefly, three main approaches for inter-population statistics can be used, including site frequency spectrum, linkage disequilibrium and reduced local variability. These approaches are based on the distribution of allele frequencies in a population, homozygous regions with haplotypes of high frequencies, and genomic regions with reduced variation relative to the genomic average (Saravanan et al. 2020). Additionally, two main approaches for intra-population statistics, include single-site differentiation and haplotype-based differentiation. These approaches are either based on the differences in allele frequencies between populations (F_{ST}) or based on the haplotype information from multiple populations.

Different approaches use different tools to look at different aspects of the signature of selection in genomic data. Examples include the detection of ROHs and the calculation of F_{ST} . ROH is an intra-population statistic describing regions in the genome containing contiguous segments of homozygous loci that are IBD (Ferenčaković et al. 2013). Natural or artificial selection increases the homozygosity in the targeted genomic regions and leads to the occurrence of ROH (Pemberton et al. 2012). Therefore, genomic regions with high ROH frequency can be used to detect the association between genes and traits selected within a population (Ferenčaković et al. 2013; Szmatoła et al. 2016; Saravanan et al. 2020). F_{ST} is an inter-population statistic that uses differences in allele frequency to infer the genetic differentiation between populations or generations (Weir & Cockerham 1984) and also high F_{ST} values can be used to detect signatures of selection (Holsinger & Weir 2009). The cross-population extended haplotype homozygosity (XP-EHH) statistic assesses disparities in haplotype between two potentially divergent populations, in which the selected allele has approached or reached fixation in one population while remaining polymorphic in another (Sabeti et al. 2007).

Using individual statistical tests (applying either F_{ST} , ROH, or XP-EHH) often produces inconsistent results (Lotterhos & Whitlock 2015; Schlamp et al. 2016). The discrepancy may be attributed to factors such as varying sensitivity to sampling methods, specifics of the selective sweep, and the demographic background of the populations being studied (Lotterhos & Whitlock 2015; Schlamp et al. 2016). To tackle these challenges, a common strategy is to prioritize selection signals detected by multiple individual statistical tests (Lotterhos & Whitlock 2015; Wang et al. 2016; Mastrangelo et al. 2020), although this approach may lead to the loss of some loci that show weak signals (Lotterhos & Whitlock 2015; Ma et al. 2015). Consequently, methods have been developed that combine p -values of different statistical tests (Randhawa et al. 2014; Ma et al. 2015). One of these is a de-correlated composite of multiple signals (DCMS) method (Ma et al. 2015). Ma et al. (2015) observed that DCMS enhanced the resolution of selection signature mapping and improved the ability to detect selection signals compared to most statistical tests by themselves. Furthermore, composite measures of selection, like DCMS, have been demonstrated to more accurately identify the causal variant (Lotterhos et al. 2017).

2.3.3. Signatures of selection in goats

Following the successful development of genomic approaches and tools for signatures of selection in humans and cattle, there is an increasing effort to develop these studies in goats (Brito et al. 2017; Bertolini et al. 2018b; Waineina et al. 2022). These studies have identified candidate regions and potential genes that are associated with adaptation to particular environmental conditions or linked to production traits.

Previous studies have identified regions associated with adaptation to specific environmental conditions for Barki goat in Egypt, and Tibetan goat in China (Kim et al. 2016; Jin et al. 2020). While the Karki goats are adapted to hot and dry climates in Egypt, the Tibetan goats are adapted to high-altitude environments in China. Other studies have revealed candidate regions and genes that are linked to immune functions in various goat breeds (Kim et al. 2016; Talenti et al. 2017; Yao et al. 2023). Eloiflin et al. (2021) reported genes against the Peste des petits ruminants in goats. Henkel et al. (2019) described genes associated with survival in Pakistani goats. Onzima et al. (2018) revealed genes that are associated with immune response and thermotolerance in six Uganda goat breeds.

Several studies have detected candidate regions and genes associated with production traits such as carcass, milk and fibre production (Brito et al. 2017; Bertolini et al. 2018b; Waineina et al. 2022), and reproduction traits (Lai et al. 2016; Brito et al. 2017). Selection signature studies in goats also found regions containing genes influencing coat colour, body size, lipid metabolism, energy metabolism and thermo-tolerance (Kim et al. 2016; Bertolini et al. 2018b; Yao et al. 2023).

2.4. Animal tracking technology as a tool to inform breeding management in developing countries

2.4.1. Interpreting gene flow through home ranges

The distribution and consumption of resources such as time and place can be better understood by determining the animal's home range. Home ranges are defined as the locations where an animal spends its adult life in pursuit of food, mating, and caring for offspring, excluding seasonal migration and forays outside of the normally travelled areas (Burt 1943). A commonly recognized definition of an animal's home range is the smallest area associated with a 95% probability of finding the animal (White and Garrott 1990).

The location of an animal during the day or seasons provides the primary unit of movement pathways and shows where animals interact with the environment around them (Cagnacci et al. 2010). Those interactions eventually determine animal capability (Nathan et al. 2008). Animal location will help biologists, conservation managers, or farmers understand animal ecology and behaviour. It is feasible that intensive movement sampling, along with thorough information on habitat elements at various scales, may enable us to visualize an animal's cognitive map of its environment, as well as the close link between behaviour and fitness (Dore et al. 2020). Animal tracking can allow researchers to assess animal movements across the landscape, geographic heterogeneity of field occupation by animals, grazing habits, animal performance, behaviour, and social ties within a herd (Cagnacci et al. 2010; Forin-Wiart et al. 2015; Dore et al. 2020). Visualising grazing behaviour assist with grazing management by revealing the amount of land available for animal nutrition. Distances and speeds travelled by the animal, including the amount of time spent lying down, grazing, and the number of hours during the day when the animals are unable to either feed or lie down, indicates how much energy is expended, allowing nutritionist to optimise diets.

Traditionally, animal tracking has relied on researchers making observations in the field, which is time-consuming, and has the potential to influence animal behaviour (Cooke et al. 2004). Nowadays, animal tracking technology with GPS devices allows researchers to collect substantially larger spatial location data sets with greater precision to measure an animal's utilization distribution (UD). This is the probability distribution of the animal's use of space (Van Winkle 1975). The UD provides a useful summary of space use for a given individual, and therefore, UD has been considered a key parameter in other types of analyses using telemetry data. Marzluff et al (2001) reported that UD may provide the most informative measure of habitat use in animal selection studies.

Home-range overlap indices are useful in animal research and management for a variety of reasons including determining the degree of interaction between individuals as well as a group's site fidelity. Furthermore, overlap measures can be used to assess the accuracy of various home range estimators (Fieberg and Kochanny 2005). In recent years, the studies in home range overlap or sharing of space

between animals, or between the same animal at different times, has risen. When simultaneous observation of animal locations is available, it is possible to assess the degree of dynamic interaction between individuals by comparing the temporal sequence of their movement patterns (Kernohan et al. 2001).

2.4.2. Application of GPS in investigating livestock behaviour

A global position system (GPS) is defined as a navigation system using satellites, a receiver, and algorithms to synchronize location, velocity, and time data. GPS technology can be battery operated, working 24 hours a day, 7 days a week, in almost any weather. It has been used to determine the location, navigation, mapping, and time of measurements. GPS was first introduced in 1973 and used by the United States military, before being adapted for animal tracking in 1994 (Gaur et al. 2013). GPS technology now has been used successfully to track domestic sheep, and cattle as well as numerous wildlife species (Edenius 1997; Douglas-Hamilton 1998; Dore et al. 2020). GPS technology is usually worn by the animal on a collar. To review and collect that recorded tracking data, the collars are manually removed, and stored data is downloaded, allowing retrospective monitoring of animal movements.

Over the last two decades, GPS collars have significantly improved in both quality and quantity. Even under humid tropical conditions in many developing countries, these devices can now frequently capture GPS data and pinpoint the location of a collar with great precision (Moriarty & Epps 2015). It is now possible to collect spatiotemporal data automatically and on a predetermined schedule using GPS collars, making systematic collection of location data less impacted by topography and surrounding foliage, which can limit observers' ability to track animals and directly record their positions, resulting in more reliable data (Reyna-Hurtado & Chapman 2019). Data analysis programs can calculate distance between GPS coordinates, which provide information about speed, periods of activity vs. inactivity, and elucidate nocturnal activity in diurnal species, and data collection devices are now capable of collecting data on variables such as temperature, elevation, and acceleration (Isbell et al. 2017).

The data can be downloaded directly from a satellite or from a memory card that is inserted in GPS collars. To assure accuracy, this data can be examined, sorted, and statistically analysed (Frair et al. 2010).

2.4.3. Application of GPS in animal genetics studies

GPS data was used by livestock experts to better understand behavioural variations in free-grazing tests. The problem of guaranteeing the experimental unit's independence arises as the attention shifts from the environment to the animal. The application of spatial modelling approaches to GPS data allows researchers to assess the degree of independence of data acquired from a single animal in behaviour-

based investigations. Using position and movement information acquired from GPS data, researchers were able to estimate the environmental impact of grazing animals as well as to measure animal responses to management operations or environmental disturbances. The ability to identify landscape avoidance and selection behaviours is increased by combining satellite-derived remote sensing data with GPS-derived landscape preference indices.

Another possible application of GPS tracking is to monitor breeding and mating behaviour in animals. The whereabouts of adult working males could be tracked to ensure they stayed in their allotted pasture, and managers could be notified if breeding males strayed from their chosen herds and pastures by a sophisticated monitoring system (Forin-Wiart et al. 2015; Dore et al. 2020). The precision and efficacy of planned mating systems based on natural service and various breeding pastures would be improved with this technique. In addition, GPS or real-time tracking might be used to monitor animals in large, mountainous pastures and alert management if females were grazing in locations where there were no adult working males during the breeding season. Males and females may become isolated throughout the breeding season in large and rugged pastures, which may minimize mating close relatives and lower inbreeding rates. Oestrus detection is another possible application of animal tracking, where female grazing rangelands could be identified in oestrus through a combination of tracking and accelerometer monitoring.

2.5. Genetic improvement for indigenous goat breeds

Genetic improvement of livestock can be done through selection in a breeding program. Local goat breeds are typically well-adapted to local environment and regional management systems. They present valuable genetic resources to improve farmers' likelihood (FAO 2010). However, the indigenous breeds are generally characterized by smaller body sizes, and slower growth rates compared to commercial breeds (Haile et al. 2023). Achieving success in genetic improvement requires careful planning, implementation, and maintenance of appropriate breeding programs.

Breeding programs are complex processes designed to enhance animal performance for traits that align with specific breeding objectives. The initial step in designing a breeding program is to define clear and realistic breeding objectives (van der Werf 2000). These objectives can be established at national or regional levels, reflecting long-term development goals and specific needs of the areas and markers. At the state level, these objectives should align with the agricultural policies, market demands, and production systems (FAO 2010). At a regional level, these breeding objectives focus on improving traits tailored to the local production environment (Philipsson et al. 2011). Additionally, these objectives must reflect the needs, perspectives and preferences of farmers (Mueller et al. 2015; Haile et al. 2023). A lack of farmer participation in defining objectives has been a significant cause of the failure of many livestock improvement programs, particularly in tropical regions (Kahi et al. 2005; Duguma et al. 2011; Haile et al. 2023). Therefore, these objectives must be supported by the farmers/communities (Kosgey

et al. 2006). Various tools, such as structured surveys, choice experiments, group and individual rankings, bio-economic analyses, or combinations of these methods, can be used to define breeding objectives (Duguma et al. 2011; Haile et al. 2023).

The next critical step in a breeding program is data recording and genetic evaluation. Accurate data recording enables the identification of superior animals, and greater data availability improves selection accuracy and genetic gain (van der Werf 2000). However, in smallholder systems, indigenous breeds often lack performance and pedigree records, unlike commercial farms in developed countries (Gizaw et al. 2014b; Gray et al. 2019; Haile et al. 2020). To initiate data recording, two key questions arise: which traits should be measured, and which animals should be recorded (van der Werf 2000). The choice of traits depends on the breeding objectives, the cost of measurement, and the relative importance of the trait. Data recording is not necessary to record all animal performance in each household; instead, a representative subset of the population can be targeted. If resources are limited, trait measurement may be confined to a small group of animals, e.g. only nucleus animals are measured. When starting from scratch, a part of the population could be measured, usually consisting of a group of ‘progressive farmers’. Such a group will automatically form the nucleus. Cost-benefit analyses can assist in deciding how many animals should be recorded for optimal genetic improvement.

The data recording is then used for genetic evaluation. Animal performances are transformed into estimated breeding values (EBVs). Pedigree records are used to establish genetic relationship matrices, but in smallholder systems where pedigree data is often unavailable, genomic data can provide an alternative (Mrode et al. 2018; Burrow et al. 2021). Advanced statistical methods, such as Best Linear Unbiased Prediction (BLUP), genomic BLUP, and single-step GBLUP, are widely used for genetic evaluation (Henderson 1985; Meuwissen et al. 2001; Hayes et al. 2009a; Misztal et al. 2009; van der Werf 2013). These tools are essential for accurately estimating EBVs, and GEBVs, and optimizing selection strategies. The effectiveness of genetic evaluation depends on the quality and availability of data, including phenotypic, pedigree, and genomic information, as well as the suitability of the statistical models used.

The selection criteria are directly linked to the breeding objectives. In the mating structure, all selected bucks and does are mated to improve productivity. Genetic improvement for indigenous breeds can be achieved through within-breed selection or by crossbreeding with exotic breeds.

2.5.1. Utilize exotic germplasm to improve the performance of indigenous goat breeds.

Crossbreeding with exotic germplasm can increase genetic diversity in a population but often comes at the cost of losing part or all of the original indigenous genetic diversity (Polak et al. 2022). The introduction of exotic germplasm has been shown to enhance genetic improvement in local breeds in pigs (Phuc et al. 2010; Ph  m et al. 2018), and cattle (Mekonnen et al. 2020). In goats, the Boer goat

breed has been used to improve the body weight of Central Highland goats in Ethiopia (Tesema et al. 2021). In Brazil, goat breeds from Portugal, Spain, and Asia were introduced to increase the productivity of local goat breeds (Lôbo et al. 2010). In Vietnam, the Co goat was crossbred with bucks from India and New Zealand to improve body size and carcass traits (Binh & Lin 2005; Norton et al. 2009). Similarly, the Bohuai goat in China was developed by crossing the local Huai goat with Boer goats, resulting in improved growth rate, reproduction, and meat quality traits (Barry & Godke 1991; Yao et al. 2023).

Despite these successes, crossbreeding programs face significant challenges. For instance, in Ethiopia, crossbreeding indigenous goats with exotic breeds such as Saanen, Toggenburg, and Boer did not result in genetic improvement (Chiemela et al. 2015). After 27 years of crossbreeding programs supported by Non-government organizations (NGOs) and the Ethiopian government, Boer x Konso crossbreds were reported to be less productive than the indigenous goats (Dessie et al. 2014). In the intensive review of small ruminant breeding programs in the tropics, Kosgey et al. (2006) concluded that the performance of crossbred animals in smallholder systems is low. This could be explained by poor adaptation to the local environment of exotic breeds, lack of infrastructure, and limited farmer motivation (Kosgey et al. 2006; Haile et al. 2023).

2.5.2. Within-in indigenous breed selection

An alternative to crossbreeding is within-breed selection, which focuses on genetic improvement while maintaining the unique characteristics of indigenous breeds. There are several breeding programs were designed to improve the indigenous breeds, including nucleus breeding programs, cooperative village or village-based breeding programs (CBBP), centralized nucleus breeding programs at research stations (CNBP), and combined nucleus-village breeding programs (Galal 1986; Sölkner et al. 1998; Kosgey 2004; Gizaw et al. 2009).

Nucleus breeding programs have been proposed (Galal 1986; Kosgey 2004). These programs aim to establish elite groups of animals for genetic improvement at research stations or government farms. Selected males are then distributed to farmers to improve the genetic quality of the broader population. There are two types of nucleus breeding programs, including open and closed. Open nucleus breeding programs (ONBPs) allow animals to flow both to and from the nucleus. The superior animals in ONBPs are selected from both nucleus herds and local herds. While in close nucleus breeding programs (CNBPs), the animals are selected only within nucleus herds (Sölkner et al. 1998; Gizaw et al. 2009). These programs were proposed and implemented for Djallonke sheep in the Ivory Coast, Damara sheep in Namibia, and Boer goats in South Africa but failed to remain and succeed (Yapi-Gnoare 2000; Wielligh 2003). It was because these programs are difficult to implement in smallholder systems as they require a long-term commitment from sponsors and active participation from farmers (Kosgey 2004).

Developing breeding programs tailored to smallholder systems is complex. These programs must balance genetic gain in the short term with maintaining genetic diversity and avoiding inbreeding depression in the long term (van der Werf 2000). Community-based breeding programs (CBBPs) are a new approach to genetic improvement programs proposed for the low-input traditional smallholder farming system (Sölkner et al. 1998; Kahi et al. 2005; Gizaw et al. 2014a). In the CBBP, the farmers within specific geographical boundaries collaborate to improve livestock through community participation and decentralized selection directly in local herds (Sölkner et al. 1998; Gizaw et al. 2009). CBBPs integrate indigenous knowledge, breeding practices, and objectives of local communities, ensuring their active participation at every stage—from planning to implementation. These programs holistically address the production system and typically feature a single-tier structure where farmers act as both breeders and producers (Gizaw et al. 2014a). Key steps in CBBP were described in the essentials for Community-based Livestock breeding program by Mueller et al. (2015) and “How to succeed in implementing community-based breeding programs: Lessons from the field in Eastern and Southern Africa” by Haile et al. (2023). These steps included community engagement with the participation of local farmers in decision-making and the implementation of breeding programs; identification of breeding objectives by determining desirable traits based on local production systems and farmer preferences; systematic data collection on animal performance for selection decisions; genetic selection and mating strategies; and long-term support from the government and NGOs through training, funding, and infrastructure development. CBBPs are widely implemented in smallholder systems for goats and sheep in Africa (Gizaw et al. 2009; Tesema et al. 2021), dairy goats in Mexico (Wurzinger et al. 2013), and indigenous pigs in Vietnam (Herold et al. 2010).

2.5.3. Approaches for optimizing breeding programs

Optimizing breeding programs involves developing strategies that balance genetic gain with economic, practical considerations, and optimal selection balancing genetic gain and genetic diversity (van der Werf 2006; Herold et al. 2012). Simulation studies are widely used to test breeding scenarios, predict genetic progress, and assess economic returns. The breeders can simulate the different breeding programs which reflect either current breeding practices or alternative ones without requiring significant resources. Additionally, simulations can show the long-term impacts of strategies by simulating multiple generations within a short time frame (Gaynor et al. 2021). This information could contribute to breeders/farmers’ decision-making and the choice of their breeding program.

There are two types of simulation commonly used: deterministic and stochastic. Deterministic simulations apply mathematical models to the entire population, providing rapid insights into genetic gains and potential inbreeding. These methods are particularly useful for large-scale breeding planning due to their computational efficiency and ability to model essential genetic dynamics, such as the

Bulmer effect, inbreeding adjustments, and correlations between EBVs. However, deterministic methods may involve simplifying assumptions, making them less detailed than stochastic simulations.

Stochastic simulations, in contrast, generate unique genetic and phenotypic values for individual animals. This method enables a more detailed examination of individual variation, mating patterns, and complex genetic interactions. Although these simulations require longer processing times, they offer the advantage of capturing more complex genetic processes and generating more realistic outcomes.

Various software and packages have been developed to facilitate both deterministic and stochastic simulations. For example, SelAction (Rutten et al. 2002) is a deterministic program that enables fast, group-based response predictions and can calculate inbreeding rates but does not provide options for economic analysis or discounted returns (Herold et al. 2012). In contrast, stochastic programs like MoBPS (Pook et al. 2020), AlphaSimR (Gaynor et al. 2021), and QMSim (Sargolzaei & Schenkel 2009) model whole populations, tracking individual mating and genetic variability over generations.

Lao native goats are a key livestock product for smallholder farmers in Laos contributing up to 46% of their annual income (Walkden-Brown et al., 2024), yet their productivity remains lower compared to other local goat breeds (Gray, 2019). Like many indigenous breeds, they exhibit small body sizes and slow growth rates but are well adapted to the local environment and traditional management practices. Understanding their genetic characteristics is essential for sustainable breeding and conservation. However, there are no scientific studies that have comprehensively examined the genetic resources of Lao native goats or how they were managed. The extent of their genetic diversity, the genomic basis of their adaptation, the influence of movement patterns on gene flow, and the effectiveness of different breeding strategies in smallholder systems remained unexplored. To addressing these gaps, this study aimed to provide a foundation for genetic improvement while ensuring the long-term sustainability of Lao native goats through informed breeding strategies.

Chapter Three: Genetic diversity, population structure and origin of the native goats in Central Laos

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Published in the “Journal of Animal Breeding and Genetics”

3.1. Abstract

Maintaining genetic diversity and variation in livestock populations is critical for natural and artificial selection promoting genetic improvement while avoiding problems due to inbreeding. In Laos, there are concerns that there has been a decline in genetic diversity and a rise in inbreeding among native goats in their village-based smallholder system. In this study, we investigated the genetic diversity of Lao native goats in Phin, Songkhone and Sepon districts in Central Laos for the first time using Illumina's Goat SNP50 BeadChip. We also explored the genetic relationships between Lao goats with 163 global goat populations from 36 countries. Our results revealed a close genetic relationship between Lao native goats and Chinese, Mongolian and Pakistani goats, sharing ancestries with Guangfen, Jining Grey, and Luoping Yellow breeds (China) and Teddi goats (Pakistan). The observed (H_o) and expected (H_e) heterozygosity were 0.292 and 0.303 (Laos), 0.288 and 0.288 (Sepon), 0.299 and 0.308 (Phin), and 0.289 and 0.305 (Songkhone), respectively. There were low to moderate genetic differentiation (F_{ST} : 0.011 to 0.043) and negligible inbreeding coefficients (F_{IS} : -0.001 to 0.052) between goat districts. The runs of homozygosity (ROH) had an average length of 5.92 to 6.85 Mb, with short ROH segments (1-5 Mb length) being the most prevalent (66.34%). Longer ROH segments (20-40 and >40 Mb length categories) were less common, comprising only 4.81% and 1.01%, respectively. Lao goats exhibit moderate genetic diversity, low inbreeding levels and adequate effective population size. Some genetic distinctions between Lao goats may be explained by geographic and cultural features.

3.2. Introduction

Goats play a significant role in Lao People's Democratic Republic (Laos), serving as a crucial component of the smallholder production system due to their economic, nutritional and cultural contributions. In Laos, goats are mainly raised in a semi-intensive grazing production system for export to neighbouring Vietnam, where demand for goat meat is rapidly growing (Bui et al. 2023). Only an estimated 10% is destined for domestic consumption (Gray et al. 2019). Consequently, the goat population in Laos has experienced an almost six-fold increase, rising from 128,000 in 2005 to approximately 711,200 in 2021 (FAOSTAT 2022). Furthermore, goats provide essential socio-cultural functions and contribute to the mixed production system by supplying manure for crop cultivation (Devendra 2013).

Goats are distributed throughout Laos, with variation in frequency across regions. Central Laos hosts 42% of the goat population, while the South and North regions accounted for less than 17% and 41%, respectively (Xayalath et al. 2021). Savannakhet province is a province of Central Laos with the greatest goat population (Gray et al. 2019). The goat population raised in Laos mainly consists of native breeds, with a small proportion of exotic breeds, and crossbreds between indigenous breeds and Southeast Asian Mountain goats (Wilson 2007; Trach & Phiovankham 2011). The native breed is Kangbing-Katjang (Phengsavanh 2006) which is kept for meat rather than milk production. This breed exhibits

traits such as a small body size of on average 26 kg and a high mortality rate of 37.5% (Gansberghe 2005; Colvin et al. 2022). Some native goats have been crossbred with the Boer goat breed, which was imported from Thailand (Wilson 2007), and Back-Thao bucks, a Vietnamese composite breed, resulting in improved growth rates compared to indigenous goats (Trach & Phiovankham 2011).

The majority of goats in Laos are managed by smallholder farmers according to traditional practices. Herds are small, typically comprising 2 to 12 goats (Wilson 2007; Windsor et al. 2018), generated from random mating (Dubeuf et al. 2014). Goats are typically housed at night and range freely during the day in unsegregated groups with overlapping grazing areas between flocks and villages Windsor et al. (2018). Breeding occurs throughout the year (Olmo et al. 2022a), driven by natural mating and the absence of human intervention. Bucks often reach sexual maturity before they are sold, which increases the risk of inbreeding and hampers genetic progress (Gray 2005). However, there is a lack of research on the genetic composition and extent of inbreeding within this population. Additionally, goats are frequently kept as assets to be sold when cash is needed (Gray 2005), leading to the inadvertent sale of superior animals due to their larger size and higher market value.

Given the importance of goats in the smallholder system, investigation of the genetic composition of goats in Laos can help inform breeding strategies to enhance goat production. Genetic diversity studies are important for understanding natural and artificial selection processes and assessing genetic relationships within and between breeds, particularly in indigenous breeds (Chokoe et al. 2022) which are better adapted to the local feed resources, environmental conditions, diseases and parasites (Brito et al. 2017). Managing and utilizing genetic diversity in these breeds is key to designing sustainable breeding programs aimed at achieving desirable phenotypes and avoiding mating close relative animals within a population.

Inbreeding coefficients derived from genomic data, such as F_{IS} and F_{ROH} , are important indicators of genetic diversity and the degree of inbreeding. F_{ROH} estimates the fraction of the total length of continuous homozygous segments, in the total length of autosomes, which is increased due to inbreeding (Purfield et al. 2012). The F_{IS} parameter estimates the average decrease in heterozygosity of individuals due to non-random mating within a population (Wright 1965; Peripolli et al. 2017). Genetic distance can be measured with the pairwise fixation index (F_{ST}) that indicates low (0.00-0.05), moderate (0.05-0.15), high (0.15-0.25) and exceptional (>0.25) genetic relatedness between populations (Wright 1978).

In recent years, genomic analyses, such as runs of homozygosity (ROH) have been extensively employed to study genetic diversity and indicate recent and ancient inbreeding in various livestock species (Muir et al. 2008; Makina et al. 2014; Al-Mamun et al. 2015; Munoz et al. 2019). The frequency of ROH provides insights into the demographic history and management of the population over time. ROH usually arise from the transmission of identical haplotypes from each parent to offspring (Purfield

et al. 2012) and its accumulation in the genome can have significant impacts on overall biological fitness (Manunza et al. 2016).

The genetic diversity of cosmopolitan and indigenous goat breeds has been studied in Asia (Berihulay et al. 2019; Deniskova et al. 2021; Mukhina et al. 2022), Africa (Tucho & Tesfaye 2004; Onzima et al. 2018; Nandolo et al. 2019; Tarekegn et al. 2019), Europe (Cañón et al. 2006; Lenstra et al. 2017; Oget et al. 2019), and Oceania (Brito et al. 2017). These studies have utilized genomic markers to investigate population structure, assess genetic diversity, linkage disequilibrium patterns and effective population size, together providing insight into population characteristics, demographic history and the degree of inbreeding. In a country like Laos, where pedigree and phenotype data are limited, genomic markers are valuable tools for inferring various genetic properties of its goat population based on a small sample of genotyped individuals and derive from that proposed informed management decisions and breeding strategies.

In this study, we aimed to describe the population structure of native goats across three districts in Central Laos, to estimate the inbreeding and genetic diversity, both within and between districts, and elucidate the genetic relationship between Lao native goats and global goat breeds, providing insights into their genetic origins and potential admixture.

3.3. Materials and methods

3.3.1. Ethics statement

All the procedures conducted in this study were approved by the Animal Ethics Committee of the University of New England under approval number AEC21-084.

3.3.2. Sample collection and genotyping

A total of 420 ear-notch samples were collected between February and April 2022 from three districts in the Savannakhet province of Laos (Figure 3.1). In Laos, there are limited genetic introductions from outside Laos and therefore, all samples in this study were considered as the same breed, Lao native goats. These samples were obtained from 140 households situated in seven villages located in Phin (184 samples), Songkhone (176 samples), and Sepon (60 samples) districts. In each household, three healthy male or female goats were collected. Field staff were instructed to avoid taking samples from full-sibs. Staff verified that the goats were not full-sibs by asking the goat owners. These samples were stored in the Allflex Tissue Sample Units (Neogen, Australia) with preservatives and kept in a fridge in Laos before being exported to New Zealand for analysis. DNA extraction and genotyping were conducted by GenomNZ (AgResearch Ltd., Mosgiel, New Zealand). Genotyping was performed with the goat 50K Illumina BeadChip (Tosser-Klopp et al. 2014) containing 59,727 SNPs with 56,204 SNPs on autosomes.

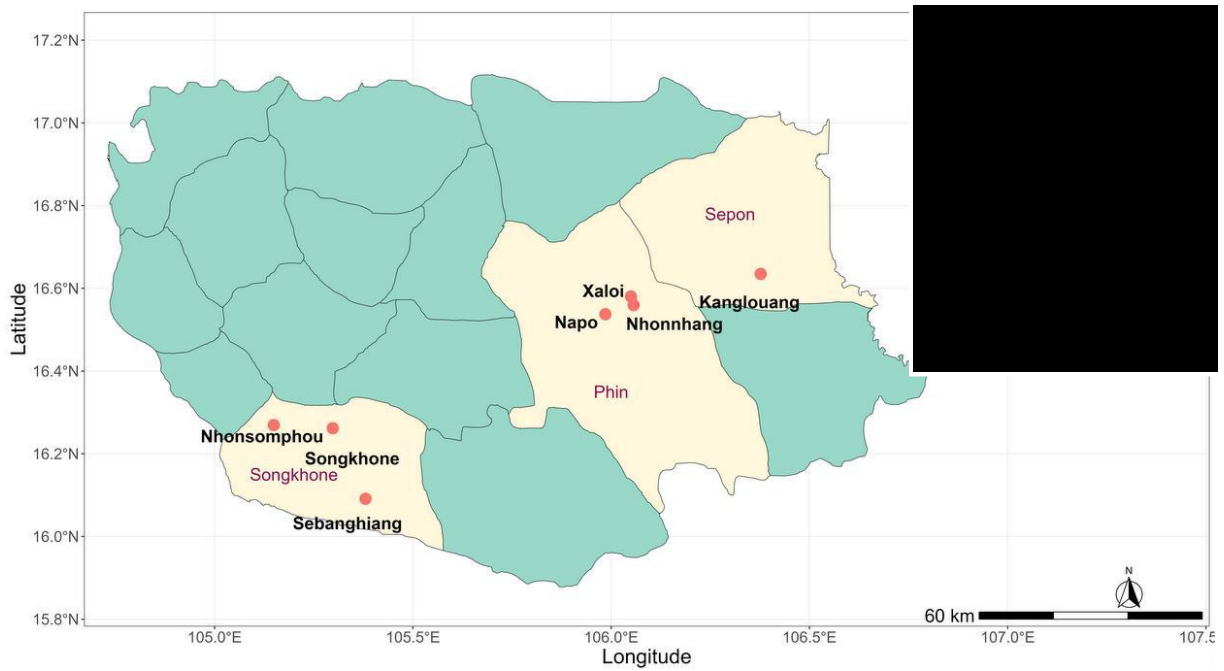


Figure 3. 1. Geographical location of goat samples used in this study. The samples were collected in Savannakhet, a Central province in Laos. The red circles in the map are shown as samples collected in seven villages in Songkhone, Phin and Sepon districts.

3.3.3. Construction of the working datasets

Three working data sets were constructed for this study. The first one, the Lao dataset, included 420 samples from three sampling districts in Laos as described above. To compare the genetic diversity of Lao goats with other goat breeds in Asia and the rest of the world, we combined the SNP profiles from the first dataset with four public reference datasets (Colli et al. 2018; Berihulay et al. 2019; Deniskova et al. 2021; Mukhina et al. 2022). The second working dataset, the Global dataset, contained 5,688 goats from 165 breeds, including 69 populations from Africa, 43 from Asia, 37 from Europe, 13 from America and 2 from Oceania. The third working dataset, the Asian dataset, encompassed 1,552 goats from 43 populations in Asia, including 16 populations from Pakistan, 8 from Russia, 6 from China, 5 from Mongolia, 3 from Turkey, 3 from Laos (from this study) and 2 from Iran. Details of full breed name and geography distribution are presented in Supplementary Table S1.

Quality control was performed in PLINK v1.9 (Purcell et al. 2007) for each dataset. This process involved excluding SNPs on the sex chromosomes and unmapped locations, as well as those with a minor allele frequency (MAF) lower than 0.05, a call rate lower than 90% or a deviation from Hardy-Weinberg equilibrium (p -value $< 10^{-6}$). Individuals with more than 10% missing SNPs were also excluded. After quality control, the Lao dataset consisted of 419 genotyped goats with 42,666 SNPs, the Asian dataset included 1,546 goats with 43,612 SNPs, and the Global dataset comprised 5,574 goats with 43,886 SNPs. The MAF filter was not applied for the run of homozygosity (ROH) based analyses.

3.3.4. Genetic diversity

In order to assess the genetic diversity for the Lao dataset, the observed (H_o) and expected (H_e) heterozygosity and inbreeding coefficient (F_{IS}) along with a 95% confidence interval (CI 95%) were calculated in the R package “hierfstat” (Goudet 2015). The PLINK files were converted to hierfstat format using the PGDSpider program (Lischer & Excoffier 2012)

3.3.5. Effective population sizes

Effective population size (N_e) is a genetic parameter that contributes to our comprehension of the population's evolutionary history and its diversity. In this study, we estimated N_e for the Lao dataset and for each district separately using the SNeP version 1.1 software (Bertolini et al. 2018a), where N_e is derived based on measures of linkage disequilibrium (LD). We applied the default parameters with an exception for the sample size correction, occurrence of mutation (-alpha 2.2 as suggested by (Corbin et al. 2012)), along with a recombination rate between a pair of genetic markers determined using the Sved and Feldman (1973) method: $c = (1-d/2)$, where c is recombination rate, d is the linkage distance.

3.3.6. Run of homozygosity (ROH) and genomic inbreeding (F_{ROH})

Runs of homozygosity (ROH) are the estimated length of segments of continuous homozygous genotypes inherited in an identical-by-descent manner from an animal's parents and present in its genome (Purfield et al. 2012). ROH was detected in all autosomes and examined in each district individually. We used the “detecRUNS” package in R (Biscarini et al. 2018) with the consecutive run methods proposed by Marras et al. (2015) for the analysis of ROH.

The pattern of ROH coverage can provide insights into both recent and historical inbreeding events (Cardoso et al. 2018). For the identification of ROH, we imposed the restriction that no more than one SNP with a missing genotype could be included per window and up to one possible heterozygous genotype was allowed. The minimum ROH length was 1 Mb. In order to minimize the false positive results, we applied a threshold for the minimum number of SNPs (l) per sliding window, which was computed using the formula introduced by Lencz et al. (2007) and subsequently adapted by Purfield et al. (2012):

$$l = \frac{\log_e \frac{\alpha}{n_s - n_i}}{\log_e (1 - het)}$$

where n_s represents the number of genotyped SNPs per animal, n_i is the number of genotyped individuals, α corresponds to the percentage of false positive ROH (set to 0.05 in this study), and het denotes the mean heterozygosity across all SNPs. We determined that the minimum number of SNPs per sliding window for this study was 47.

The identified ROH were classified into five groups based on their length: 1-5 Mb, 5-10 Mb, 10-20 Mb, 20-40 Mb and >40 Mb to determine the distribution of recent and ancestral inbreeding in Laos and then compare the distribution of ROH length among sampling areas in Laos. The mean sum of the number of ROH within each ROH length category was calculated by averaging the total number of ROH per animal. Additionally, the percentage of SNPs involved in ROH was determined by counting the number of times an SNP appeared in an ROH in the district.

Genomic inbreeding coefficients (F_{ROH}) for individuals and districts were estimated using the ROH data. The F_{ROH} defined as the genomic autosomal proportion of ROH of an individual, was the sum of the lengths of all ROH detected in that individual divided by the total length of the autosomes covered by SNP markers (in this case, 2,463.88 Mb) (McQuillan et al. 2008).

3.3.7. Genomic relationship and population structure

To estimate the extent of genetic differentiation F_{ST} -values (Weir & Cockerham 1984) were calculated between goat populations from different districts with PLINK v1.9. The matrix of pairwise F_{ST} values was visualized in a distance tree with iTOL (<http://itol.embl.de>) (Letunic & Bork 2016).

A principal component analysis (PCA) was performed to provide insights into the goat population structure in Central Laos and assess the Lao goat relationships with other breeds at the global and Asian levels. The PCA was performed in PLINK v1.9 and visualized with the R package “ggplot2” (Wickham 2011).

To describe common ancestry between Lao goats and other goat breeds, the ADMIXTURE v1.3.0 program (Alexander et al. 2015) was used. The optimal number of clusters (K) was determined for each dataset and multiple runs with varying K levels were performed. Specifically, for the Lao dataset, ADMIXTURE was run from K=2 to 20, for the Asian dataset from K=2 to 70, and for the global dataset from K=2 to 170, using a ten-fold cross-validation (CV=10). Each run was repeated 10 times to evaluate the lowest cross-validation error. The resulting admixture outputs were visualized using the R package “BITE” (Milanesi et al. 2017).

3.3.8. Linkage disequilibrium analysis

To determine different LD patterns for each Lao goat district, PLINK v1.9 was used with default parameters. The LD coefficient (r^2) was used as a measure of LD strength, as it is considered more reliable and unaffected by allele frequency and population size (Zhao et al. 2005). For visualizing the relationship between LD and physical distance between SNPs, the average r^2 within a 1,000 kb interval was calculated and plots were created using the “ggplot2” package in R.

3.3.9. Migration analysis

Historical introgression events and past migrations between Asian goat populations were investigated with the maximum likelihood algorithm implemented in TreeMix v1.13 (Pickrell & Pritchard 2012). The analysis involved testing a range of migration edges (m) from 1 to 20, employing the bootstrap command, excluding sample size correction, and allowing for global rearrangements. The optimal number of migration events was determined using the Evanno method (Evanno et al. 2005) from the “OptM” package (Fitak 2021) and the results were visualized using the TreeMix function “plot_tree” in the “BITE” package in R.

3.4. Results

3.4.1. Comparative analysis of genetic diversity and genetic structure: Lao goats at the global level

In the global dataset (Figure 3.2A and Figure S3.1A), the first principal component (PC1) explained 29.24% of the total variation and separated Asian breeds from the breeds from Africa, Europe and America. The PC2 accounted for 20.01% of the total variation and divided the global goat breeds into two groups, North American, European and some African goat breeds in quadrant II and most African, Oceanian and South American goat breeds in quadrant III and IV. The PC3 (Figure S3.1A) accounted for 9.99% of the total variation and mainly separated the Oceanian breeds. The first three PCs (Figure 3.2A and Figure S3.1A) accounted for 59.24% of total variation and divided the global goat breeds into four main clusters: one including Asian goats, a second cluster consisting of the majority of African breeds and South American breeds, a third cluster enclosing European and North America breeds, and a fourth cluster enclosing Oceanian breeds along with some breeds from Asia and Africa. The result of PCA at the global level (Figure 3.2A) and Asian level (Figure 3.2B) show Lao goats are in closer proximity to Chinese breeds than other breeds in Asia.

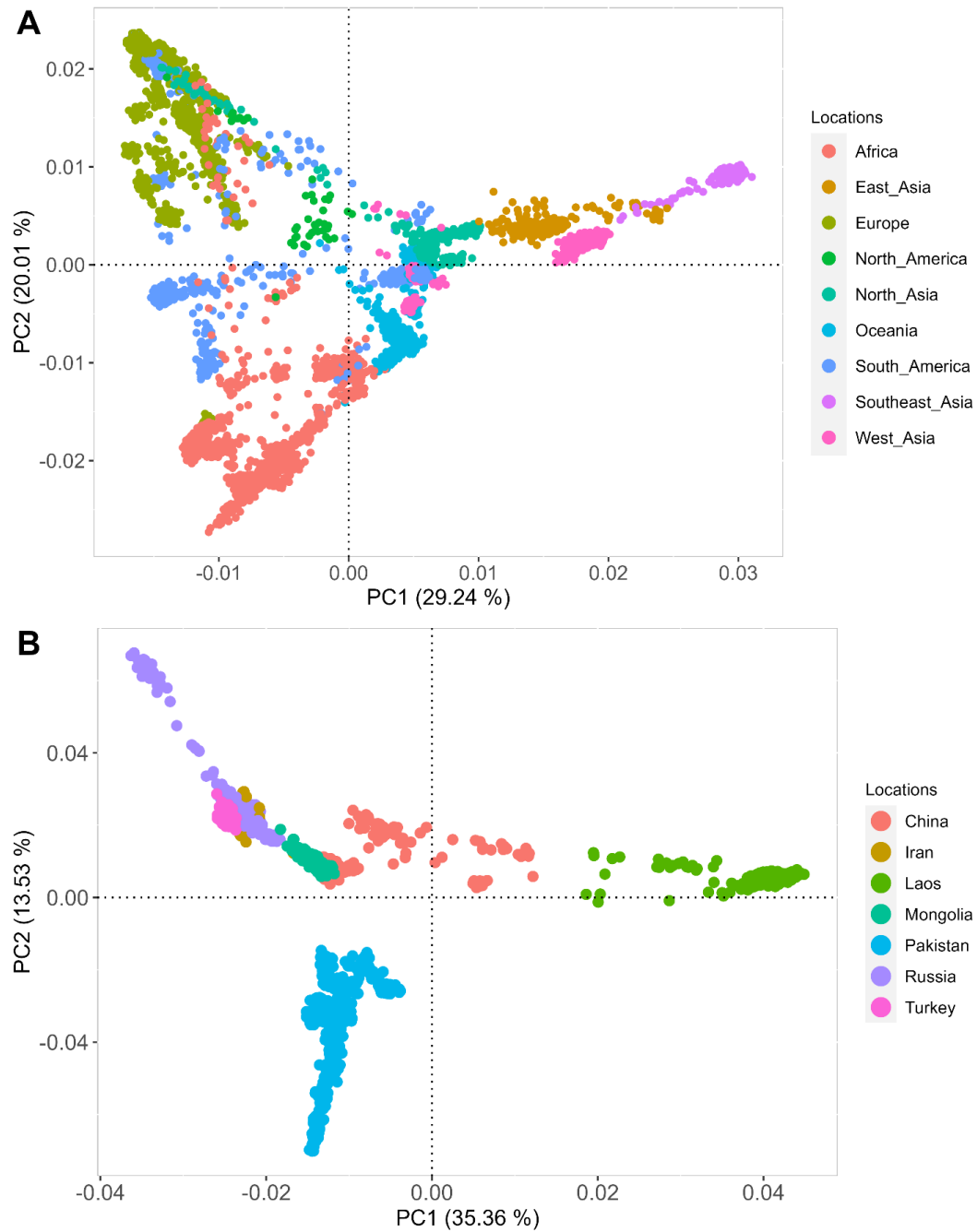


Figure 3. 2. Principal component analysis at the global (**A**) and Asian (**B**) levels. One dot represented an individual, and colours represented populations.

Admixture analysis applied for global (Appendix A, Figure S3.2) and the Asian datasets (Figure 3.3) were similar to the PCA results. Lao goat breeds showed a high differentiation among the global goat breeds but clustered together with goats from China, Pakistan and Mongolia. At K levels 2, 4, 6, and 9 (Figure 3.3) the major blue-coloured cluster is displayed in Lao goats and those were also found in smaller proportions in Guangfen (CHN_GF), Jining Grey (CHN_JN), and Luoping Yellow (CHN_LP) goats in China, and in Teddi goats (PAK_TED) in Pakistan (Figure 3.3). At K = 2, the blue colour cluster comprised 97-99% of the genetic composition in Laos, 46% in CHN_LP, 45% in CHN_GF,

30% in CHN_JN, 25% in PAK_TED, and 17% in Mongolian goats. At K = 4, these percentages were 96-99%, 24%, 22%, 36%, 15%, and below 5%, respectively. At K = 9, the blue cluster remained dominant in Lao goats at 95-99%, while accounting for 21% in CHN_GF, 13% in CHN_JN and CHN_TED, and less than 1% for CHN_LP and Mongolia goats. Across all K levels, the lowest CV error for the Asian breeds was acquired for K = 50 (Figure S6).

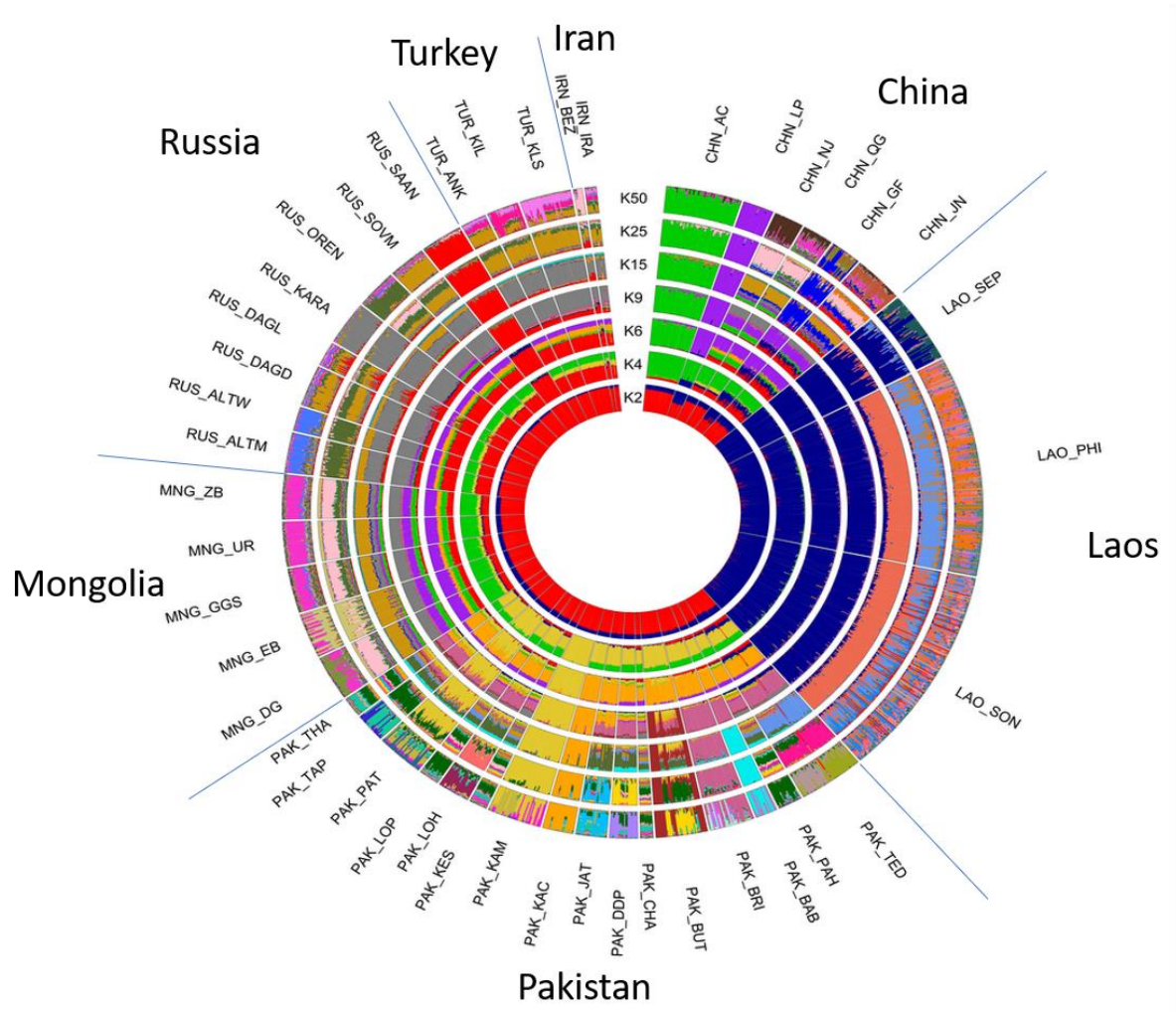


Figure 3.3. Admixture analysis of 1,546 individuals from the 43 goat populations in Asian regions. Results for number of clusters K = 2, 4, 6, 9, 15, 25 and 50 are shown from inner to outer circles. Goats are grouped by population and each individual is represented as a single vertical line. The proportion of the coloured segment in each K cluster band represents their estimated ancestry from different populations with each colour representing a different ancestry. For a description of the goat breeds, see Table S3.1.

The genetic distances measured as pairwise F_{ST} between 43 Asian goat breeds (Appendix A, Table S3.2) showed that the average pairwise F_{ST} values among these breeds were 0.087 and ranged from 0.003 to 0.221. This indicates a range of genetic differentiation, from low to high, across the

populations. Notably, the Russian breeds ALTW and ALTM exhibited the lowest genetic differentiation in all pairwise F_{ST} , while the highest level of differentiation was observed between the breeds Luoping Yellow in China and Barbari in Pakistan.

Among all the Asian goat breeds, the Lao goat populations showed little genetic differentiation within themselves ($F_{ST} < 0.05$) while displaying moderate to high genetic differentiation from other Asian breeds (Table S3.2). However, the F_{ST} values between Sepon (LAO SEP) and Asian goat breeds (ranging from 0.056 to 0.175) were slightly higher than the F_{ST} value between Phin (LAO PHI) and Songkhone goats (LAO SON) with Asian goat breeds (F_{ST} from 0.054 to 0.165). This indicates a significant genetic disparity between Sepon and other Asian goat breeds, ranging from moderate to high differentiation. Low genetic differences were observed between Lao goats and Chinese goats ($F_{ST} = 0.0481$), as well as Mongolian goats ($F_{ST} = 0.0512$) confirming the results from PCA analysis.

The neighbour-Net graph based on Weir and Cockerham F_{ST} between Lao goat breeds and Asian goat breeds is presented in Figure 3.4. It revealed that there are three main cluster groups, the first including Lao, Chinese and Mongolian goat breeds, the second including the Russian, Iranian and Turkish goat breeds, and the third including the Pakistani goats. In the first genetic cluster group, Lao goat breeds had an independent branch and goat populations in Phin (LAO PHI) and Songkhone (LAO SON) clustered together before joining with those in Sepon (LAO SEP) within the relevant genetic cluster. The Chinese Guangfen (CHN GF) and Jining Grey (CHN JN) goats clustered together with Lao goats in the next sub-cluster before other Chinese and Mongolia goat breeds were classified within the first main group cluster.

F_{ST}

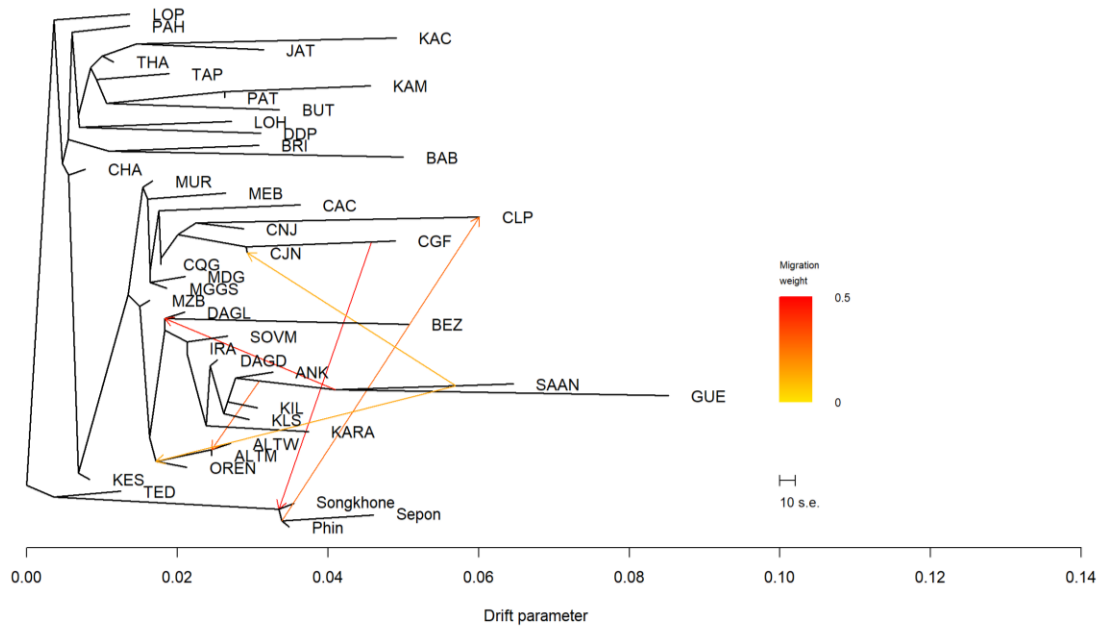


Figure 3. 5. Maximum likelihood tree with 6 migration events between 43 goat breeds in Asian regions. Migration edges are coloured according to their migration weight (reflects the strength of inferred gene flow between populations). The scale bar indicates 10 times the average standard error of the entries in the sample covariance matrix. For a description of the goat breeds, see Table S3.1.

3.4.2. Genetic diversity, genetic structure and inbreeding level within Lao native goats

PCA indicated that genetic structure exists within the Lao goat population. Goats in Sepon were different from those in the Phin and Songkhone districts. It also revealed low differentiation between Phin and Songkhone where in PC1, PC2, and PC3, the cluster of these districts overlapped to some extent. The principle components PC1, PC2 and PC3 accounted for 12.64%, 8.75% and 7.48% of the total variation (Figure 3.6A and 3.6B), respectively.

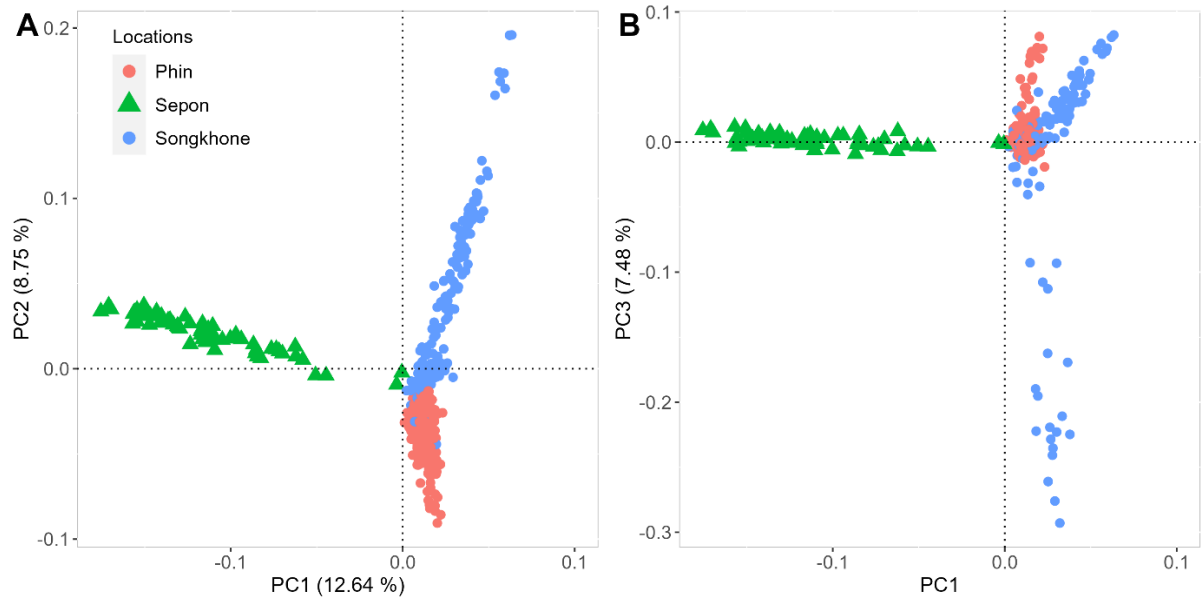


Figure 3. 6. Principal component analysis for goats from three districts in Laos. The PC1 vs PC2 (A) and PC1 vs PC3 (B). A symbol represented an individual and colours represented sampling areas.

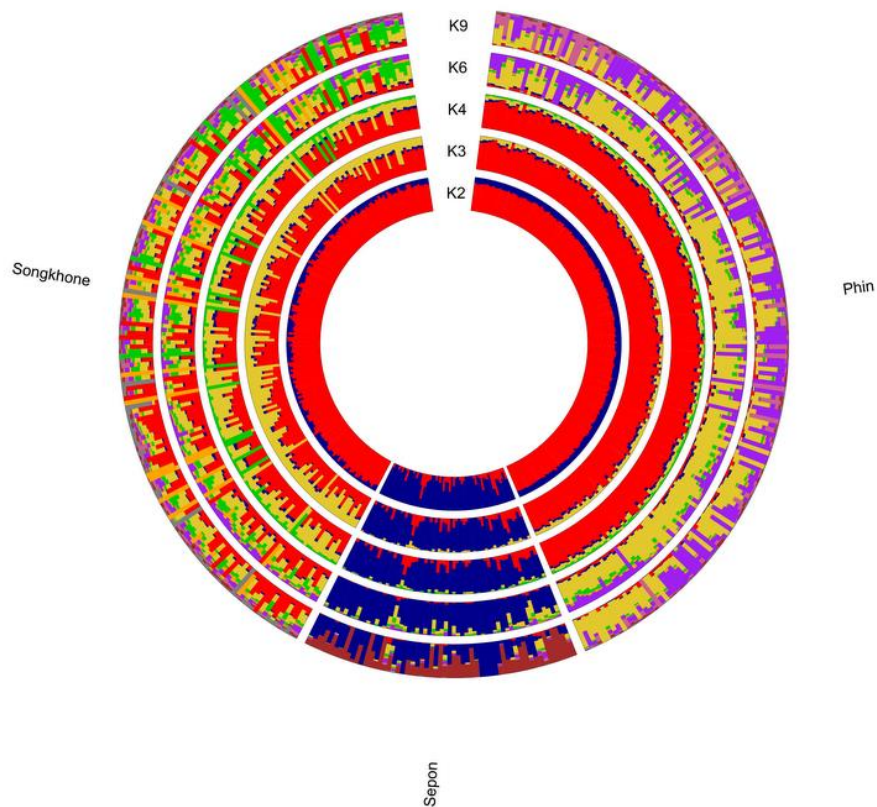


Figure 3. 7. Admixture analysis of 419 goats from three districts in Central Laos. Goats are grouped by district and each individual is represented as a single vertical line. The proportion of the coloured segment in each K represents their estimated ancestry deriving from different populations.

Admixture results of the Lao dataset for $K = 2$ to 9 are presented in Figure 3.7 and a cross-validation (CV) error is presented in Figure S5. In Lao goats, the analysis of admixture revealed a clear differentiation of goats in Sepon from other Lao goats in $K=2, 3$, and 4, which is consistent with results obtained from the PCA (Figure 3.6A and Figure 3.6B).

Across all K levels, admixture was observed among goat populations in Laos but the proportion of each cluster varied depending on the common ancestral level. In Sepon, for instance, the blue colour cluster accounted for a majority of the proportion (from 80% at $K=6$ to 84% at $K=2$) in all K levels. However, this cluster showed a small proportion at $K=2$ in both Phin (18%) and Songkhone (13%) and this significantly decreased as the K level increased. At $K = 6$, this cluster accounted for 4% of both Phin and Songkhone populations. In contrast, while the red colour cluster held a minor proportion in Sepon, it emerged as a significant component in Songkhone and Phin. When $K = 2$, the red colour cluster represented 16% of Sepon, 82% of Phin, and 87% of Songkhone. This distribution shifted at $K = 4$, where the cluster constituted 14% in Sepon, 81% in Phin, and 44% in Songkhone. Additionally, from $K = 3$ to 9, individual goats in Phin showed less admixture compared to goats in Songkhone.

Based on the classification of F_{ST} by Wright (1965), there was overall low genetic differentiation among Lao native goats from three districts. However, a greater differentiation was found between Sepon district and both Phin and Songkhone districts compared to the differentiation between Phin and Songkhone themselves (Table 3.1). These findings align with the result from PCA (Figure 3.6) showing that goats from Phin and Songkhone districts are more related.

Table 3. 1. Pairwise fixation index (F_{ST}) among three districts in Laos.

	Phin	Sepon	Songkhone
Phin	-		
Sepon	0.041	-	
Songkhone	0.011	0.043	-

To estimate genetic diversity, we computed H_o and H_e for goats in three Lao districts (Table 3.2). The average values for H_o and H_e were 0.292 and 0.303, respectively, with the lowest observed in Sepon and the highest in the Phin goat population. Except for the Sepon district, H_o value was slightly greater than the H_e value. In Phin and Songkhone, H_o values were, on average, 0.012 lower than H_e , while in Sepon, H_e was 0.0002 lower than H_o .

In general, the estimated inbreeding coefficient was close to zero with an average F_{IS} of 0.037, varying from negative values in Sepon (-0.001) and positive values in Phin (0.028) and Songkhone (0.052). Based on the 95% confidence intervals, F_{IS} values in Phin and Songkhone were moderately positive and

significant, while the F_{IS} value in Sepon was not significantly different from zero. In addition, the mean F_{ROH} values in all Lao goat populations were generally low. However, some individual animals exhibited high inbreeding, with the highest F_{ROH} values found in Phin, Sepon, and Songkhone at 0.412, 0.405, and 0.422, respectively (Table 3.2).

Table 3. 2. Genetic diversity and inbreeding estimates in Lao goats by observed (H_o) and expected heterozygosity (H_e), estimates of the inbreeding coefficient (F_{IS}) with 95% confidence interval, fixation index (F_{ST}) within districts, mean, standard deviation (SD), min and max of genomic inbreeding coefficients (F_{ROH})

Location	N	H_o	H_e	F_{IS} [95% CI]	F_{ROH}		
					Mean $\pm$ SD	Min	Max
Phin	184	0.299	0.308	0.028 [0.027; 0.030]	0.080 $\pm$ 0.073	0.005	0.412
Sepon	59	0.288	0.288	-0.001 [-0.002; 0.001]	0.100 $\pm$ 0.061	0.023	0.4049
Songkhone	176	0.289	0.305	0.052 [0.051; 0.053]	0.108 $\pm$ 0.096	0.001	0.422
Laos	419	0.292	0.303	0.037 [0.036; 0.038]	0.094 $\pm$ 0.083	0.001	0.422

To estimate the level of inbreeding, we calculated the ROH segments for each Lao goat population, as shown in Table 3.3 and Figure 3.8. The average ROH length varied from 5.92 Mb in Phin to 6.85 Mb in Songkhone, with the average number of ROHs per goat ranging from 33.22 (Phin) to 38.69 (Songkhone). Longer ROHs are indicative of more recent inbreeding events since each recombination event reduces the length of an ROH. The Songkhone district displayed the largest variability in ROH lengths and number of ROHs per goat, while the Sepon district showed the lowest variability. Nevertheless, the majority of goats from the three districts exhibited similar patterns in individual homozygosity, with a number of ROH segments of 60 and genome coverage ranging between 250-300 Mb (Figure 3.8A).

Table 3. 3. Mean ROH length and mean ROH number in three goat populations in Laos

Population	N	ROH length (Mb)			Number of ROH		
		Mean $\pm$ SE	Min	Max	Mean $\pm$ SE	Min	Max
Phin	184	5.92 $\pm$ 0.09	0.03	80.79	33.22 $\pm$ 0.87	5	66
Sepon	59	6.42 $\pm$ 0.15	0.12	62.92	38.44 $\pm$ 1.3	18	62
Songkhone	176	6.85 $\pm$ 0.1	0.03	106.17	38.69 $\pm$ 1.13	2	84

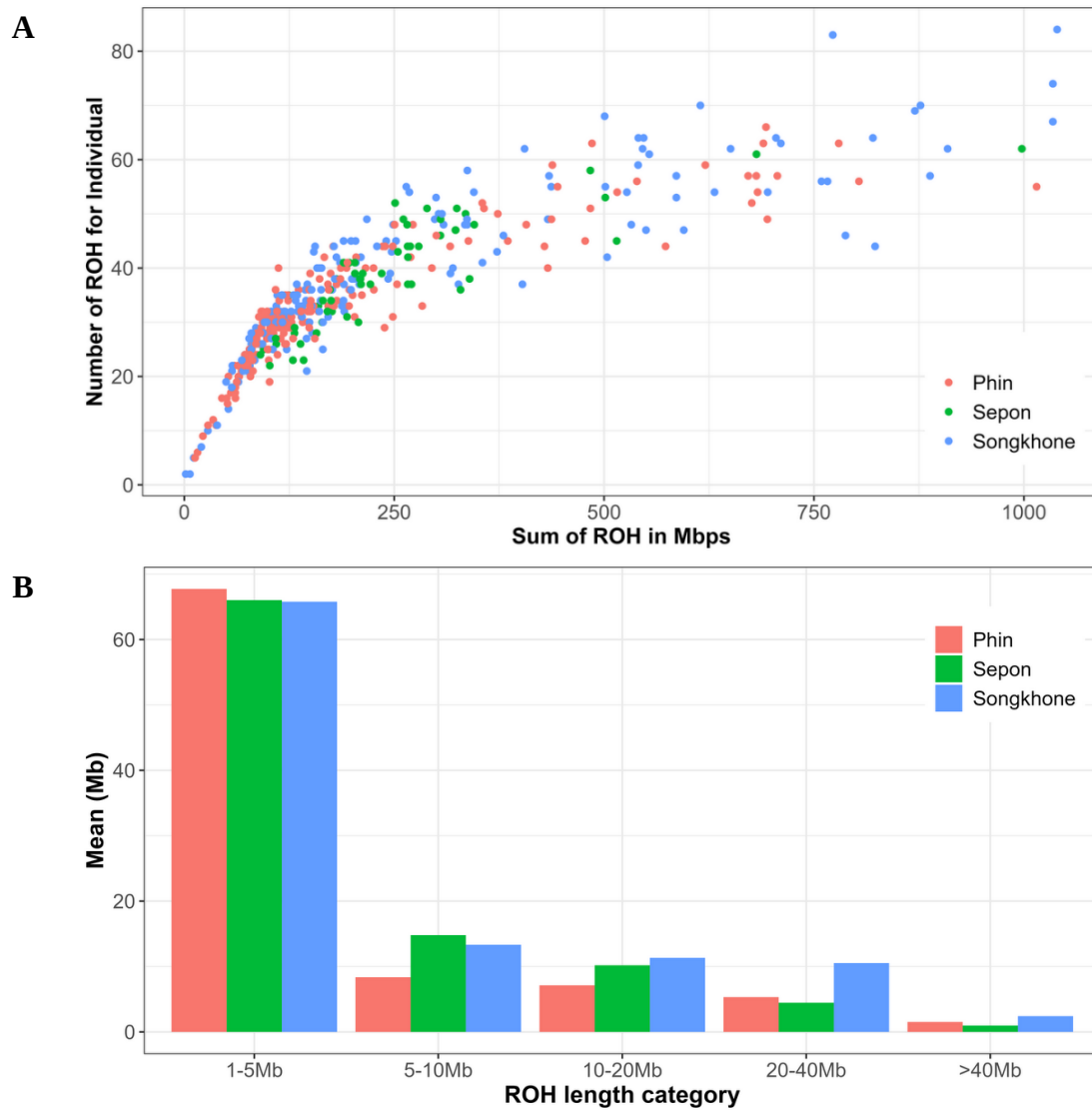


Figure 3. 8. Patterns of ROH in Lao goats across districts. (A) Genomic coverage in ROH and ROH number per individual; (B) Mean sum of ROH per animal. The sum of ROH was performed per individual, measured in megabases (Mb) within each ROH length category averaged per district.

Overall, goats showed a higher frequency of ROH segments in the shorter-length categories, as represented in Figure 3.8B. The most common ROH length category was 1-5 Mb, accounting for 63.93% of the total ROH segments in Sepon, 64.28% in Songkhone and 70.80% in Phin. The amount of genome coverage of this class of ROH length segments was 67.74 Mb, 66.03 Mb, and 65.78 Mb in Phin, Sepon, and Songkhone, respectively. The second most frequent ROH length category was 5-10 Mb, with a proportion of 15.84% (Phin), 18.37% (Songkhone), and 19.62% (Sepon) with a mean genome coverage of 8.37 Mb, 13.33 Mb and 14.80 Mb, respectively. Long ROH segments (10-20 Mb and 20-40 Mb) accounted for 9.9% (ranging from 8.18% to 11.07%) and 4.81% (varying from 4.22% to 5.62%) of the total number of ROH segments. The frequency of the longest ROH length category (>40 Mb) ranged from the rarest in Sepon (0.79%) to low in Phin (0.97%) and Songkhone (1.26%). The

average sum of the total ROH segment length per animal for long ROH length categories (10-20 Mb, 20-40 Mb, and >40 Mb) was less than 12 Mb.

The estimation of LD was based on r^2 values between pairs of SNPs for each of the three Lao goat districts (Figure 3.9). The result demonstrated a consistent trend in which the average r^2 values decrease as the genetic distance between pairwise SNPs increases, with a pronounced decline observed within the initial 0.5 Mb of genomic distance. A comparison of the average r^2 values among the three districts revealed similar results for Phin and Songkhone, both of which exhibited lower values than those observed in Sepon. The average LD of Sepon, Songkhone and Phin were 0.083, 0.032 and 0.03, respectively. The average LD up to 1,000 Kb was highest in Sepon at 0.203.

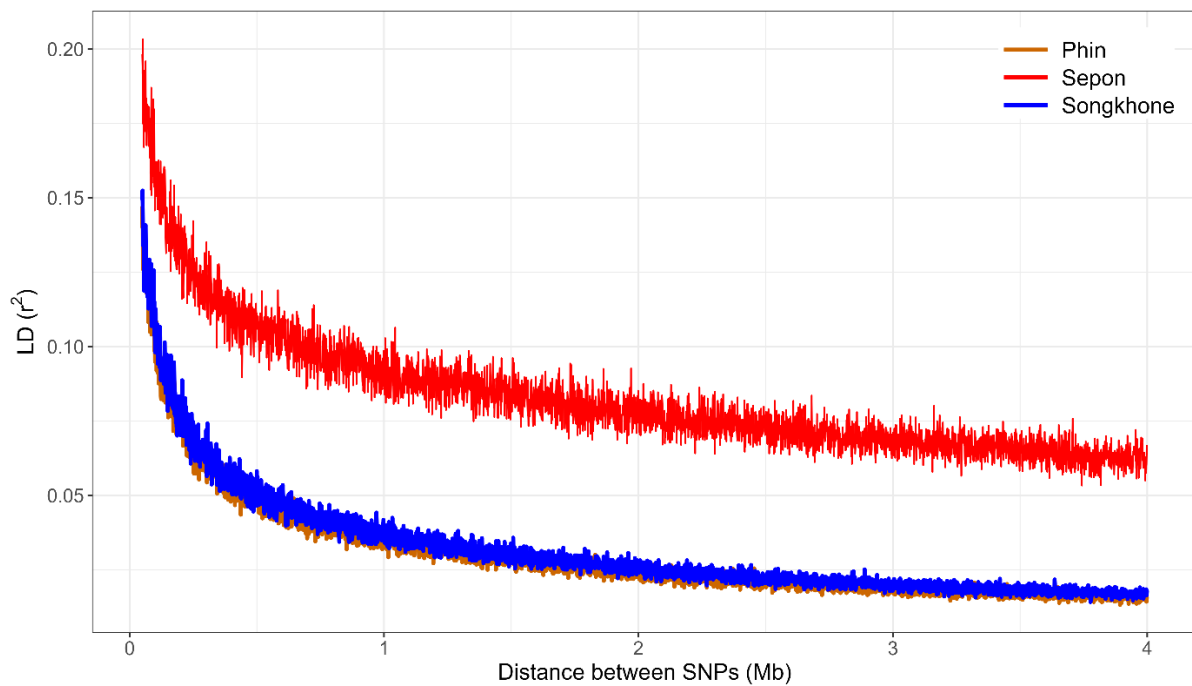


Figure 3. 9. Genome-wide average LD decay estimated for each district.

The values for recent and ancestral N_e estimated for the Lao goat population are presented in Figure 3.10. The estimated N_e showed a stable declining trend in the most recent generations across the three districts. The Phin goat population consistently had the highest N_e , while the Sepon goat population had the lowest N_e . The recent effective population sizes, 13 generations ago, were 92 for Sepon, 372 for Songkhone, 401 for Phin and 626 for the whole Lao datasets. The peak of the historical effective population size was found 915 generations ago, with 1,487 for Sepon, 2,368 for Songkhone, and 2,446 for Phin.

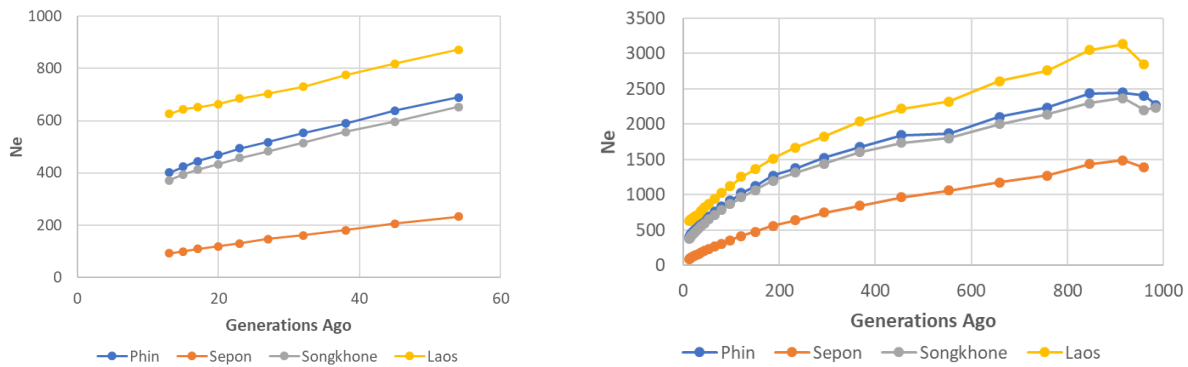


Figure 3. 10. Recent (A) and long-term (B) trends in effective population size (N_e) for Lao goats in three districts and a total of Laos.

3.5. Discussion

3.5.1. Goat migration to Southeast Asia and genetic relationships between Lao native goats and global breeds

Archaeological and genetic evidence showed that the goats were one of the first livestock species to be domesticated around 10,000 years before present (YBP), during the Neolithic period in the Fertile Crescent (Zeder & Hesse 2000). Following the initial domestication, the dispersal of goats across Asia occurred through two primary corridors. One migration route passed through Pakistan and India, eventually reaching Southeast Asia through overland and/or maritime routes (Devendra & Nozawa 1976; Porter et al. 2016). These historical communication routes between Western Asia, the Indian subcontinent, and Southeast Asia, provided an opportunity for the diffusion of crops and livestock (Fuller et al. 2011). The second corridor involved goats traversing through Caucasus and Siberia, eventually reaching Mongolia and China (Nozawa 1991; Porter et al. 2016; Amills et al. 2017). Barker et al. (2001) reported that some goat breeds in Southeast Asia shared the same cluster with Chinese goat breeds, suggesting a possible separate dispersion via China, similar to the spread of swamp buffalo through Southeast Asia (Barker et al. 1997). Furthermore, Yi et al. (2022) found that Lao goats have shared the haplogroup A and B with Chinese, Mongolian, Vietnamese, Cambodian and Pakistani goat breeds, supporting the notion of Western Asian goat influence on Southeast Asia goats.

The result in the PCA plots from 165 goat breeds (Figure 3.2A and Figure S3.1A) demonstrated that Lao goats clustered with Asian goat breeds and were more distant from goat breeds in Africa, America and Europe. The result from Asian PCA plots (Figure 3.2B and Figure S3.1B) in this study illustrated that Laos goats are closer to Chinese, Mongolian and Pakistani goats than other Asian goat breeds. Those findings are consistent with the result of admixture analysis where admixture results indicated the common genetic background between goat breeds in Laos, Mongolia, China and Pakistan, especially

with three Chinese goat breeds (Guangfen, Jining Grey, and Luoping Yellow) and one Pakistan goat breed (Teddi). In addition, moderate gene flows were found between Teddie (Pakistan) and Guangfeng (China) breeds and the goat population in Central Laos. Goats in Central Laos also had weak gene flow with Luoping Yellow and Jinning Grey breeds in Southwest and Eastern China, respectively. These findings are consistent with previous studies that described Guangfen and Jining Grey goats from China clustered in the same clade (Berihulay et al. (2019). Later, Mukhina et al. (2022) reported those two Chinese goats in the same clade as Erchim goats from Mongolia and suggested that these breeds may share a common ancestry. These findings in this study supported the hypothesis that goats in Central Laos migrated from China and Pakistan.

Goats arrived in Mongolia and Northern China at approximately 4,500 YBP (Pereira & Amorim 2010; Colli et al. 2018). Goats also entered the Indian subcontinent and the broader regions of Southeast Asia. Due to the lack of archaeological evidence and genetic studies in these regions, the exact dates for their arrival are uncertain (Pereira & Amorim 2010; Amills et al. 2017). Based on the long-term trends in effective population size in this study and an average generation interval of 4 years (Wang et al. 2021), goats would have arrived in Laos around 4,000 YBP.

3.5.2. Genetic Diversity, Structure, and Inbreeding Patterns in Lao Native Goats

Since the availability of the Illumina Goat 50K SNP BeadChip in 2014 (Tosser-Klopp et al. 2014), a number of studies to understand the genetic variation of local and international goat breeds using SNP datasets were conducted (Colli et al. 2018; Islam et al. 2019; Tarekegn et al. 2019; Le et al. 2023; Zhong et al. 2023). To our knowledge, this is the first application of a medium SNP array and genomic approaches to assess the genetic diversity and inbreeding levels of Lao native goats. The results of genetic variation showed moderate levels of diversity within Lao goat populations.

The level of genetic diversity in Lao goat populations is indicated by heterozygosity levels (H_o and H_e). The average H_o and H_e for Lao breeds were 0.292 and 0.303, respectively which were lower than the reported estimated values for goats in West Asia, China, Greece, and Mongolia (Colli et al. 2018; Berihulay et al. 2019; Michailidou et al. 2019; Mukhina et al. 2022). The H_o and H_e of Lao goats were comparable to those of Pakistani goats (Kumar et al. 2018). One study using 65 SNPs reported H_o and H_e values of 0.305 and 0.342 for Laos, 0.311 and 0.340 for Vietnam, 0.292 and 0.356 for Cambodian plains goats, and 0.332 and 0.324 for the Philippines (Lin et al. 2013). Table 3.4 depicts values of H_o and H_e reported by previous studies using SNP data. These findings are in alignment with the results of the present study, suggesting that Lao native goats exhibit moderate genetic diversity. Multiple factors, including inbreeding, small population size, and demographic history, could contribute to the different levels of heterozygosity observed (Cardoso et al. 2018).

Table 3. 4. The genetic diversity of goats in different locations

Location	Ho	He	Genetic marker	References
Mongolia	0.393-0.406	0.388-0.410	SNP	Mukhina et al. 2022
China	0.306-0.402	0.371-0.405	SNP	Berihulay et al. 2019
Greece	0.94-0.405	0.392-0.395	SNP	Michailidou et al. 2019
West Asia	0.375	0.379	SNP	Colli et al. 2018
Pakistani	0.200-0.348	0.236-0.347	SNP	Kumar et al. 2018

The effect of population size (N_e) is a crucial parameter in population genetics due to its association with genetic variation loss, rate of inbreeding, mutation accumulation, and the accuracy of genomic selection (Goddard, 2009). The N_e of Lao goats has decreased over generations, aligning with the global trend observed in goat breeds (Visser et al. 2016; Brito et al. 2017; Colli et al. 2018; Berihulay et al. 2019; Deniskova et al. 2021). The decline over time in effective population size could be due to natural and artificial selection (Monau et al. 2020). Given that goats in Laos are more likely to belong to a random mating population but with limited exchange of bucks or does between regions, the rapid change in N_e of Lao goats is possibly due to a lack of migration, rather than the consequence of domestication, selection, breed formation, and breed endangerment (Shin et al. 2013). N_e values in Lao populations are not considered low in comparison with recent N_e estimates with global and indigenous goat breeds. For instance, N_e at 13 generations ago ranged from 52 for Booted goats (Burren et al. 2016), 87 for Boer (Monau et al. 2020), 96 for Eghoria (Michailidou et al., 2019) to 266 for Tswana goats (Monau et al. 2020) and 796 for Dagestan (Deniskova et al. 2021). Furthermore, the N_e at 13 generations ago in Lao native goats were higher compared to those reported for goat breeds in Australia, Canada (Bruto et al. 2015) and Russia (Deniskova et al. 2021). The higher N_e of the Lao goat populations, compared to global breeds, could be attributed to the absence of artificial insemination in the breed development process and the application of less intensive management and breeding systems. This hypothesis is partially supported by the findings of Colli et al. (2018), which demonstrated that extensively managed local breeds tend to have higher N_e values compared to more intensively managed goat populations.

In order to ensure the preservation of genetic diversity and prevent negative effects from inbreeding, it is recommended to maintain the N_e values above 50 (Meuwissen & Goddard 2007). The current N_e values observed in the native goat population in Laos (N_e : 626) exceed this critical threshold required for population maintenance. However, it has been proposed that a higher N_e value, exceeding 100, is necessary for the long-term viability of the livestock population (Meuwissen 2009). The N_e value of Sepon 13 generations ago (N_e : 92) falls just below this threshold, indicating the need to increase the genetic pool in this area to achieve long-term selection and genetic response. It is advisable to consider

interventions such as the exchange of breeding bucks between regions or the application of artificial insemination (Tada et al. 2013).

Wright (1978) noted that low F_{ST} values indicate a close genetic relationship between populations. Low F_{ST} values among Lao goat population suggested minimal genetic differentiation and the presence of gene flow among those populations. Our findings showed that the global F_{ST} value within the Lao goat population was slightly higher than the global F_{ST} value in the Mongolian goats (Mukhina et al. 2022) but lower than the global F_{ST} values observed in Russian (Deniskova et al. 2021) and Chinese goat populations (Islam et al. 2019).

Results from F_{ST} , PCA, and admixture analyses illustrate more gene flow between Songkhone and Phin districts, and less between those districts and Sepon. The difference in gene flow between populations can often be explained by geographic isolation (Islam et al. 2019). Phin and Songkhone districts are not located far from each other and they both have access to the main road network. Farmers in these two districts benefit from easily trading goats between each other's locations in Xathamua town which is located almost halfway between the two districts and is close to the Savannakhet province centre. On the other hand, Sepon is more culturally and geographically isolated, being a more distinct ethnic and linguistic group (Mong Kong) that speaks a different language from Lao Loum (the main ethnic group) and Phu Tai in Songkhone and Phin. These differences in ethnic and language groups may potentially result in less frequent trade with the other two districts. Additionally, Sepon is closer to the Vietnam border, making it easier for farmers to trade goats with Vietnamese dealers and previous studies using microsatellite and mitochondrial DNA have reported low genetic differentiation between Lao and Vietnamese goats (Lin et al. 2013; Nguyen et al. 2022).

The results of the LD analysis suggest that greater levels of mixing in the Phin and Songkhone populations are responsible for the faster rate of decline in the LD between SNPs and this would be consistent with the results of the admixture analysis. The disruption of the LD patterns caused by the introduction of genetic variation through mixing is likely the cause of the observed decline in LD. Sepon, on the other hand, has higher levels of LD and lower levels of mixing, indicating a breeding history with a smaller gene pool and limited exchange with other populations.

This study has disproven concerns about a high level of inbreeding in native goats, as both F_{IS} and F_{ROH} were found to be close to zero. It also implies that the small body size, slow growth rate and high mortality rate observed in Lao goats are not caused by inbreeding depression. Furthermore, the inbreeding coefficient of Lao native goats in this study was lower than that reported in Malaysian native goats (Ernie Muneerah et al. 2021) and Lao goats (Lin et al. (2013)). The inbreeding coefficient values were comparable to those in other goat breeds globally, such as in Angola, Alpine, Saanen and Toggenburg (Visser et al. 2016) as well as indigenous goats in Mongolia (Mukhina et al. 2022), China (Islam et al. 2019) and Vietnam (Thuy et al. 2017).

In this study, the mean ROH number and mean ROH coverage (33-39 ROH and 5.92-6.85 Mb) for Lao goats were similar to those observed in Chinese (Zhong et al. 2023) and Mongolian native goats (Mukhina et al. 2022). However, the number of ROH in this study was lower than those reported for goat breeds in Russia (Deniskova et al. 2021), Turkey and Central Asia (Bertolini et al. 2018a) which have been selected for specific traits. The lower relative ROH values in native breeds compared to global breeds are potentially due to an increased homozygosity pattern caused by small population size and geographic isolation (Bertolini et al. 2018a). Similarly, a larger number of ROH and greater ROH coverage is commonly observed in breeds under selection compared to indigenous breeds (Bertolini et al. 2018a).

Longer ROH segments indicate more recent inbreeding, while shorter ROH segments reflect more ancient inbreeding (Cardoso et al. 2018). In this study, long ROH segments in the Lao goat population accounted for a minority of all ROH segment length classes. The long ROH segments might be a consequence of artificial selection, demographic decline or recent inbreeding (Purfield et al. 2012; Bertolini et al. 2018a). On the other hand, the majority of ROH segments fell in the short category. According to (Bertolini et al. 2018a), short ROH segments often result from ancestral family relatedness and similar observations have been made in other global and indigenous goat populations (Onzima et al. 2018; Michailidou et al. 2019; Deniskova et al. 2021; Zhong et al. 2023). This suggests the native goat breeds in this study have historical relatedness.

This study has some limitations, primarily related to sample location and size. Due to travel restrictions during and post COVID-19 pandemic in Laos, samples were only collected in three districts in Savannakhet province which has the largest proportion of Laos' goat population at 26% in 2014 (Gray et al. 2019). There was also an uneven sample size among districts, with three villages in each Phin and Songkhone district, while only one village in Sepon, due to the limited access in that area. To capture the full genetic diversity across the country, it is recommended to obtain samples from different locations in Northern and Southern Laos. Furthermore, the migration analysis could not definitively explain whether goats migrated directly from China and Pakistan to Laos or through another country due to a lack of samples from other countries in Southeast Asia. This discrepancy was due to some farmers in Sepon not being willing to participate in the project. Despite these limitations, the study revealed moderate genetic diversity and low inbreeding in Lao native goats in central areas. Historical gene flow between the districts was evident, with Songkhone and Phin goats showing a closer relationship than those in Sepon.

3.6. Conclusion

Our analysis of Lao goats revealed their close relationship with Chinese, Mongolian and Pakistani goats and shared ancestry with Chinese and Pakistani goats.

Our findings revealed that overall moderate level of genetic diversity and a low level of inbreeding in Lao native goats, with variations ranging from low to moderate across different populations. The goat population in Sepon was more differentiated compared to that in Songkhone and Phin, while the latter two populations displayed similar characteristics to each other.

Although goats in each district exhibited a strong trend of decreasing effective population sizes, none of them currently meet the criteria for being classified as endangered breeds. This indicates that efforts should be made such as increasing the number size and exchanging breeding bucks with other regions to prevent further decline in the N_e of Sepon goats.

3.7. Author contributions

JvdW, SWB, LO, SdlHS and SVL conceived the study. SVL performed the statistical analysis and wrote the manuscript. SdlHS, PA and JvdW supervised the statistical analysis and writing of the manuscript. All authors read and approved the final manuscript.

3.8. Acknowledgements

The authors gratefully acknowledge the financial support from Project LS/2017/034 for sample collection and genotyping. Special thanks to Dr. Ammaly Phengvilaysouk and his team from the National Agriculture and Forestry Research Institute in Laos for collecting ear-notch samples. We also express our gratitude to Dr. Watthana Theppangna from the National Animal Health Laboratory in Laos for assistance with paperwork and arranging the shipments of samples from Laos to New Zealand. Lastly, we thank Prof. John McEwan from AgResearch for his guidance with the genotyping strategy. The first author gratefully acknowledges financial support from the Australian Commonwealth Government through the Research Training Program stipend scholarship at the University of New England, Armidale, NSW, Australia.

3.9. Conflict of interest statement

The authors declare no conflict of interest.

3.10. Funding

This study was supported by the Australian Centre for International Agricultural Research under project LS/2017/034.

3.11. Data accessibility

The data are owned by Project LS/2017/034 and access to the data can be negotiated by request.

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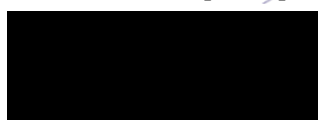
STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name (please print clearly)	% of contribution
Candidate	Sang Van Le	70
Other Authors	Julius van der Werf	9
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26/11/2024
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Higher Degree Research Thesis by Publication University of New England

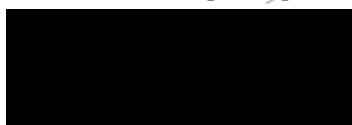
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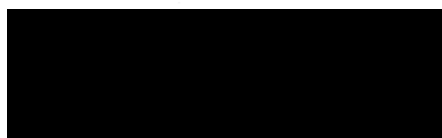
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**Chapter Four: Signature of selection analysis reveals candidate genes
related to tropical monsoon climate adaptation and production traits in
Lao native goats**

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Submitted to Journal of Animal breeding and genetics in July 2024

4.1. Abstract

Detecting selection footprints offers valuable insight into evolutionary processes and the mechanisms underlying phenotypic diversity in selected traits. Domestication, natural and artificial selection, and breeding have produced indigenous goats well-adapted to their local environments, making them crucial genetic resources. Understanding the genetic foundation of these adaptations can guide the development of effective breeding strategies to preserve and improve local goat breeds. This study investigated selection signatures in Lao native goats using Illumina's Goat SNP50 BeadChip, analysing 420 Lao native goats, 87 goats from three Chinese breeds, and 51 Teddi goats from Pakistan as test populations. We applied the de-correlation composite multiple signals (DCMS) method, incorporating *p*-values from nine statistical tests, including runs of homozygosity in the Lao goat population, and fixation index and cross-population extended haplotype homozygosity between Lao goats and test populations. Significant genomic regions were identified using a 0.05 threshold adjusted for multiple testing. Our results uncovered 24 genomic regions harbouring 68 unique-coding genes. Analysis revealed both annotated and novel candidate genes linked to a variety of characteristics, including adaption to the tropical monsoon climate (e.g. *ABHD6*, *GATA4*, *MSRA*) and economic traits like growth and status (e.g. *CNTNAP5*, *FAM135B*, *GATA4*), reproduction (e.g. *NPHP3*, *ARSL*, *GATA4*), milk production (e.g. *MRPL32*, *PRSS51*, *EPHA7*), and carcass characteristics (e.g. *GNAL1*, *SOX7*, *FAM135B*). These results offered insightful information about genetic mechanisms driving economic traits and tropical climate adaptation of Lao native goats. Combining *p*-values from various statistical tests into a single DCMS framework effectively assists in selecting and prioritizing candidate genes for further analysis.

4.2. Introduction

Animal domestication has played a crucial role in human demographic and cultural development. The important evolutionary forces acting along with domestication such as genetic drift, natural and artificial selection have produced an immense diversity of livestock populations observed today (Diamond, 2002). Goats were one of the first livestock species to be domesticated, around 10,000 years before the present, from wild goats (*Capra aegagrus*) in the Zagros mountains in modern-day Iran (Zeder & Hesse 2000). Following the initial domestication, goats dispersed with humans to different parts of the world.

Evolutionary processes such as genetic drift, natural and artificial selection have caused changes in specific genomic regions that contribute to particular breed characteristics. They can include body size, stature, growth, production performance, resistance to disease, and adaptation to different environments (Saravanan et al. 2020). Positive selection pressure leads to an increase in the frequency of advantageous alleles, resulting in unique signatures within the genome (Nielsen, 2005; Jensen et al., 2016). Signatures of selection studies aim to identify loci under selection providing opportunities to find targeted regions and genes related to economic traits or traits relevant to adaptation to specific environments. This can provide insights into functionally important genetic variants and a deeper understanding of population

origin and the genetic process influencing phenotypic differentiation and genetic improvement in the livestock population (Yurchenko et al., 2018).

In goats, detection of selection signatures using single nucleotide polymorphism (SNP) has been carried out for several goat breeds, exploring their genomes for adaptations to various breeding systems and environments. Studies have identified regions containing genes associated with different breeding objectives such as carcass, milk and fibre production (Brito et al. 2017; Bertolini et al. 2018b; Waineina et al. 2022). Additionally, these studies have revealed regions that are linked to reproduction traits (Lai et al. 2016; Brito et al. 2017) and immune functions in various goat breeds (Kim et al. 2016; Talenti et al. 2017; Yao et al. 2023). Selection signature studies in goats also found regions containing genes influencing coat colour, body size, lipid metabolism, energy metabolism and thermo-tolerance (Kim et al. 2016; Bertolini et al. 2018b; Yao et al. 2023). Some studies have identified regions associated with adaptation to specific environmental conditions, such as hot and dry climate in Barki goats in Egypt (Kim et al. 2016), and high-altitude environments in Tibetan goats in China (Jin et al. 2020).

Numerous methods have been proposed for detecting signatures of selection, including runs of homozygosity (ROH), fixation index (F_{ST}) and cross-population extended haplotype homozygosity (XP-EHH) analyses (Saravanan et al. 2020). ROHs are regions in the genome containing contiguous segments of the homozygous genome that are identical by descent (Ferenčaković et al. 2013). Natural or artificial selection pressure increases the homozygosity in the targeted genomic regions and leads to the occurrence of ROH (Pemberton et al. 2012). Therefore, genomic regions with high ROH frequency can be used to detect the association between genes and traits selected within a population (Ferenčaković et al. 2013; Szmatoła et al. 2016; Saravanan et al. 2020). Fixation index (F_{ST}), first defined by Wright (1965), is a metric that exploits variations in allele frequencies to infer the genetic differentiation between populations or generations (Weir & Cockerham 1984). Differences in allele frequencies between populations manifested as high F_{ST} values can be used to detect signatures of selection (Holsinger & Weir 2009). Certain loci under selection pressure exhibit changes in allele frequencies. Thus, high values of F_{ST} indicate a signature of selection due to differences in locus frequency between populations. The XP-EHH statistic assesses disparities in haplotype between two potentially divergent populations, in which the selected allele has approached or reached fixation in one population while remaining polymorphic in another (Sabeti et al. 2007).

Using individual statistical tests (applying either F_{ST} , ROH, or XP-EHH) often produces inconsistent results (Lotterhos & Whitlock 2015; Schlamp et al. 2016). The discrepancy may be attributed to factors such as varying sensitivity to sampling methods, specifics of the selective sweep, and the demographic background of the populations being studied (Lotterhos & Whitlock 2015; Schlamp et al. 2016). To tackle these challenges, a common strategy is to prioritize selection signals detected by multiple individual statistical tests (Lotterhos & Whitlock 2015; Wang et al. 2016; Mastrangelo et al. 2020), although this approach may lead to the loss of some loci that show weak signals (Lotterhos & Whitlock

2015; Ma et al. 2015). Consequently, methods have been developed that combine p -values of different statistical tests (Randhawa et al. 2014; Ma et al. 2015). One of these is a de-correlated composite of multiple signals (DCMS) method (Ma et al. 2015). Ma et al. (2015) observed that DCMS enhanced the resolution of selection signature mapping and improved the ability to detect selection signals compared to most statistical tests by themselves. Furthermore, composite measures of selection, like DCMS, have been demonstrated to more accurately identify the causal variant (Lotterhos et al. 2017).

The Lao goat population was estimated at 700 thousand heads in 2021 (FAOSTAT 2022) and distributed throughout the country which is located within the tropics. Most Lao goats belong to the native breed (Kangbing- Katjang), with a small proportion of exotic breeds, and crossbreds between indigenous goats and meat (e.g. Boer) or dual purpose (e.g. Bach-Thao) breeds (Phengsavanh 2006; Wilson 2007; Trach & Phiovankham 2011; Bui et al. 2023). Lao goats are generally kept for meat purposes rather than for milk, fiber or skin. Previous analysis suggested that goats possibly migrated to Laos from the centre of goat domestication via China and Pakistan (Le et al. 2024). Lao native goats share common ancestors with Chinese goat breeds (Guang Feng - GF, Jining Grey - JN and Luoping Yellow - LP) and a Pakistani goat breed (Teddi - Ted). Ted goats thrive in Pakistan's diverse environments, from cold and dry in winter (from December to February), to hot and dry during the spring (from March to May) and with a wet season during the Summer (from June to September). Ted goats have a small average yearling weight of 21.45kg and are primarily raised for meat (Kuthu et al. 2013). Characteristics of GF, JN, and LP were described by Islam et al. (2019). Briefly, these breeds were raised in various environments and under different breeding practices and kept at altitudes ranging from 45m to 1480m.

All these breeds are well adapted to the environmental conditions where they habitat either in China, Pakistan or Laos. This study aimed to detect selection signatures for Lao goat genome footprints compared with three goat breeds from China (GF, LP, JN) and one from Pakistan (Ted) and to better understand the function of candidate genes detected.

4.3. Materials and methods

4.3.1. Ethical statement

All the procedures conducted in this study were approved by the Animal Ethics Committee of the University of New England under approval number AEC21-084.

4.3.2. Animal and genotyping data

The dataset included the genotypic information from 420 goats from three districts in Savannakhet province in Laos (Lao dataset, Figure 4.1). Sample size, locations and genotyping were detailed by Le et al. (2023). Briefly, those animals were genotyped with the goat 50K Illumina BeadChip (Tosser-Klopp et al. 2014) containing 59,727 SNPs. Additionally, 87 Chinese goats from three breeds, GF

(N=24), JN (N=39), and LP (N=24) (Berihulay et al. 2019), as well as 51 Ted goats from Pakistan (Colli et al. 2018) were included as a test population in this study.

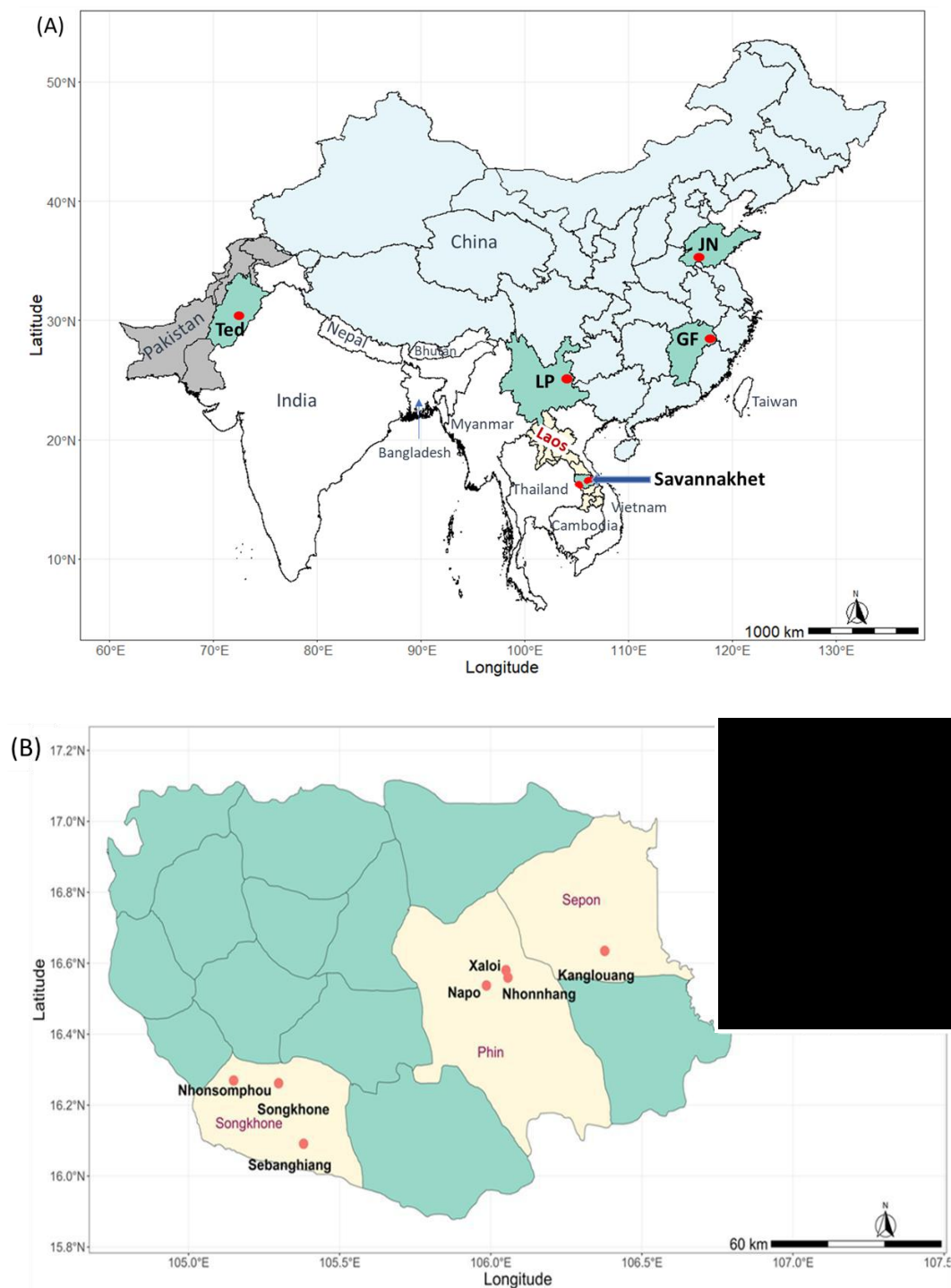


Figure 4. 1. Geographical location of goat samples used in this study. (A) Samples were collected from the Savannakhet province, Laos, and test populations GF, JN, and LP in Jiangxi, Shandong, and Yunnan provinces, China, respectively (Islam et al. 2019), and Ted in the Punjab province, Pakistan (Colli et al. 2018). (B) Samples were collected from seven villages in Songkhone, Phin and Sepon districts of Savannakhet province in Laos.

Quality control steps were conducted across the datasets using Plink v1.9 (Purcell et al. 2007), which involved removing SNPs with GenCall score <0.5 , SNPs on the sex chromosome, SNPs with a call rate $<90\%$, and those that deviated from Hardy-Weinberg equilibrium (p -value $< 10^{-6}$). Additionally, individuals with more than 10% missing SNPs were removed. Following the quality control, 2 Ted goats were discarded, while no animals from the other datasets were removed. After quality control, the common SNPs between the Lao dataset with all test populations were 38,946 SNPs. For haplotype-based analysis, each dataset was phased using Eagle v2.4.1 with default parameters (Loh et al. 2016).

4.3.3. Population structure

Using the shared SNPs (38K), a principal component analysis (PCA) was performed on the genomic relationship matrix (GRM), both generated in Plink v1.9, to identify any clustering pattern between the Lao native goats and the test populations. The PCA was visualized with the “ggplot2” R package (Wickham 2011).

4.3.4. Signature of selection analyses

The identification of selection signatures for Lao native goats relied on identifying areas with reduced variation relative to the genome average and the properties of haplotypes segregating in the populations. A total of nine tests were employed, including one test within the Lao goat population (ROH) and eight tests based on comparisons between Lao goats and each of the test populations (Ted, GF, JN, and LP), using either the F_{ST}

or the XP-EHH methods.

ROH Islands: Identification of ROH islands within the Lao dataset was performed using the “detectRUNS” v0.9.6 package in R (Biscarini et al. 2018) and employing the consecutive run methods proposed by Marras et al. (2015). The detection of the ROH segment was the same as the one described by Walkden-Brown et al. (2024). To minimize the occurrence of false positive results, we implemented a threshold by setting the minimum number of SNPs within each sliding window at 47, following the approach outlined in Purfield et al. (2012). To identify genomic regions with a high frequency of ROH, the percentage of times an SNP occurs within an ROH segment out of the total occurrences of each SNP within any segment was calculated across the population.

Fixation index: In order to ensure unbiased data for the comparison between breeds, we selected the same sample size having 50, 39, 24 and 24 most unrelated Lao goats for an F_{ST} analysis with Ted, GF, JN, and LP, respectively. Relatedness was derived from the genomic relationship matrix. In these statistics, animals from the test population were selected with an average relationship of less than 0.125. Weir and Cockerham (1984) F_{ST} was estimated in PLINK v1.9 (Purcell et al. 2007) between the Lao

native goat population and each of the test populations. Any negative F_{ST} values were converted to zero. To minimize potential noise in the estimate and address the linkage disequilibrium between adjacent SNPs, the “runmed” R function (Hardle & Steiger 1995) was employed to smooth F_{ST} values using a moving window of 47 markers per chromosome as described for the ROH analysis.

Cross-population extended haplotype homozygosity: Four pairwise XP-EHH analyses between the Lao goats with each of the four test populations were performed. The XP-EHH scores were calculated using the “rehh” package v3.2.2 (Gautier et al. 2017) to identify the alleles that have increased frequency to the point of fixation in Lao native goats compared to other test breeds. In these pairwise analyses, four test breeds (Ted, GF, JN, and LP) were considered as the test population to identify potential selection signatures in Lao native populations. XP-EHH identifies SNPs under selection in one population but not in another, so only the extremely positive XP-EHH scores identified SNPs under selection in Lao native goats, but not in the test population breeds.

4.3.5. De-correlated composite of multiple signals calculation

To avoid potential inconsistencies often produced by individual statistical tests (Lotterhos & Whitlock 2015; Schlamp et al. 2016), results from the signature of selection methods were integrated into a single de-correlated composite of multiple signals (DCMS), as described by Ma et al. (2015) and Yurchenko et al. (2018). The DCMS method combines p -values from various test statistics for each locus into one measure, accounting for the correlation between the statistics. We utilized the *stat_to_pvalue* function from the “MINOTAUR” R package (Verity et al. 2017) to calculate the genome-wide rank of the p -value for each of the SNPs for each test statistic, using a one-tail test (left-tailed for ROH and right-tailed test for F_{ST} and XP-EHH). Subsequently, we calculate the covariance matrix for nine statistics using the *CovNAMcd* functions (with parameters $\alpha = 0.75$ and $nsamp = 50000$) from the “rrcovNA” v0.5-1 package (Todorov et al. 2011) to assign different weights to each statistics’ p -value based on their overall correlation (Ma et al. 2015). This covariance matrix was used as one of the input files to calculate the DCMS values with the *DCMS* function in the “MINOTAUR” package. The formula for calculating DCMS at position l is as follows (Ma et al. 2015)

$$DCMS_l = \sum_{t=1}^n \frac{\log \left[\frac{1 - p_{lt}}{p_{lt}} \right]}{\sum_i^n |r_{it}|}$$

where $DCMS_l$ is the DCMS p -value for SNP at position l , p_{lt} represents the p -value at position l for test statistic t ; r_{it} denotes the correlation between the test statistics of the i^{th} and t^{th} methods, and n refers to the total number of test statistics in the DCMS. The $1/\sum_i^n |r_{it}|$ term refers to the weighting factor for each method, ranging from $1/n$ to 1. These weights are based on the genome-wide correlation of test

statistics pairwise between methods, helping to prevent overly correlated statistics from disproportionately influencing the DCMS calculation.

The DCMS values were then fitted to a normal distribution using the robust linear model (*rlm*) function from the “MASS” v7.3-61 package (Venables & Ripley 2013) as outlined by Yurchenko et al. (2018). The fitted DCMS statistics were then converted into *p*-values by using the *pnorm* function in R with parameters lower.tail=FALSE and log.p=FALSE. Finally, we used the *p.adjust* function in R with the Benjamini and Hochberg method to convert the DCMS *p*-values to DCMS *q*-values (Storey & Tibshirani 2003). The $q - \text{value}(i) = \frac{p\text{-value}(i) * m}{i}$ where *p*-value (*i*) is the original DCMS *p*-value at the position (*i*), *m* is the total number of DCMS tests (*m*=9) and (*i*) is the rank of the *p*-value when all *p*-values are sorted in ascending order.

4.3.6. Gene annotation of candidate regions

A candidate region for a signature of selection was defined as significant intervals. The boundaries for a significant interval were determined by identifying the SNPs, first adjacent to the significant SNP (*q*-value < 0.05), with a *q*-value greater than 0.1. Therefore, these intervals included consecutive SNPs, with at least one SNP exhibiting a significant *q*-value lower than 0.05. The candidate regions were investigated to detect candidate genes mapped inside them using the “biomaRt” v1.0.7 package (Durinck et al. 2009) based on the goat reference genome assembly (ARS1). Lastly, we conducted a comprehensive literature review to annotate the functions of the identified genes.

4.4. Results

4.4.1. Population structure

Figure 4.2 displays the PCA plots generated using SNP chip data for the five investigated goat breeds. All breeds were distinctly separated by the first three principal components. The three breeds from China were closely clustered together, distinct from the Lao and Ted goats. However, there was no overlap between them, with the GF breed being closer to JN than to LP, with the LP breed more clearly separating according to the 3rd PC.

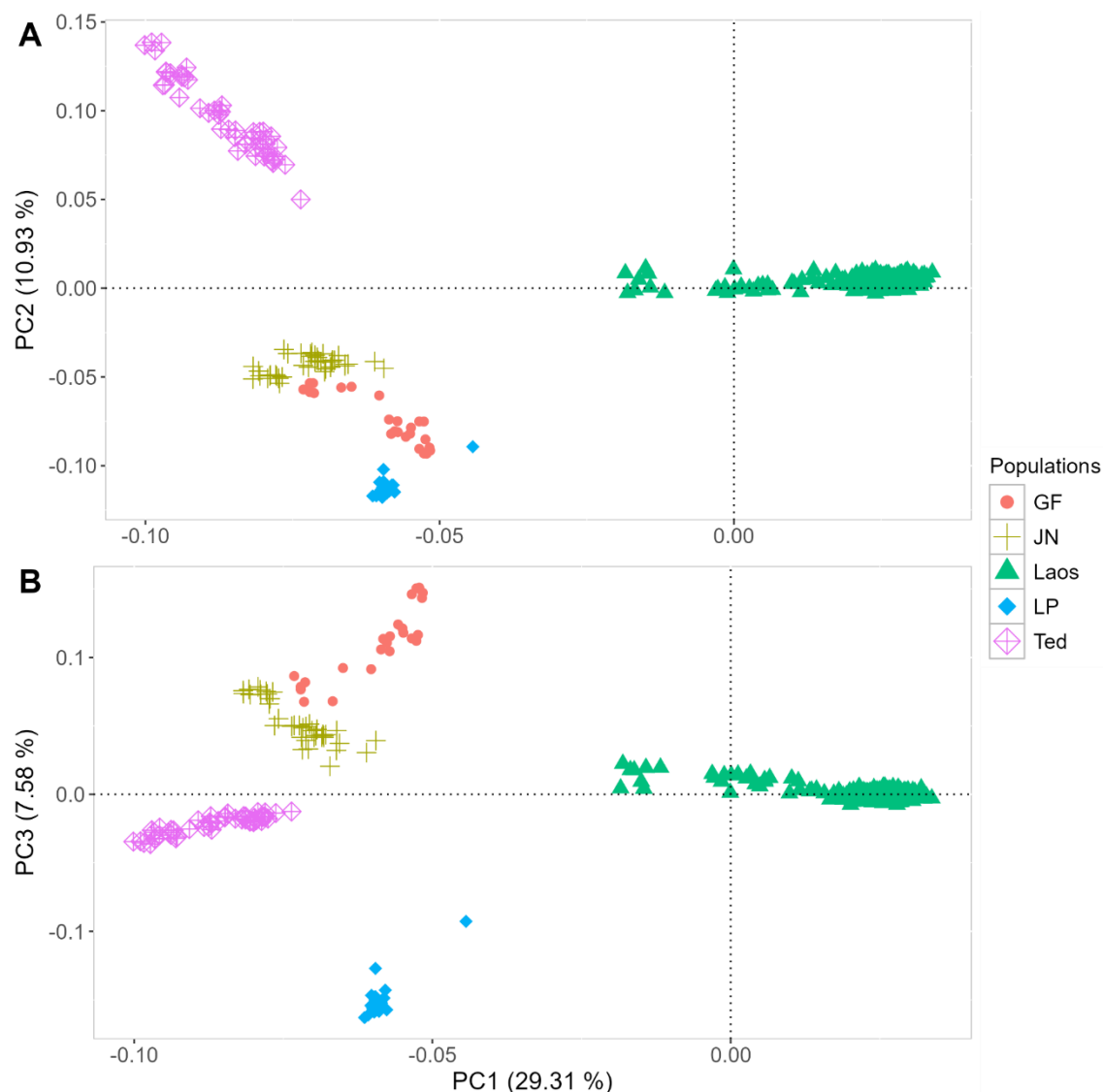


Figure 4. 2. Principal component analysis for five goat breeds as (A) PC1 vs PC2 and (B) PC1 vs PC3. Each dot represents a goat, and colours represent breeds. GF (Guang Feng), JN (Jining Grey) and LP (Luoping Yellow) are from China, Ted (Teddi) is from Pakistani and Laos (Lao native goats).

4.4.2. De-correlated composite of multiple signals (DCMS)

After adjusting for p -values for multiple tests with FDR, there were 24 genomic regions for Lao native goats with DCMS q -values less than 0.05 (Table 4.4.1 and Table 4.4.2). The total length of the genomic regions covered with significant signals and the number of the identified protein-coding genes was 12.7 Mb, with the average length of the significant region being 529kb, ranging from 110kb to 1610kb. In 24 genomic regions, 68 unique protein-coding genes were identified for Lao native goats (Table 4.4.1). We observed there were no protein-coding genes in six genomic regions.

Table 4. 1. Descriptive statistics of the genomic regions identified through the DCMS for Lao native goats

Breed	N regions	Average length $\pm$ SD (Kb)	Number of SNPs ¹	Total size (Mb)	Genes ²
Lao native	24	529 $\pm$ 390	195	12.70	68

¹ Number of SNPs: Number of significant SNPs detected in a candidate region (q -value < 0.05)

² Number of Genes: number of protein-coding genes located in the significant regions detected by the DCMS approach

The Manhattan plot illustrating the distribution of selection signature regions across the genome of the Lao native goats is presented in Figure 4.4.3. The most significant genomic region was identified on chromosome 8, from 7.45 to 9.06 Mb. The next most significant genomic regions were observed on chromosomes 22 (39.83 – 40.65 Mb), 19 (17.28 – 18.15 Mb), 4 (85.97 – 86.42 Mb) and 9 (81.29 – 81.62) (Table 4.4.2 and Table S4.1).

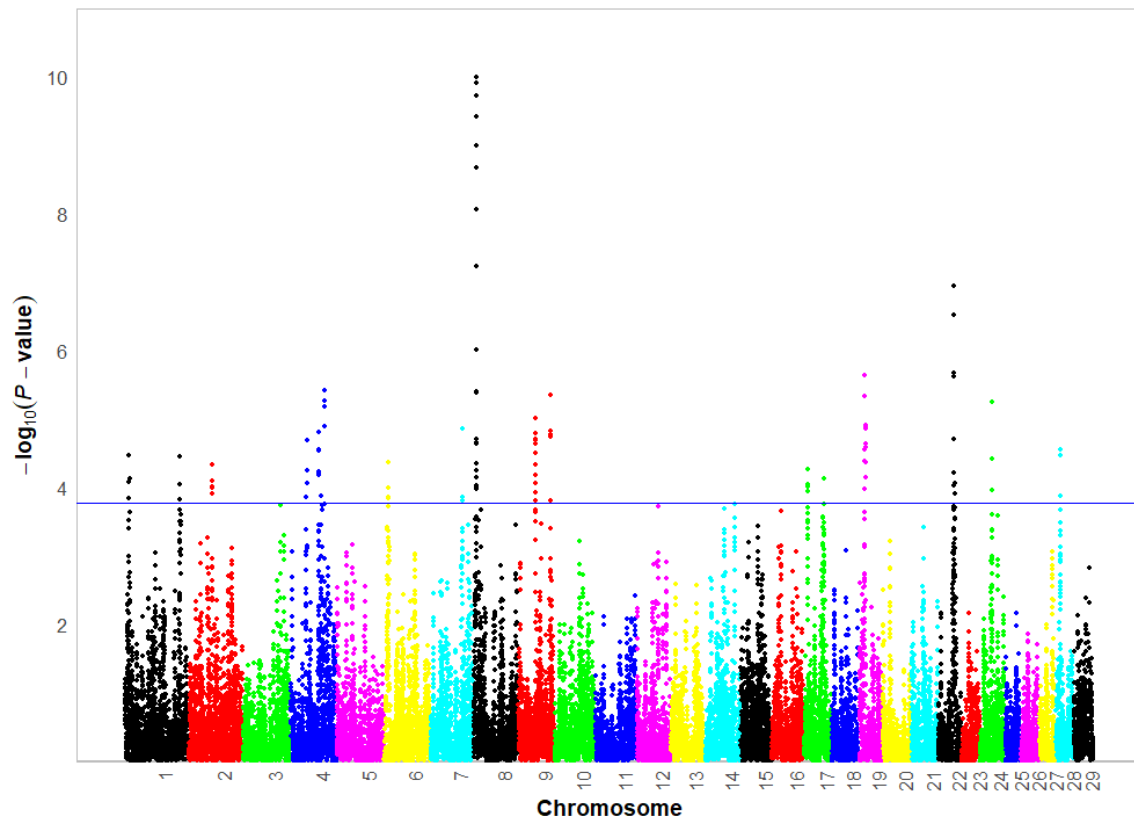


Figure 4. 3. Manhattan plot of the genomic regions detected by the DCMS approach identified in Lao native goats. The significant threshold (q -value ≤ 0.05) is indicated by the horizontal blue line.

Table 4. 2. The number of significant SNPs, the number of genes and annotated genes found in the region under the DCMS approach across the Lao native goat genome

CHR	Region (Mb)	Number of SNPs ¹	Number of Genes ²	Candidate genes
1	135.89 - 136.51	13	1	<i>NPHP3</i>
2	59.52 - 59.78	7	1	<i>CNTNAP5</i>
4	41.8 - 42.1	6	3	<i>C7orf25, PSMA2, MRPL32</i>
4	72.45 - 73.14	12	3	<i>SYPL1, CCDC71L, NAMPT</i>
4	79.14 - 79.44	6	1	<i>GNAI1</i>
6	11.67 - 12.24	13	1	<i>ARSJ</i>
7	79.69 - 79.93	5	1	<i>PPIC</i>
7	80.07 - 80.35	4	1	<i>CEP120</i>
8	7.45 - 9.06	28	13	<i>GATA4, MTMR9, PRSS51, MSRA, SOX7, FAM167A, XKR6, BLK, C8orf74, FDFT1, NEIL2, PINX1, MSRA</i>
9	44.1 - 45.29	16	1	<i>EPHA7</i>
9	81.29 - 81.62	8	1	<i>ZDHHC14</i>
14	77.45 - 77.86	7	1	<i>FAM135B</i>
17	11.98 - 13.13	16	6	<i>MED13L, HRK, MED13L, SPRING1, FBXW8, RNFT2</i>
17	52.87 - 52.98	4	1	<i>MGST2</i>
19	17.28 - 18.15	17	14	<i>CDK5R1, PSMD11, ADAP2, ZNF207, MYO1D, RHOT1, ATAD5, COPRS, CRLF3, RNF135, TEFM, C17orf75, RHBDL3, SUZ12</i>
22	39.83 - 40.65	11	-	
22	41.63 - 41.78	3	-	
22	42.75 - 43.81	8	15	<i>FAM107A, ASB14, SLMAP, DENND6A, ABHD6, ACOX2, PDE12, KCTD6, FLNB, APPL1, RPP14, DNASE1L3, DNAH12, HESX1, PXX</i>
24	30.58 - 30.9	6	2	<i>KCTD1, TAF4B</i>
24	31.26 - 31.42	5	-	
28	10.49 - 10.64	5	2	<i>ANXA11, ZCCHC24</i>

¹ Number of SNPs: Number of significant SNPs detected in a candidate region (q -value < 0.05)

² Number of Genes: number of protein-coding genes located in the significant regions detected by the DCMS approach

4.4.3. Gene annotation

Gene annotation of the candidate regions detected various verified and novel candidate genes that are associated with adaptation and economically important production traits. Genes associated with adaptation include those for altitude (*GNAI1*), heat stress and heat tolerance (*PSMA2*, *MRPL32*, *ARSJ*, *FDFT1*, *NEIL2*, *MGST2*, *MYO1D*, *ABHD6*, *RPP14*, *KCTD1*), stress response (*CEP120*, *GATA4*, *MSRA*, *XKR6*, *MGST2*), cold acclimation (*ABHD6*), immune response (*GATA4*, *BLK*, *MED13L*, *MGST2*, *PSMD11*, *RNF135*, *PDE12*, *DNASE1L3*), resistance to disease and bacterial infection (*PSMA2*, *EPHA7*, *ZDHHC14*, *RHBDL3*), DNA repair (*MGST2*), and survival (*DNAH12*). Genes linked to a diverse range of traits, including body size and stature (*CNTNAP5*, *NAMPT*, *GATA4*, *FAM135B*, *MED13L*, *FBXW8*, *RNFT2*, *SLMAP*, *ACOX2*, *FLNB*), growth and feed intake (*NAMPT*, *MTMR9*, *PINX1*, *FAM135B*, *ABHD6*, *APPL1*, *HESX1*), carcass-related traits (*CNTNAP5*, *MRPL32*, *NAMPT*, *GNAI1*, *MSRA*, *SOX7*, *FAM167A*, *XKR6*, *PINX1*, *EPHA7*, *FAM135B*, *RHOT1*, *ASB14*, *SLMAP*, *DNASE1L3*), reproduction (*NPHP3*, *ARSJ*, *CEP120*, *GATA4*, *SOX7*, *BLK*, *MGST2*, *RNF135*, *ASB14*, *ABHD6*, *PDE12*, *FLNB*, *RPP14*, *DNASE1L3*, *DNAH12*, *HESX1*, *PXK*, *KCTD1*, *ANXA11*), milk production (*MRPL32*, *GNAI1*, *CEP120*, *PRSS51*, *EPHA7*, *FAM135B*, *RNFT2*, *MGST2*, *CDK5R1*, *ADAP2*, *MYO1D*, *RHBDL3*, *FAM107A*, *ABHD6*, *KCTD6*, *FLNB*, *DNAH12*, *ZCCHC24*), and horn (*EPHA7*, *HRK*). Additionally, genes involved in the metabolism process (*GNAI1*, *EPHA7*, *ABHD6*, *PXK*) (Table 4.4.3).

Table 4. 3. Genomic regions detected and potential candidate genes related to tropical monsoon climate adaptation and economically important traits in Lao native goats

Region (Mb) ¹	q -value ²	Candidate gene	Gene function and citation
1: 135.89 - 136.51	2.04E-02	<i>NPHP3</i>	Reproduction (Othman et al. 2022)
2: 59.52 - 59.78	2.32E-02	<i>CNTNAP5</i>	Body size and stature (Bermudez-Wagner et al. 2013; Rohrer et al. 2015; Rahmatalla et al. 2018; Chen et al. 2020; Vanvanhossou et al. 2020). Carcass (Vanvanhossou et al. 2020)
	1.66E-02	<i>PSMA2</i>	Heat stress (Weitzel et al. 2017)

4: 41.8 - 42.1		<i>MRPL32</i>	Disease resistance (Ullah et al. 2022)
			Carcass (Imumorin et al. 2011)
			Milk composition and milk production (Pimentel et al. 2011)
4: 72.45 - 73.14	1.55E-02	<i>NAMPT</i>	Body size and stature (Wang et al. 2009; Basse et al. 2021)
			Carcass-related traits (Cepica et al. 2010)
			Growth and feed intake (Zappaterra et al. 2015)
4: 79.14 - 79.44	4.27E-02	<i>GNAI1</i>	High-altitude adaptation (Jin et al. 2024)
			Milk production (Laodim et al. 2024)
			Carcass and lipid metabolism (Wang et al. 2020)
6: 11.67 - 12.24	2.32E-02	<i>ARSJ</i>	Heat tolerance (Nguyen 2021)
			Reproduction (Michenet et al. 2016)
7: 80.07 - 80.35	1.49E-02	<i>CEP120</i>	Milk composition (Du et al. 2019)
			Reproduction (Song et al. 2022)
			Stress response (Duarte et al. 2022; Song et al. 2022)
8: 7.45 - 9.06	1.87E-06	<i>GATA4</i>	Immune response (Zhang et al. 2023) (Patel et al. 2022)
			Body size and stature (Li et al. 2024)
			Reproduction (Michenet et al. 2016; Bennett-Toomey & Stocco 2018; Grigoletto et al. 2020; Wang et al. 2023)
			Stress response (Aries et al. 2004)
		<i>MTMR9</i>	Residual feed intake (Brunes et al. 2021)
		<i>PRSS51</i>	Milk production (Mohammadi et al. 2022)
		<i>MSRA</i>	Meat quantity and quality (Jourshari et al. 2023)
			Stress response and environmental adaptation (Gheyas et al. 2021; Vahedi et al. 2022)
		<i>SOX7</i>	Reproduction (Grigoletto et al. 2020)
			Carcass traits (Li et al. 2022)
		<i>FAM167A</i>	Adaptation (hair follicle cycle) (Wu et al. 2022)
			Carcass traits (Kenny 2022)

				Stress response (Littlejohn et al. 2018)
			<i>XKR6</i>	Carcass-related traits (Hieber et al. 2018; Shang et al. 2019; Blaj et al. 2022; Kenny 2022)
			<i>BLK</i>	Immune response (Maruyama et al. 2019; Scott et al. 2022) Reproduction (Gao et al. 2019)
			<i>FDFT1</i>	Heat stress (Garner et al. 2020)
			<i>NEIL2</i>	Heat stress (Garner et al. 2020)
			<i>PINX1</i>	Carcass (Li et al. 2022) Residual feed intake (Li et al. 2021)
9: 44.1 - 45.29	1.27E-02	<i>EPHA7</i>		Horn colour (Zsolnai et al. 2021) Milk composition (Bekele et al. 2023) Meat quality traits (Leal-Gutierrez et al. 2019) Resistance to disease (Cinar et al. 2023) Lipid metabolism (Poirier 2020)
9: 81.29 - 81.62	7.34E-03	<i>ZDHHC14</i>		Disease resistance (Mallikarjunappa et al. 2021)
14: 77.45 - 77.86	4.93E-02	<i>FAM135B</i>		Hip width and rump width (Doyle et al. 2020) Growth and residual feed intake (Serão et al. 2013; Carvalho et al. 2020) Carcass (Kim et al. 2022) Milk production (Liu et al. 2021) Milk composition (Jiang et al. 2014; Freitas et al. 2021)
17: 11.98 - 13.13	2.70E-02	<i>MED13L</i>		Body size and stature (Ma et al. 2023) Immune response (Li et al. 2023)
		<i>HRK</i>		Hornless (Carlson et al. 2016)
		<i>FBXW8</i>		Body weight (Braz et al. 2021)
		<i>RNFT2</i>		Body size (Lim & Kim 2022) Milk production (Du et al. 2019)

17: 52.87 - 52.98	3.18E-02	<i>MGST2</i>	Heat stress (Duffy 2019)
			Oxidative stress response (Wu et al. 2014)
			Adaptation (DNA repair) (Chebii et al. 2021)
			Immune response (Sorbolini et al. 2016)
			Milk urea metabolites (Honerlagen et al. 2021)
			Reproduction (Udder structure) (Nazar et al. 2022)
19: 17.28 - 18.15	5.26E-03	<i>CDK5R1</i>	Milk composition (Ma et al. 2021)
		<i>PSMD11</i>	Immune responses (Estrada-Reyes et al. 2022)
		<i>ADAP2</i>	Milk production (Habimana et al. 2023)
		<i>MYO1D</i>	Heat tolerance (Freitas et al. 2021)
			Milk production (Lu et al. 2022)
		<i>RHOT1</i>	Bone weight traits (Gao et al. 2023)
		<i>RNF135</i>	Immune response (Cai et al. 2022)
			Reproduction (Gaddis et al. 2016)
22: 42.75 - 43.81	3.41E-02	<i>RHBDL3</i>	Milk yield and mastitis (Schneider et al. 2024)
		<i>FAM107A</i>	Milk production (Koringa et al. 2016; Fonseca et al. 2023)
		<i>ASB14</i>	Carcass-related traits (Martins et al. 2021)
			Reproduction (Rios et al. 2023)
		<i>SLMAP</i>	Body size and stature (Mukherjee et al. 2020).
			Rump fat thickness (Martins et al. 2021)
		<i>ABHD6</i>	Cold tolerance (Poursharifi et al. 2020)
			Heat tolerance (Luo et al. 2022)
			Average daily gain (Schweer et al. 2018; Mukiibi et al. 2019)
			Lipid metabolism (Mukiibi et al. 2019)
			Milk cholesterol content (Do et al. 2018)
			Reproduction (Bertevello et al. 2018; Reding et al. 2023)

		<i>ACOX2</i>	Muscle production and growth (Mohammadabadi et al. 2021)
		<i>PDE12</i>	Immune response (Wood et al. 2015; Eloiflin et al. 2021) Reproduction (Khayatzadeh et al. 2019; Rios et al. 2023)
		<i>KCTD6</i>	Milk composition (Do et al. 2018)
		<i>FLNB</i>	Body size and stature (Farrington-Rock et al. 2008) Milk production (Volkandari et al. 2021) Reproduction (Rios et al. 2023)
		<i>APPL1</i>	Growth and feed intake (Schweer et al. 2018; Davoudi et al. 2024)
		<i>RPP14</i>	Heat stress (González Luna 2022) Reproduction (Reding et al. 2023)
		<i>DNASE1L3</i>	Immune system processes (Chen et al. 2021) Reproduction (Barnwell et al. 2016) Carcass-related traits (Sood 2023)
		<i>DNAH12</i>	Milk production and composition (Pimentel et al. 2011; Di Gerlando et al. 2019). Reproduction (Oud et al. 2021) Survival (Madden et al. 2014)
		<i>HESX1</i>	Growth and average daily gain (Lai et al. 2009) Reproduction (Rios et al. 2023)
		<i>PXK</i>	Energy metabolism (Khayatzadeh et al. 2019) Reproduction (Reding et al. 2023)
24: 30.58 - 30.9	8.17E-03	<i>KCTD1</i>	Heat stress/tolerance (Garner 2017; Aboul-Naga et al. 2022) Reproduction (Klein 2021)
28: 10.49 - 10.64	1.82E-02	<i>ANXA11</i>	Reproduction (Oliveira et al. 2019)
		<i>ZCCHC24</i>	Milk production (Pedrosa et al. 2021; Massender et al. 2023)

¹ Region (Mb): **Chromosome:** Start (Mb) - End (Mb)

² q-value: Adjusted p-value of the most significant SNP within the significant genomic regions

4.5. Discussion

Our study identified selection candidate genes and regions by using genome-wide SNP data. Genomic regions under selection were assessed by comparing indigenous Lao goats with goat breeds from China (GF, JN and LP) and Pakistan (Ted) using F_{ST} , ROH, and XP-EHH analyses. Although the statistical power to detect selection signatures can vary with each approach, combining different methods can increase detection accuracy and decrease bias (Grossman et al. 2010; Ma et al. 2015). Our results identified several genomic regions and genes that are associated with adaptation to tropical climate, body size and stature, growth and feed intake, carcass-related traits, reproduction, milk production, disease resistance, and immune response.

The principal component analysis confirmed that Lao goats form a distinct cluster, separate from the test populations (Figure 4.2), aligning with the results of Le et al. (2024). Within the test populations, the Ted and LP groups also formed distinct clusters. Conversely, the GF and JN groups clustered together despite being subjected to different breeding practices and environmental conditions (Islam et al. 2019). In addition, Le et al. (2024) reported that GF and JN shared a common ancestor with Lao native goats but with different proportions, ranging from 7% to 15%. Therefore, we maintained Ted, GF, JN and LP as independent test populations.

The genomic regions under selection identified in this study included genes that may be associated with adaptation to the Laos tropical monsoon climate such as genes involved in heat and stress tolerance, immune response, and disease resistance. A large number of identified genes can be indicative of complex adaptation processes that involve multiple genes acting together (Lv et al. 2014; Kim et al. 2016). The genomic regions identified in this study showed limited overlap between breeds, indicating that the selection of genes involved in adaptation to a tropical environment can be breed-specific, as previously identified in African goats (Onzima et al. 2018). Additionally, the selection signatures identified in our study did not display any of the hard selective sweep characteristics found in European goat breeds (Talent et al. 2017). Instead, they were more associated with adaptation to the local climate and disease.

4.5.1. Signature of selection related to adaptation to tropical climate and disease resistance

Several genes found in this study have been previously reported to be associated with heat stress and thermal tolerance (Table 4.3). For example, *ABHD6* is involved in adaptive thermogenesis and linked to both cold and heat tolerance in cattle (Poursharifi et al. 2020; Luo et al. 2022), *NEIL2* has shown differential expression in bovine white blood cells during heat challenges (Garner et al. 2020), while *PSMA2* has been linked to heat stress responses in late pregnant cows (Weitzel et al. 2017). *MGST2* and *RPP14* play a role in heat stress response in sheep (Duffy 2019; González Luna 2022), and *ARSL*,

KCTD1, and *MYO1D* have been reported to be linked to heat tolerance in different cattle breeds (Garner 2017; Freitas et al. 2021; Nguyen 2021; Aboul-Naga et al. 2022). Variations in these genes could explain how Lao goats adapted to the tropical monsoon climate which is characterized by abundant rainfall during the wet season from May to October with hot, drier conditions during the dry season from November to April (Gupta 2005).

Lao goats are subjected to traditional management with free grazing during the day coupled with housing at night in often poor-quality shelters and are subject to many disease syndromes (Gray et al. 2019). Additionally, the tropical monsoon climate contributes to extreme weather events such as droughts and floods, which can lead to prolonged stress and malnutrition and also facilitate the spread of infectious diseases to Lao goats (Miyan 2015). In this study, we found 16 genes located across chromosomes that may be involved in immune response, disease resistance and stress response for Lao native goats. *BLK* is involved in the immune response against tick infestation in calves and skews the immune response towards Th2-type immunity in cattle (Maruyama et al. 2019; Scott et al. 2022). *GATA4* and *MED13L* play significant roles in immune regulation and inflammatory responses (Patel et al. 2022; Li et al. 2023; Zhang et al. 2023). *PDE12* and *PSMD11* regulate the innate immune response, especially *PDE12* is involved in resistance to *peste des petits ruminant's virus* replication in goats (Eloiflin et al. 2021). *DNASE1L3* contributes to immune system processes in cattle under different diets (low and high concentrate diets) and in humans, where its dysfunction can lead to autoimmune diseases (Chen et al. 2021).

Genes such as *MSRA*, *MGST2*, and *PSMA2* are pivotal for stress response. *MSRA*, located near the peak of DCMS on chromosome 8, is essential in repairing oxidative stress-induced protein damage, playing an important role in stress response in mammals (Vahedi et al. 2022). *MGST2* is correlated with oxidative stress responses, featuring unique amino acid changes in camels (Wu et al. 2014), while *PSMA2* is involved in response to stress, cytokine and metabolic processes (Weitzel et al. 2017; Zhuang et al. 2022). In addition, we identified *CEP120* on chromosome 7, which is associated with cortisol response to stress (Duarte et al. 2022), and *XKR6* on chromosome 8, which is associated with stress before giving birth to cows (Littlejohn et al. 2018). Lastly, *GATA4* is linked to adaptative stress response in mice (Aries et al. 2004; Madden et al. 2014).

4.5.2. Signatures of selection for body size, stature, growth and feed intake

Goats in Central Laos are primarily free or semi-freely grazed on communal land with often have access to forested areas for forage (Gray et al. 2019). In this study, the most significant peak identified by the DCMS approach was located on chromosome 8 (7.45 to 9.06 Mb), with the most significant SNP having a *q*-value of 1.87E-06. Previous studies have indicated that regions around this locus harbour numerous genes and QTLs influencing stature and related traits in ruminants and other species (Farrington-Rock

et al. 2008; Wang et al. 2009; Chen et al. 2020; Doyle et al. 2020; Vanvanhossou et al. 2020; Lim & Kim 2022; Li et al. 2024).

Genes associated with body conformation and growth included *CNTNAP5*, *FAM135B*, *MED13L*, *GATA4*, *RNFT2*, and *NAMPT*. Genome-wide associated studies have shown the roles of *CNTNAP5* in body conformation traits such as bicoastal diameter and body length in Sudanese goats (Rahmatalla et al. 2018), body length of Benisese indigenous cattle (Vanvanhossou et al. 2020), and hip cross height in Brahman cattle (Chen et al. 2020). As a member of the neurexin family, *CNTNAP5* functions as a cell adhesion molecule and receptor in the vertebrate nervous system. Additionally, *CNTNAP5* was associated with conformation in humans (Bermudez-Wagner et al. 2013) and vertebral number in pigs (Rohrer et al. 2015).

FAM135B has been reported to be associated with hip width or rump width in Herford cattle (Doyle et al. 2020). *MED13L* is associated with body mass index, body weight, appendicular lean mass, and body height in humans (Ma et al. 2023). Additionally, *GATA4* influences the growth of Shaanbei and Guizhou goats by regulating bone genesis and differentiation (Li et al. 2024). *RNFT2* has been associated with body size in dogs (Lim & Kim 2022). *NAMPT* influences birth weight and six-month-old body weight in cows (Wang et al. 2009) and is crucial for maintaining cellular Ca^{2+} homeostasis and skeletal muscle development in mice (Basse et al. 2021).

Genes related to skeletal and muscle development include *SLMAP*, *EPHA7*, and *FLNB*. *SLMAP* has been identified to be associated with muscle growth in Indian Mithun cattle (Mukherjee et al. 2020). *EPHA7* was reported to be associated with bovine skeletal muscle in multibreed Angus-Brahman (Leal-Gutierrez et al. 2019). *FLNB* is involved in cartilage and bone morphogenesis in Piemontese and Marchigiana cattle (Sorbolini et al. 2015).

Genes associated with growth, feed efficiency and body composition include *ABHD6*, *APPL1*, *CEP120*, *FAM135B*, *MTMR9*, and *PINX1*. Mukiibi et al. (2019) reported that *ABHD6* was linked to average daily gain in Angus cattle and it is involved in lipid metabolism. Variations in lipid synthesis between fast and slow-growing animals may suggest variances in energy utilization efficiency, as fast-growing animals prioritize energy towards protein deposition rather than fat synthesis and deposition. *ABHD6* was observed to be downregulated in the liver tissue of high-ADG Angus cattle, suggesting a role in efficient energy utilization (Mukiibi et al. 2019).

The *APPL1* gene has been reported to be linked to feed efficiency traits in beef cattle through the regulation of glucose (Schweer et al. 2018) and is also linked to growth and feed efficiency traits in mink (Davoudi et al. 2024). Similarly, *CEP120* has been noted for its involvement in the regulation of feed intake and energy homeostasis in Rongchang and Jinhua breeds (Li et al. 2017). *FAM135B* is associated with residual average daily gain in SimAngus cattle (Serão et al. 2013), and yearly weight in

Nellore cattle (Carvalho et al. 2020). *MTMR9* is linked to residual feed intake (RFI) in Nellore cattle (Brunes et al. 2021), while *PINX1* is associated with RFI in a multibreed population of beef cattle (Li et al. 2021). These genes contribute to efficient feed utilization, suggesting a role in growth efficiency.

NAMPT was identified in a specific region on chromosome 4 and in pig populations, it is linked to feed intake, growth, body stature, fatty acid composition, muscle, backfat tissues and backfat thickness (Cepica et al. 2010; Zappaterra et al. 2015). This suggests that *NAMPT* might play a significant role in regulating body composition and metabolic efficiency in Lao native goats. *HESX1* is associated with growth hormone deficiency or combined pituitary hormone deficiency, which regulates overall somatic growth and various aspects of metabolism (Lai et al. 2009). Furthermore, *HESX1* is linked with growth traits such as body height, body length, chest girth, huckle bone width, body weight, and average daily gain in four Chinese cattle breeds (Lai et al. 2009).

4.5.3. Signature of selection for carcass and meat production traits

The DCMS analyses identified potential genes in chromosomes 8, 19, 4, 22, 2 and 14 associated with carcass-related traits. Lao goats are mainly raised for meat, there is a small proportion of crossbred with the Bach-Thao breed, which is dual-purpose for meat and milk production (Trach & Phiovankham 2011). Although there has been no study on the carcass and meat quality of Lao native goats, nearly half of Vietnamese goat consumers are willing to pay an average 15% price premium for Lao goats over the goat breeds available in Vietnam (Morales et al. 2023).

Eight genes identified are associated with specific carcass traits. *NAMPT* on chromosome 4 is a notable gene involved in energy metabolism and is preferentially secreted by visceral fat tissue in humans and mice (Imai 2009). This gene plays a role in metabolism, gluconeogenesis, glycolysis, and insulin secretion, and has been linked to muscling, growth, fat deposition, and fat-to-meat ratio in pigs (Cepica et al. 2010). *ASB14*, *CNTNAP5*, *FAM167A*, *FAM135B*, *PINX1*, and *RHOT1* are linked to various aspects of carcass composition, such as rump fat thickness, fat thickness, marbling, and bone weight traits (Zhang et al. 2018; Vanvanhossou et al. 2020; Martins et al. 2021; Kenny 2022; Kim et al. 2022; Li et al. 2022; Gao et al. 2023). *MRPL32* is related to slaughter weight and hot carcass weight in multiple Brahman-Angus breeds (Imumorin et al. 2011). *MSRA* is moderately expressed in various organs and has been associated with meat quantity and quality muscle in cattle (Jourshari et al. 2023).

Further, several identified genes play roles in determining meat quality. *XKR6* is associated with carcass fat, hot carcass weight, backfat thickness, meat-to-fat ratio, and body fat distribution across various livestock (Hieber et al. 2018; Shang et al. 2019; Blaj et al. 2022; Kenny et al. 2022). *SYPL1*, abundant in adipose tissue and linked to GLUT4-containing vesicles, is linked to marbling QTL in Wagyu cattle (Yokouchi et al. 2009). *DNASE1L3* is linked to lean meat yield and muscle contraction, respectively, highlighting their roles in meat production (Sood 2023).

4.5.4. Signature of selection for reproduction and milk production

Lao goats potentially have moderately high reproductive traits. Results from surveys based on farmer recall suggested a kidding rate of 3 litters over 2 years (Gray et al. 2019). On average, Lao native goats produce 2.1 kids per litter, with a range from 1 to 5 kids (Colvin et al. 2022). Our analysis identified genes across chromosomes that are associated with both reproduction and milk production traits.

Several genes associated with male fertility and spermatogenesis in previous studies were identified from the signatures of selection results. We found three genes, *ABHD6*, *PXK*, and *RPP14*, that are associated with scrotal circumference, which is essential for male reproductive health (Reding et al. 2023). *DNAH12*, *SYPL1*, and *CEP120* contribute to spermatogenesis success, for example, the flagellum development, sperm cytoplasmic droplet formation, and sperm maturation (Oud et al. 2021; Chen et al. 2022; Song et al. 2022; Liu et al. 2023). The genes associated with sperm quality such as sperm motility, abnormal sperm morphology, number of sperm cells, sperm progressive motility, and semen volume, include *DNAH12*, *BLK*, and *PXK* (Gao et al. 2019; Oud et al. 2021; Reding et al. 2023). *SYPL1* is also reported to be associated with sire fertility traits in Holstein cattle (Chen et al. 2022).

Genes associated with female fertility include *ABHD6*, *GATA4* and *MGST2*. *GATA4* is linked to ovarian function and is also associated with follicular development of oocytes (Bennett-Toomey & Stocco 2018). Bertevello et al. (2018) reported that *ABHD6* was expressed in bovine ovarian cells. Additionally, *MGST2* has been identified as a potential gene influencing udder traits in Chinese Holstein cattle (Nazar et al. 2022).

Numerous genes significantly influence various reproductive traits, including conception rate, gestation length, litter size, and overall reproductive efficiency. The gene expression of *DNASE1L3* was linked with conception rate length in Holstein (Barnwell et al. 2016), while *FLNB* was associated with conception rate in US Jersey sire Cattle (Rezende et al. 2018). *FLNB* and *ARSJ* were associated with embryonic development (Zhou et al. 2007; Ratzka et al. 2010). The gestation length varies between species and within the breeds. *ASB14*, *FLNB*, and *PDE12*, located in chromosome 22, affect gestation length in Blanco Orejinegro cattle of Colombia (Rios et al. 2023). Also, in chromosome 22, genes *ARSJ* and *SOX7* were linked to calving performance and fertility traits in cattle (Michenet et al. 2016; Grigoletto et al. 2020). The *GATA4* gene has been reported as a potential gene that is associated with litter size in goats (Wang et al. 2023). *ANXA11* on chromosome 28 and *KCTD1* on chromosome 24 affect lactation length and the interval from calving to first insemination in cattle (Oliveira et al. 2019; Klein 2021).

In this study, we found numerous genes on different chromosomes (4, 7, 8, 9, 14, 17, 19, 22, and 28) associated with milk production and milk composition traits. *ADAP2* and *CEP120* are associated with overall milk production traits in Brown Swiss cattle and water buffalo, respectively (Venturini et al.

2014; Saravanan et al. 2021), while *ZCCHC24* was associated with milk production traits in both cattle and dairy goats (Pedrosa et al. 2021; Massender et al. 2023). *RNFT2*, *CEP120*, *DNAH12*, *FAM107A*, *GNAI1*, and *MRPL32* also contribute to milk yield in water buffalo, sheep, and cattle (Pimentel et al. 2011; Venturini et al. 2014; Di Gerlando et al. 2019; Fonseca et al. 2023; Laodim et al. 2024). Additionally, *FAM135B* is linked to milk yield in different livestock in multiple studies (Jiang et al. 2014; Liu et al. 2021).

In terms of milk composition, *ABHD6*, *EPHA7*, *MGST2*, *GNAI1* and *FAM135B* play significant roles in milk fat and cholesterol content (Do et al. 2018; Gebreyesus et al. 2019; Freitas et al. 2020; Bekele et al. 2023; Laodim et al. 2024), while *RNFT2*, *FLNB*, *FAM135B*, *CDK5R1* and *KCTD6* are linked to milk fat and cholesterol levels (Jiang et al. 2014; Do et al. 2018; Freitas et al. 2020; Volkandari et al. 2021). Additionally, *CDK5R1*, *MYO1D*, and *PRSS51* impact milk protein traits (Ma et al. 2021; Lu et al. 2022; Mohammadi et al. 2022). *DNAH12* and *MRPL32* are not only associated with milk yield in sheep and cattle, respectively (Pimentel et al. 2011; Di Gerlando et al. 2019), but *DNAH12* is also associated with daily fat yield, protein percentage, and fat percentage in sheep (Di Gerlando et al. 2019).

4.6. Conclusion

Signatures of selection for Lao native goats were identified using the DCMS framework, revealing 24 genomic regions with 68 unique protein-coding genes. These genomic regions indicate selection events in Lao native goats that are likely related to how they have adapted to the tropical monsoon climate, disease resistance and local breeding practices. Furthermore, these regions harbour genes that are associated with economic traits such as growth, feed intake, reproduction, milk production and carcass-related traits. Our genomic analysis identified several genes relevant to production that could be targeted for breeding programs to apply future strategies such as genomic prediction. This understanding could lead to more reliable genetic markers, strengthening both current and future breeding programs for native goat breeds in Laos as well as providing reference for molecular breeding of other breeds. Additionally, further studies focusing on these putative regions of selection signature and incorporating recorded phenotypes of Lao native goats may help identify specific candidate genes under selection.

4.7. Author contributions

JvdW, SdlHS, PA, and SVL conceived and designed the study. SVL performed the statistical analysis and wrote the manuscripts. SdlHS, PA and JvdW supervised the statistical analysis and writing of the manuscript. All authors read and approved the final manuscript.

4.8. Acknowledgements

The authors gratefully acknowledge the financial support from Project LS/2017/034 for sample collection and genotyping. Special thanks to Dr. Ammaly Phengvilaysouk and his team from the National Agriculture and Forestry Research Institute in Laos for collecting ear-notch samples. We also express our gratitude to Dr. Watthana Theppangna from the National Animal Health Laboratory in Laos for assistance with paperwork and arranging the shipments of samples from Laos to New Zealand. The first author gratefully acknowledges financial support from the Australian Commonwealth Government through the Research Training Program stipend scholarship at the University of New England, Armidale, NSW, Australia.

4.9. Conflict of interest statement

The authors declare no conflict of interest.

4.10. Funding

This study was supported by ACIAR project LS/2017/034.

4.11. Data accessibility

The data are owned by project LS/2017/034 and access to the data can be negotiated by request.

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University of New England

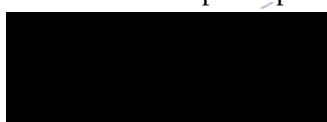
STATEMENT OF AUTHORS' CONTRIBUTION

We PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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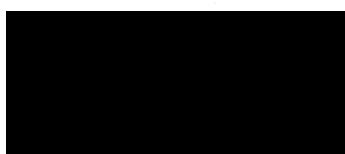
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26/11/2024

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26/11/2024

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Chapter Five: Analysis of home range and the level of mixing between herds of native goats in Central Laos

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Prepared to publish in "Small Ruminant Research"

5.1. Abstract

In pastoral agricultural systems, understanding the movement and mixing of animal cohorts is important for the interpretation of mating patterns in free-roaming herds or flocks, as these factors impact the degree of genetic diversity and levels of inbreeding. This study investigated the home range, home range overlap, gene flow and genetic relatedness between herds within and between villages of Lao native goats by using the global positioning system (GPS). Data from 54 goats was recorded from August 2022 to July 2023 and genotype data on 293 goats was collected from five villages in Central Laos. Our results revealed variation in home range size between villages, with an average annual home range of 0.35 km² (ranging from 0.13 to 0.73 km²). Home range size tended to be larger in the dry season than in the wet season, and bucks explored larger areas than does, but these differences were not significant. The degree of home range overlap between herds varied between villages, ranging from zero (Nhonnhang) to very high (Kanglouang). For all villages, the results of home range overlap were consistent with gene flow and relatedness estimates between herds within villages, when assessed based on genotype data. Goats from the Kanglouang village were found to be more genetically related between herds ($F_{ST} = 0.082$) and with moderate gene flow between herds (F_{ST} ranges from 0.02 to 0.143) due to the high level of mixing. This study highlights the impact of different grazing and breeding management strategies at the village level, on the degree of genetic exchange between herds.

5.2. Introduction

As the main goat breed in Laos, Lao native goats serve as an important component of the smallholder production systems due to their economic and nutritional contribution. Goats are distributed throughout Laos with approximately 42% located in Central Laos (Xayalath et al. 2021). Goats are mainly kept in smallholder systems with small herd sizes, ranging from 1 to 37 goats (Walkden-Brown et al. 2024). They are mainly raised in a semi-extensive grazing production system where they are free-grazing in the forest and communal lands during the day and are housed at night (Gray et al. 2019).

There was speculation about the level of inbreeding which might be high for Lao native goats (Gray et al. 2019). This was because of low trading in bucks between herds, mating was not controlled, and castration was not practised in these systems increasing the chances of mating among relatives. However, in previous studies based on genotype data from a sample of goats, we identified low inbreeding levels within the Lao native goat population (Le et al. 2023; Le et al. 2024a). Data on the actual roaming behaviour is effective in explaining the relationships between individuals among herds within a village and between villages. In pastoral agricultural systems, the movement and mixing of animal cohorts are important for understanding potential mating patterns in free-roaming herds or flocks, as they impact the degree of genetic diversity and levels of inbreeding (van der Werf 2000). There were concerns about a high level of inbreeding in Lao native goats due to limited movement of bucks between herds, uncontrolled mating, and the absence of castration, which could increase the likelihood of mating among relatives (Gray et al. 2019).

Animal movement and mixing between herds can be assessed by using the global positioning system (GPS). GPS has been widely used to track animal movement, home ranges and overlap in home ranges in comparison with observational monitoring (Urbano et al. 2010; Forin-Wiart et al. 2015; Justicia et al. 2018). An animal's home range refers to the areas it regularly travels within, searching for food, shelter, or mates (Burt 1943; Spencer 2012). The home range of an animal or a group of animals depends on population density, abundance, distribution of food and predators, social behaviour, weather and many other factors (Lott 1991). For example, males and females have different home ranges due to their distinct reproductive strategies and spatial requirement scales with their bodies (Schoener & Schoener 1982; Wolf et al. 2007). Changes in behaviour due to environmental factors in different seasons can also alter spatial behaviour, affecting the home range and overlap among individuals of the same species (Gehrt & Frtzell 1997; Hamede et al. 2009). Home range overlap refers to the degree of interaction among individuals within a herd or between herds and can help to explain disease transmission, genetic material exchange and genetic structure between herds (Kitchen et al. 2005; Spencer 2012).

Determining an individual's home range can be challenging because the area is not used uniformly. Core areas, where an individual spends significantly more time, often indicate nesting sites, resting places, or regions of high resource abundance (Lott 1991; Spencer 2012). The size of the home range is constrained by the distance an individual can travel and still return to their core area (Börger et al. 2008). An animal's home range is commonly quantified by the animal's utilization distribution (UD), the probability distribution that defines the animal's use of space (Fieberg & Kochanny 2005). There are a number of methods available to estimate the home range of animals such as minimum convex polygon, kernel density estimator, grid cell approach, and low convex hull (Calabrese et al. 2016). One of the most commonly used methods to determine the home range area is the kernel density estimator (Börger et al. 2008; Supp et al. 2021), an approach that can be used to determine the home range of Lao native goats in Central areas.

Animals from different herds are more related when there is a higher home range overlap in comparison with those that have a lower home range overlap. Two animals are related when they share a common ancestor resulting in more similar genotypes at each locus since their alleles are more likely to be identical by descent than those of unrelated animals (Weir et al. 2006), in particular when the effective size of a population is small and few males are responsible for all offspring. Gene flow within and between herds or populations can contribute to genetic relatedness when animals or their genetic material are transferred from one group to another (Wright 1921). The rapid development of genotyping and sequencing technology has made it possible to generate genomic data which can be used to estimate genetic relatedness in animals and gene flow between populations. Genetic relatedness is measured using a genomic relationship matrix (GRM) and gene flow between herds or populations can be quantified using the fixation index (F_{ST}) (Lynch & Ritland 1999; Weir et al. 2006; Wang 2011). F_{ST}

ranges from 0 to 1, where 0 means complete sharing of genetic material and 1 means no sharing (Wright 1984).

This study aimed to utilize GPS collars and genomic data to associate the variation in native Lao goat movement patterns and home range overlap between sex, seasons and locations, with the genetic relatedness and gene flow between herds within and between villages. The findings of this study would aid in developing village breeding programs that control inbreeding while selecting economically important traits.

5.3. Materials and methods

5.3.1. Ethics statement

All the procedures conducted in this study were approved by the Animal Ethics Committee of the University of New England under approval number AEC21-084.

5.3.2. Study area

This study was conducted in five villages in Savannakhet province in Central Lao (16° 30' N and 105° 35' E; Figure 5.1). The Savannakhet province is located in a monsoon tropical climate with abundant rainfall and hot temperatures from May to October (wet season) and hot and dry conditions from November to April (dry season) (Gupta 2005). The maximum temperature was 42.5°C in May 2023, typically ranging from 15.3°C in January to 36.0°C in June. The average monthly rainfall in this area is 245 millimetres, ranging from 15 millimetres in December to 318 millimetres in August (Weather and Climate, 2024). The Savannakhet province is characterized by semi-forest mixed with agricultural land which is mainly cropped in the wet season and used for livestock grazing otherwise (Russell et al. 2015).

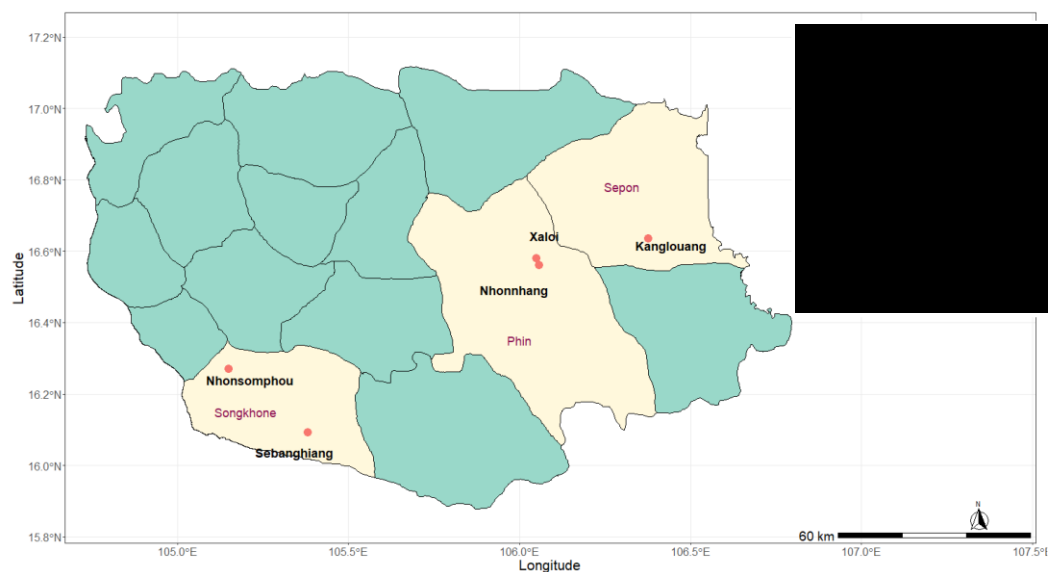


Figure 5. 1. Geographical location of areas in this study. Districts are labelled in red and villages in black with red point markers.

A total of 42 GPS collars were used to track animals from five villages in the Songkhone, Phin and Sepon districts over 12 months from August 2022 to July 2023. The dry season in this study included data collection from November 2022 to April 2023, and the wet season included data from August 2022 to October 2022 and from May 2023 to July 2023.

5.3.3. GPS devices, animal, genotype data and quality control

The GPS trackers used were 95 x 65 x 35 mm in dimension and weighed 170g (less than 1% of body weight). To ensure the batteries could last for 30 days and to obtain the highest resolution of the GPS signal, the devices were programmed to operate 24 hours a day at five-minute intervals. Every 300 seconds the devices attempted to acquire a valid global navigation satellite system (GNSS) position and searched for satellites for a maximum of 30 seconds before returning to its sleep state. When a valid GNSS position was acquired, the GPS tracked a satellite for eight seconds to allow stabilization and acquisition for further satellites, before recording five consecutive positional fixes at the frequency of 5 Hz. Once this was completed, the device would enter sleep mode until the next 300-second duty cycle began and the process was repeated.

The GPS trackers used rechargeable lithium batteries NCR18650B to provide power and micro 16 GB SanDisk Ultra memory cards to store the data. Every thirty days, the battery and memory cards were replaced by a fully charged battery and a new memory card.

In total, 15 households were selected, and in each household, at least one adult male and one adult female goat were randomly selected to be deployed with a GPS collar (Table 5.1, Figure 5.2). Field staff were instructed to select goats older than one year of age that were not full siblings. DNA samples were also collected from these goats. When a goat was sold or died during the period, another goat from the same herd was randomly selected to wear the GPS collar. At the end of the study, a total of 54 adult goats wore GPS collars during the experimental period. Animal information such as ear tag number, sex, owner and village as well as GPS collar were recorded.

Table 5. 1. Number of GPS collars deployed on goats and genotyped data animal per village in Savannakhet province, Lao

Villages	Number of Household	Number of females	Number of males	Number of animals with GPS	Number of genotyped animals wearing GPS	Number of genotyped animals
Kanglouang	3	3	4	7	7	59
Nhonnhang	3	4	3	7	7	60
Nhonsomphou	3	9	4	13	9	60
Sebanghiang	3	10	3	13	9	54
Xaloi	3	8	6	14	12	60
Grand Total	15	34	20	54	44	293

The raw GPS data were retrieved from the memory card each month. The raw GPS data included the identification number of the GPS device, Unix time stamp (which could be converted to date and time), GPS coordinates (longitude and latitude), altitude, speed, satellite, and horizontal dilution of precision (HDOP), which measures the accuracy of a horizontal position.

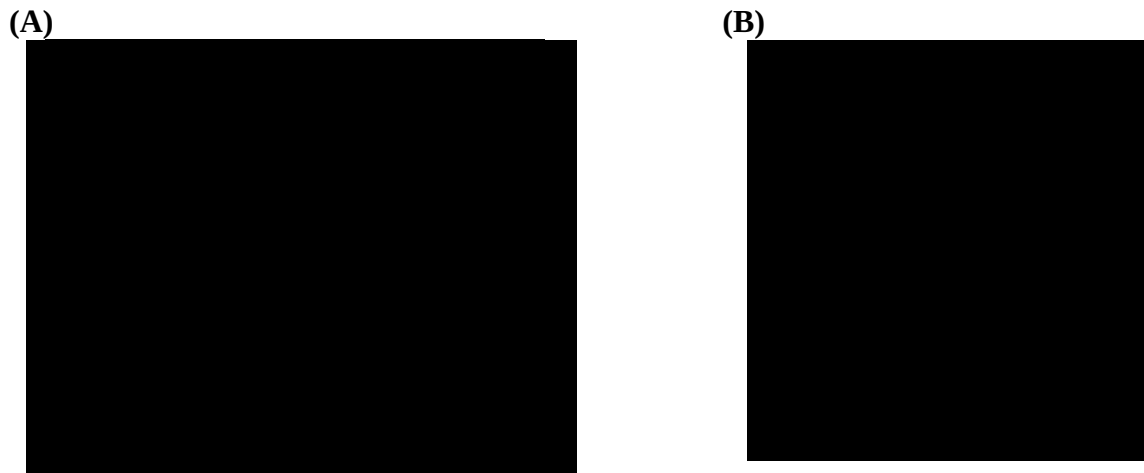


Figure 5. 2. Goats selected to wear GPS collar (A) and the device components (B)

This study included the genotyped data from the same five villages, each animal had a 50K Illumina caprine BeadChip genotype. These genotypes were a subset of the dataset from Le et al. (2023) from which out of 293 genotyped animals, 44 animals had GPS data. The sample size, location and genotyping methods were described by Le et al. (2023).

Quality control for monthly raw GPS data was conducted using the PyKalman library in Python. Erroneous individual data points were removed based on satellite counts of less than 4 and HDOP values greater than 10. The instantaneous value for distance, speed, heading and turn angle was calculated according to the Haversine method (Inman 1849). Based on the GPS coordinates, we calculated the sunrise and sunset times using Teets' method (Teets 2003). This information was used in order to keep only the data collected during the day for further analyses.

The quality control procedure for the genotypes used in this study was previously described by Le et al. (2024a). After quality control, no animals were removed, and each goat had 42,666 SNPs.

5.3.4. Home range analysis

The core areas within the home range are those that have relatively a higher intensity of use (Lott 1991; Spencer 2012). Since goats in Lao are raised in semi-intensive grazing systems with free grazing during the day and shelter at night, the home range and core areas of Lao goats were estimated based on only data collected during the daytime. Home ranges and core areas were determined via the amt v0.2.2.0 package in R (Signer et al. 2019), using the kernel density model, which determines the probability of finding an individual at any given point within their home range (Anderson 1982; Worton 1989). Home range estimates provide a 95% utilization distribution (UD), a 95% home range, and a 50% core area

for each goat. Seasonal differences between home range and core areas were compared between sexes and locations using the ANOVA with *dplyr* v1.1.4 package in R (Wickham et al. 2020) with a significance threshold of $P < 0.05$. The statistical model used was a two-way Analysis of Variance (ANOVA) to test the effect of location, sex and season on the home range of animals.

$$Y_{ijk} = \mu + \alpha_j + \beta_k + (\alpha\beta)_{jk} + \epsilon_{ijk}$$

where Y_{ijk} is the home range for each individual, μ is the mean of home range across all groups; α_j represents the effect of the j^{th} village; β_k represents the effect of the k^{th} sex or season groups; $(\alpha\beta)_{jk}$ represents the interaction effect between the j^{th} village and the k^{th} sex or season; ϵ_{ijk} represents the random error term for the i^{th} observation in the j^{th} village and k^{th} sex or season group, assumed to be normally distributed with mean 0 and variance σ^2 . Following the ANOVA, Tukey's Honestly Significant Difference (HSD) post-hoc test was conducted to determine pairwise differences among group means.

5.3.5. Home range overlap

The utilization distribution overlapping index (UDOI) is useful for assessing the degree of interaction among individuals within a herd or between herds. This index was developed by Fieberg and Kochanny (2005) and is widely used to observe overlap in the home range between species (Chynoweth et al. 2015; Moseby et al. 2020). UDOI values range from 0 (no overlap) to 1 (complete overlap). In cases where both UD's are non-uniformly distributed and highly overlapping, UDOI values can exceed 1 (Weimerskirch et al. 2020). In our study, we were interested in overlapping home ranges between animals from different herds of different villages. UDOI values were calculated with the *amt* v0.2.2.0 package (Signer et al. 2019).

5.3.6. Gene flow and analysis of genetic relatedness

To evaluate the gene flow in goats between herds within and between villages, we used genotype data to calculate the fixation index (F_{ST}) for herds within a village and between villages. The F_{ST} was calculated using the Weir and Cockerham method implemented in PLINK2 (Chen et al. 2019). The F_{ST} values range from 0 (complete gene flow) to 1 (no gene flow). To examine the genetic relatedness of individuals within and between herds and villages in Laos, a genomic relationship matrix (GRM) was built in PLINK2.

5.4. Results

5.4.1. GPS performance

During the 12-month experimental period, 16 GPS collars remained functional throughout the whole time, showing their durability. However, 26 GPS collars were lost or damaged over the course of the

trial. Among these, 19 GPS collars encountered issues such as difficulty in connecting with satellites (15 cases) or damage to their housing and memory cards (4 cases). Additionally, 7 GPS collars were lost when the goats wearing them failed to return home after grazing in the forest.

The length of measurement for each GPS also reduced over time. On average, each GPS recorded an average of 23.69 days per month, ranging from 0 to 31 days. Among the GPS collars, 53.7% recorded more than 20 days per month, while 24.4% recorded less than 10 days per month. Data from two GPS collars, GPS20 and GPS18, were excluded from further analysis due to their limited recording periods, being active for only one month (Figure 5.3).

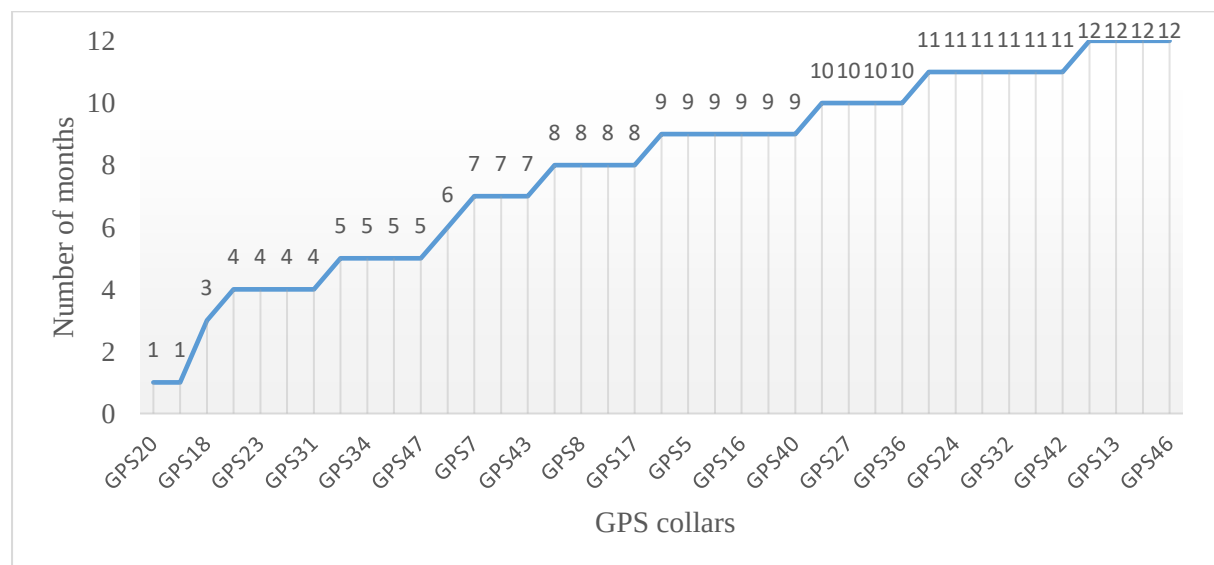


Figure 5. 3. Number of months of measurement for GPS collars averaged over 12 months

5.4.2. Home ranges

Table 5. 2. Annual home range and core areas of Lao native goats for each village

Villages	#Animals	# Days	#Points	Annual home range	Core area (km ²)
				(km ²)	
				Mean (SD)	Mean (SD)
Kanglouang	7	941	62,650	0.417 (0.302) ^b	0.028 (0.023) ^b
Nhonnhang	7	1039	59,978	0.127 (0.088) ^b	0.023 (0.017) ^b
Nhonsomphou	13	1345	96,069	0.280 (0.391) ^b	0.045 (0.064) ^b
Sebanghiang	13	1358	91,213	0.190 (0.141) ^b	0.019 (0.016) ^b
Xaloi	14	1806	110,593	0.732 (0.443) ^a	0.166 (0.127) ^a
Overall				0.349 (0.273)	0.056 (0.049)

^{a-b} Means within columns not sharing a common suffix were significantly different ($P < 0.01$). SD is the standard deviation.

The overall estimate of the home range of Lao native goats in a semi-grazing system was 0.349 (km²), when averaged over a year, ranging from 0.127 (km²) in the Nhonnhang village to 0.732 (km²) in Xaloi (Table 5.2). The annual home range for goats in Xaloi was significantly larger than those in other villages ($P < 0.01$). Similarly, a much larger core area was observed for goats in Xaloi, which was significantly larger than those in other villages ($P < 0.01$).

Overall, the average annual home range for male goats was 0.387 (km²), which was larger than the average annual home range for female goats in the same areas, which was 0.327 (km²; Table 5.3). However, the overall annual home range size between sexes was not significantly different ($P > 0.05$) and was only numerically greater for males in three of the five villages (Table 5.3).

Table 5. 3. Annual home range estimation for each village by sex

Villages	Annual home range (km ²)		Core area (km ²)	
	Male	Female	Male	Female
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
Kanglouang	0.406 (0.295) ^{ab}	0.433 (0.377) ^{ab}	0.031 (0.027) ^b	0.023 (0.019) ^b
Nhonnhang	0.145 (0.114) ^{ab}	0.114 (0.080) ^{ab}	0.027 (0.022) ^b	0.020 (0.015) ^b
Nhonsomphou	0.399 (0.382) ^{ab}	0.228 (0.406) ^b	0.064 (0.072) ^{ab}	0.036 (0.063) ^b
Sebanghiang	0.161 (0.141) ^{ab}	0.199 (0.148) ^b	0.016 (0.015) ^b	0.020 (0.017) ^b
Xaloi	0.825 (0.569) ^a	0.662 (0.346) ^{ab}	0.206 (0.153) ^a	0.136 (0.103) ^{ab}
Overall	0.387 (0.3)	0.327 (0.271)	0.069 (0.058)	0.047 (0.043)

^{a-b} Means within the same home range columns not sharing a common suffix were significantly different ($P < 0.05$).

Similarly, the core area of males was larger than females overall although this difference was not significant ($P > 0.05$). The core area for males in Xaloi was larger than the core area of female goats in other villages ($P < 0.05$). The average core area was 0.069 and 0.047 (km²) for males and females, respectively.

The difference in home range between seasons was not significant, with an average home range of 0.361 km² in the dry season and 0.317 km² in the wet season (Table 5.4). In both seasons, the home range of goats in Xaloi was the largest and it was significantly different from those in other villages. However, there was no significant difference between the home range of goats in Kanglouang during the dry season and those in Xaloi during the wet season. Additionally, the home range for goats in Kanglouang, Sebanghiang and Xaloi in the dry season was larger than in the wet season, while the opposite was observed in Nhonnhang and Nhonsomphou.

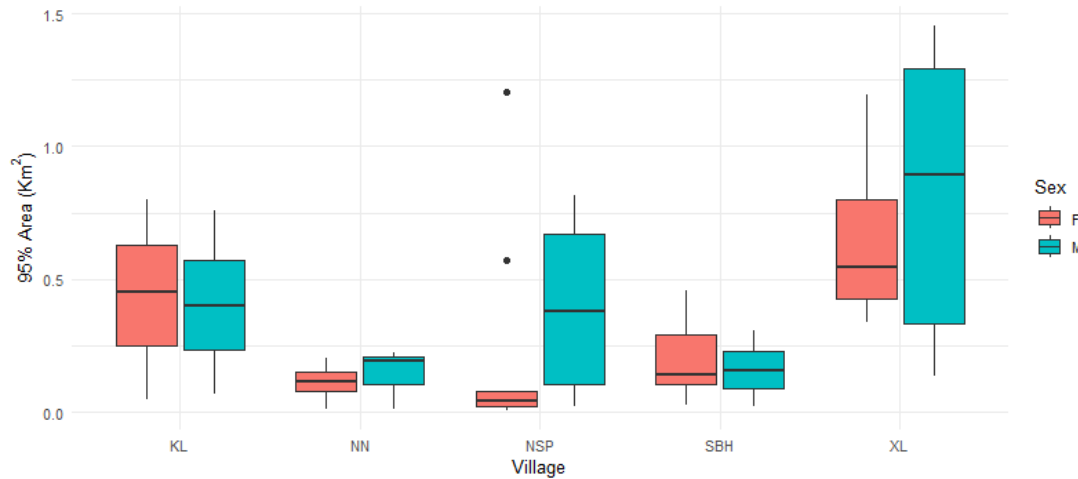


Figure 5. 4. The annual home range estimate for Lao native goats in different villages by sex. F indicates female; M indicates male. Villages include KL: Kanglouang, NN: Nhonnhang, NSP: Nhonsomphou, SBH: Sebanghiang, XL: Xaloi.

Table 5. 4. Annual home range estimation for each village by seasons (km²)

Villages	Home range per season		Core area per season	
	Dry	Wet	Dry	Wet
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
Kanglouang	0.522 (0.360) ^{ab}	0.312 (0.210) ^{bc}	0.086 (0.075) ^b	0.017 (0.010) ^b
Nhonnhang	0.101 (0.072) ^c	0.130 (0.092) ^c	0.021 (0.015) ^b	0.024 (0.018) ^b
Nhonsomphou	0.046 (0.068) ^c	0.299 (0.388) ^{bc}	0.005 (0.005) ^b	0.049 (0.064) ^b
Sebanghiang	0.241 (0.152) ^c	0.167 (0.160) ^c	0.029 (0.025) ^b	0.015 (0.010) ^b
Xaloi	0.897 (0.468) ^a	0.678 (0.430) ^{ab}	0.206 (0.144) ^a	0.158 (0.117) ^a
Overall	0.361 (0.224)	0.317 (0.256)	0.070 (0.053)	0.052 (0.044)

^{a-b} Means within the same home range columns not sharing a common suffix were significantly different ($P < 0.05$).

Similar to the seasonal home ranges, the core area showed no significant differences between the dry and wet seasons (Table 5.4). The core area for goats in Xaloi was the largest, with a significant difference between the dry and wet seasons.

5.4.3. Animal movement patterns

Movement patterns of Lao native goats from different households in five villages are displayed in Figure 5.5. Various types of goat movements are observed in these villages, with two main movement patterns being identified. Firstly, free grazing was observed for goats in communal areas and forests in Xaloi (Figure 5.5A), Sebanghiang (Figure 5.5C), and Kanglouang (Figure 5.5E). These household herds share a common area within the village precinct and then exhibit separate movement patterns in the forest

(Figure 5.5A) or share the entire grazing area throughout the year (Figure 5.5C and Figure 5.5E). Secondly, they grazed on smaller areas of land, probably closer to the owner's land (Figure 5.5B and Figure 5.5C). Goats in these household herds travelled only within the boundaries of the property (Household H4, H5, H6 in Figure 5.5B, and Household H7 in Figure 5.5D), or with only a slight mixing in common lands in Nhonsomphou (Figure 5.5D, household H8 and H9).

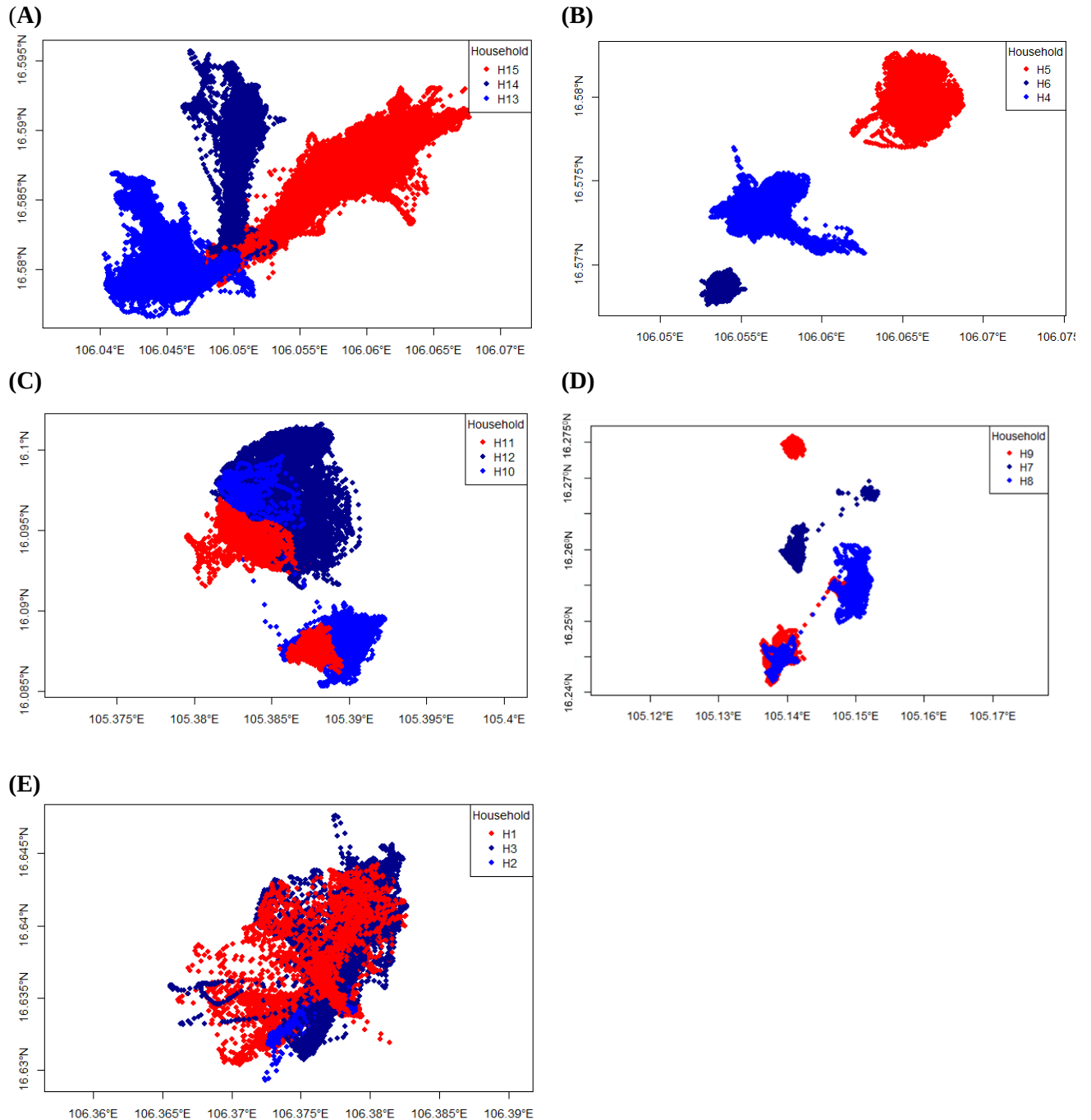


Figure 5. 5. Goat movement pattern in Xaloi (A), Nhonhang (B), Sebanghiang (C), Nhonsomphou (D), and Kanglouang (E) villages during 12 months. Each dot in the plots represented goat location and each colour represented the herd.

5.4.4. Home range overlap

The overlap of home range among herds is displayed in Table 5.5. The result illustrates that there is no home range overlap between villages, even in Xaloi and Nhonhang which share a border with Phin district. The degree of home range overlap varies between herds within each village, ranging from 0 to 4.1. No overlaps in home range were observed between herds in Nhonhang village, while goats in Kanglouang exhibited a high degree of home range overlap (UDOI ranges from 0.6 to 2). The degree of home range overlap between herds in other villages was low to moderate, varying from 0.002 to 0.391.

Table 5. 5. Annual home range overlap between herds using utilization distribution overlapping index (UDOI)

Village/Herd		Kanglouang			Nhonnhang			Nhonsomphou			Sebanghiang			Xaloi		
		H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14	H15
Kang-louang	H1	-	2.010	4.080	-	-	-	-	-	-	-	-	-	-	-	-
	H2			0.568	-	-	-	-	-	-	-	-	-	-	-	-
	H3				-	-	-	-	-	-	-	-	-	-	-	-
Nhon-nhang	H4					0.00	0.00	-	-	-	-	-	-	-	-	-
	H5						0.00	-	-	-	-	-	-	-	-	-
	H6							-	-	-	-	-	-	-	-	-
Nhon-somphou	H7								0.00	0.00	-	-	-	-	-	-
	H8									0.002	-	-	-	-	-	-
	H9										-	-	-	-	-	-
Sebang-hiang	H10											0.391	0.071	-	-	-
	H11												0.006	-	-	-
	H12													-	-	-
Xaloi	H13														0.164	0.064
	H14															0.194
	H15															

5.4.5. Gene flow

The average pairwise F_{ST} values between herds within a village ranged from 0.06 to 0.130, indicating a low to moderate gene flow within each village (Table 5.6). Gene flow was lower between herds within Nhonhang and Nhonsomphou villages than between herds within other villages.

Gene flow between villages occurred at varying degrees. There was moderate genetic exchange within and between villages in Phin and Songkhone districts, while there was a low level of gene flow between the goat population in Sepon and those in Phin, and Songkhone (F_{ST} from 0.046 to 0.062).

Table 5. 6. The average pairwise F_{ST} values for goats from different herds within and between villages

District Village		Phin		Songkhone		Sepon
		Nhonnhang	Xaloi	Nhonsomphou	Sebanghiang	Kanglouang
Phin	Nhonnhang	0.130	0.02	0.018	0.033	0.046
	Xaloi		0.069	0.025	0.039	0.053
Songkhone	Nhonsomphou			0.126	0.027	0.046
	Sebanghiang				0.060	0.062
Sepon	Kanglouang					0.082

**The average pairwise F_{ST} between herds within villages (on diagonal) and between villages (above diagonal).*

5.4.6. Genetic relatedness

The average genetic relatedness between animals within and between herds and villages was calculated based on genotype data and is shown in Table 5.7. Animals within a herd are more closely related than those within a village and animals within a village are more closely related than those between villages. Within a herd, goats in Kanglouang and Sebanghiang exhibit moderate genetic relatedness, while low genetic relatedness is observed for herds in Nhonnhang, Nhonsomphou, and Xaloi villages. Similarly, within a village, goats in Kanglouang are more related than those in other villages. Additionally, genetic relatedness between villages is very low, with values ranging from 0.002 to 0.049.

Table 5. 7. The average genetic relatedness between animals within and between villages

District Village		Phin		Songkhone		Sepon
		Nhonnhang	Xaloi	Nhonsomphou	Sebanghiang	Kanglouang
Phin	Nhonnhang	0.057	0.003	0.007	0.007	0.025
	Xaloi		0.068	0.012	0.012	0.028
Songkhone	Nhonsomphou			0.062	0.002	0.024
	Sebanghiang				0.068	0.024
Sepon	Kanglouang					0.114

**The average genetic relatedness between herds within villages (on diagonal) and between villages (above diagonal).*

5.5. Discussion

Understanding the animal movement patterns, home range dynamics and genetic structure of livestock is important to undertake informed management practices, especially in traditional agricultural systems

where free-ranging livestock plays a significant role. In these systems, there is less control of mating and the mating patterns have a significant effect on the build-up of inbreeding within herds and the potential for genetic improvement. This study investigated these aspects in Lao native goats by focusing on the differences in home range across villages, seasons and sex by using both GPS and genome-wide SNP data.

5.5.1. GPS collar performance

The technical challenges encountered with the GPS collars, including loss, damage, and reduced recording duration due to excessive battery use when devices failed to make satellite connections, highlighted the difficulties of using GPS to track goat movement in Central Laos. Despite these challenges, the data collected in Central Laos successfully provided insights into animal movement patterns and home ranges of Lao native goats in traditional management.

A total of 54 goats were tracked over 12 months by using GPS collars, resulting in 420,503 data points collected during the day (Table 5.2). The GPS tracking duration for Lao goats averaged 77% of the trial period at the beginning of the trial but decreased to 50% by the end (Figure 5.2). This tracking duration was shorter than what was observed during GPS collar testing in a goat farm in Armidale, Australia, where all GPS devices captured 100% of data over a 30-day testing period (Charlton et al. 2021). The reduced tracking duration in Laos is likely due to factors such as the GPS device, animals, and the local environment. For example, the batteries sourced locally in Laos were 1 mm shorter than those used in Australia (Olmo et al. 2022b). Although adjustments were made to GPS housing to accommodate these batteries, over time, some devices experienced unstable connections with satellites due to insufficient power.

The trial took place in Central Laos, in semi-forested tropical areas where satellite signal connections were also unstable. Additionally, goats are active animals, and when grazing in the forest, GPS collars may be damaged during fights with other goats or by impacts with rocks. The decrease in average recording over time suggests that improvements in collar design and durability are necessary for further studies. Future research could benefit from using collars with enhanced battery life and more robust housing.

5.5.2. Home range dynamics

The variation in home range sizes observed among the five villages likely indicates the varying communal and owned land availability per village and other topographic factors. Goats in Nhonhang, for instance, exhibited smaller home ranges than those in other villages, likely due to the availability of grazing areas within the owner's property and the presence of constraints on movement (fencing around the property). This management strategy is explained by a benchmarking survey in which Walkden-Brown et al. (2024) reported that farmers in the Nhonhang village are busy with other commitments

and livelihood activities, making it difficult for them to supervise their goats in communal lands. Additionally, they own a reasonable amount of land for goat grazing, on which the goats are raised. The total average land size of farmers in these villages ranges from 0.026 to 0.055 km², with 18% to 47% of that land allocated for grazing livestock, including goats (Walkden-Brown et al. 2024). This form of goat management is referred to as “permanent grazing” (Phimphachanhvongsod 2001). Liehr et al. (2024a) observed that farmers in Laos learn to manage their herds by observing others within the village and considering the availability of labour and land resources. Therefore, there is limited variation in goat management practices within each village.

Farmers in Xaloi, Sebanghiang and Kanglouang villages allowed their goats to graze freely in communal areas and forests (free range) (Phimphachanhvongsod 2001). Due to limitations in property and communal lands, goats in Nhonsomphou are under a semi-rotational grazing system, where goats are kept on the property for rice cropping during the wet season, and allowed to graze freely for the rest of the year. These practices were not only observed in Central Laos but also other areas (Xayalath et al. 2021). Depending on the availability of private property, the herd size, and the availability of communal lands, farmers keep their goats either on their property or allow them to graze in village territory but to different degrees. This type of management has also been observed in livestock management in other rural households in semi-arid Africa (Turner et al. 2014).

The study found no statistically significant difference in home range size between male and female goats. This similarity in home range size may be due to the semi-extensive system used in Central Laos, where goats graze freely during the day and are sheltered at night (Gray et al. 2019). Male goats generally require larger grazing areas because of their bigger body size and higher energy needs. Previous studies on free-ranging feral goats in Island Montane and Western Australia suggest that males typically have home ranges 3 to 6 times larger than females, likely due to their roles in breeding and territorial defence (King 1992; Chynoweth et al. 2015).

Goats in most villages had larger home ranges in the dry season, the home range differences between seasons in Nhonnhang and Nhonsomphou were of opposite signs (Table 5.4). The difference in home range between seasons tends to change due to water and feed availability (Turner et al. 2014). In the dry season, due to a lack of water resources and scarcity of feed, animals have to travel further to find the feed (Launchbaugh & Howery 2005). Olmo et al. (2022b) reported that Lao goats spent more time grazing in the dry season than in the wet season. Farmers may need to look for alternative strategies such as concentrating on optimizing forage availability within limited areas, and ensuring sufficient water and feed to meet the nutritional needs of their animals.

5.5.3. Movement patterns and home range overlap

Our study uncovered distinct movement patterns among goats across the five villages, leading to variation in the extent of home range overlap both within and between villages. In villages like Xaloi, Sebanghiang, and Kanglouang, where free grazing in communal lands is a common practice, the probability of overlap is higher than in those with permanent grazing practices.

The patterns of home range overlap within and between villages illustrate the important aspects of social structure and resource availability among herds. The high degree of overlap within herds in Kanglouang could be explained by goat movement within this village, where goats from different households graze together throughout the year (Figure 5.5E). This is in contrast with the situation in Nhonnhang, where no overlap between herds was observed.

In villages with a high degree of overlap, particularly during the dry season when feed is limited, competition for resources may be increased. For example, in Kanglouang, the home range of goats in the dry season is 1.7 times larger than in the wet season, indicating that goats in this village had to explore further to find adequate nutrition. In other villages, limited communal lands and feed shortages could negatively impact animal health and productivity if not properly managed. Additionally, high overlap increases the risk of disease transmission, which can spread rapidly through herds (Kipronoh et al. 2016). This is particularly concerning for Lao farmers as they do not vaccinate goats and maintain poor biosecurity (Phengvilaysouk et al. 2022).

The lack of overlap between villages presents both challenges and opportunities. While isolation could reduce the risk of disease spreading between villages, it may also limit genetic exchange, potentially leading to reduced genetic diversity within villages over time. Most goats raised by smallholder farmers in Laos are bred through random mating (Gray 2005; Olmo et al. 2022b). Although the level of inbreeding in the native goat population in Central Lao is low (Le et al. 2024a), the risk of inbreeding within herds and villages could increase with inadequate management of breeding practices.

5.5.4. Gene flow and genetic relatedness

The observed low to moderate gene flow and genetic relatedness within and between villages are consistent with the results from the home range and overlap analyses, which showed limited animal movement and breeding opportunities across village boundaries. For example, data from Kanglouang illustrates that the higher degree of home range overlap is consistent with the higher genetic relatedness between animals within the village. This means that when animals graze in the same areas, they are more likely to share the genetic material with that group.

It was observed that even though there was no overlap in the home range between villages, there was low to moderate gene flow between them. This illustrates that genetic exchange exists between villages

indicating that farmers not only rely on random mating for their goats in the grazing areas, but they also start intervention strategies for their goats in terms of breeding from various genetic resources. Liehr et al. (2024a) reported that some of the farmers borrow bucks from their neighbours or relatives to cross with their goats.

The degree of gene flow between herds from villages in the Phin and Songkhone districts was higher than those with herds in the Sepon district. This finding aligns with the report of Le et al. (2024a) where goats from Phin and Songkhone districts were more related than those with goats in Sepon. Also, in their study, Le et al. (2024a) revealed low inbreeding levels for the goat population in Central Laos, even with herds from Nhonhang and Nhonsomphou villages where there is low gene flow within herds and isolation management.

This study revealed the complexities and inconsistencies in goat movement patterns, home range sizes, and genetic structure in Lao native goats. The variation observed among five villages highlighted the influence of local management practices, land availability and season. This study found no significant difference in home range size between male and female goats, which contrasts with previous literature suggesting that males typically require larger areas. Additionally, the degree of home range overlap among herds within a village is consistent with the genetic relatedness observed among animals in those villages. Although there was no overlap in the home range between villages, low to moderate gene flow was detected between them.

This study has some limitations related to the small sample size of GPS-collared animals per household and the number of households in each village. In this study, only three households per village were tracked to monitor movement patterns. Since the goats grazed freely during the day on communal lands, which varied in proximity to their owner's property. This sample may not fully capture the range of movement. For instance, while goats in Nhonhang exhibited a larger home range than the land available to their owners, there was no observed overlap in home range among herds in this village. To address this limitation, future studies should consider sampling from a larger number of households per village or the physical distance between them to capture more diverse movement patterns.

Out of the five villages in this study, only Xaloi and Nhonhang are nearby, while other villages are much further apart (Figure 5.1). According to Google Maps, the distance between villages in this study exceeded 20 km, whereas the maximum recorded distance travelled by goats in Central Laos was 14.5 km (Walkden-Brown et al. 2024). For similar semi-grazing systems, as in Laos, future studies should consider the distance between villages as an important factor. Another drawback was the lack of data on the weight and age of animals, which can influence movement and distance travel. Bejan (2012) reported that larger animals tend to travel further than those with small body sizes, so including these variables could provide more accurate insights into movement patterns.

5.6. Conclusion

GPS collars were successfully used to track goat movements during both seasons in Central Laos, across semi-forested and agricultural land. The findings not only highlight the differences in goat management practices in rural areas in Laos but also reveal the significant variation in the annual home range size of goats and the degree of mixing between herds within and between villages. Goats within villages that exhibit high levels of home range overlap are more genetically related and experience higher levels of gene flow than those in villages with zero or low home range overlap. Additionally, the presence of gene flow between villages that do not have overlap suggests that Lao farmers are engaged to some extent in exchanging genetic material between villages such as borrowing or buying bucks from other herds or villages.

5.7. Author contributions

JvdW, LO, SdlHS and SVL conceived the study. LO looked after the GPS collar testing in Australia and Laos and handled shipping all the device components from Australia to Laos. AP and SVL collected data in the field. SVL performed the statistical analysis and wrote the manuscript. SdlHS, PA and JvdW supervised the statistical analysis. All authors read and approved the final manuscript.

5.8. Acknowledgements

The authors gratefully acknowledge the financial support from Project LS/2017/034 for sample collection and genotyping. We thank Mr Glen Charlton and Mr Derek Schneider from the School of Science and Technology, University of New England for designing and testing the GPS collars. We also express our gratitude to all farmers in Australia and Laos who allowed us to deploy GPS devices on their goats during the testing period and experimental trial of GPS collars. The first author gratefully acknowledges financial support from the Australian Commonwealth Government through the Research Training Program stipend scholarship at the University of New England, Armidale, NSW, Australia.

5.9. Conflict of interest statement

The authors declare no conflict of interest.

5.10. Funding

This study was supported by the Australian Centre for International Agricultural Research under project LS/2017/034.

5.11. Data accessibility

The data are owned by Project LS/2017/034 and access to the data can be negotiated by request.

Higher Degree Research Thesis by Publication
University of New England

STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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Higher Degree Research Thesis by Publication University of New England

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Chapter Six: Design of breeding programs for goat smallholder systems in Laos

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Prepared to publish in “Animal Breeding and Genetics”

6.1. Abstract

This study used stochastic simulation to evaluate breeding strategies for improving the body weight of Lao native goats in smallholder systems while maintaining genetic diversity. Simulations reflected both traditional breeding practices and alternative strategies, including random mating, selection on phenotype, and rotational mating scenarios at the herd, village and district levels. Genetic change and inbreeding were evaluated after 20 mating rounds (~13 years). Results indicated that the traditional breeding practices (random mating scenarios) achieved minimal body weight improvement, less than 0.26 units of phenotypic standard deviation (PSD units). In contrast, selection scenarios demonstrated improvement in the body weight up to 1.49 PSD units. Among these scenarios, rotational mating strategies at district and village levels showed the highest gains, with body weight improvement of 1.49 and 1.175 PSD units over 20 mating cycles, respectively. Another scenario that ranked the animals according to their phenotypes at the district, village, and herd levels achieved improvements of 1.131, 0.899, and 0.69, respectively. Inbreeding levels varied across scenarios, with the highest observed in the herd rank (0.24), followed by herd random (0.216). The lowest inbreeding rate, ranging from 0.014 to 0.033, was observed in the following order: district-rank, village-random, district-rotation, and district-random. The village-rotation strategy may be optimal for isolated villages, while district-rotational breeding could benefit areas with accessible trade networks and minimal geographical boundaries. Successful implementation of these breeding strategies will require pedigree and animal performance recording and active farmer participation.

6.2. Introduction

Lao native goats, also known as the Kangbing-Katjang breed, play an important role in Laos, contributing to the livelihoods of smallholder farmers in multiple ways. They provide meat, serve as a form of saving and insurance (selling goats when cash is needed), and supply manure for crop cultivation (Gray et al. 2019). Additionally, goats in Laos also contribute to socio-cultural functions such as spiritual rituals, festivals and ceremonies (Liehr et al. 2024a). These goats are primarily raised in smallholder systems with herd sizes ranging from 2 to 12 goats (Wilson 2007). In recent years, due to the rising demand for exports to Vietnam, the goat population has increased six-fold to 711,200 heads in 2021, with approximately 90% of goats now being exported (Gray et al. 2019; FAOSTAT 2022; Le et al. 2024a; Walkden-Brown et al. 2024). Similarly, the size of herds within the smallholder systems has also grown, now ranging from 1 to 37 goats (Walkden-Brown et al. 2024).

Goat production in Laos is largely informal and characterized by low input management practices (Windsor et al. 2018; Gray et al. 2019). Only 1% of the national goat population was raised on commercial farms, while the vast majority remains in smallholder systems (Xayalath et al. 2021). In these traditional systems, goats are typically allowed to graze freely during the day and are brought to

shelters at night (Gray et al. 2019). However, goats face challenges such as inadequate nutrition, limited feed availability, and a high prevalence of disease and internal parasites (Windsor et al. 2018).

Native goats in Central Laos have primarily evolved through natural selection, adapting well to the region's tropical monsoon climate. However, their productive performance remains low, as they have not undergone intensive selection for productivity traits. The average adult weight of Lao native goats is 26kg, with a low daily weight gain (20.8 g/d) and a high mortality rate of 37.5% (Colvin et al. 2022; Walkden-Brown et al. 2024). Contributing to these performance limitations is the absence of structured breeding programs in smallholder systems, where traditional management practices prevail (Gray et al. 2019; Walkden-Brown et al. 2024). Breeding occurs throughout the year, typically in communal lands, without human intervention (Olmo et al., 2022). In Laos, as well as in other developing countries, it is challenging to develop an animal breeding program due to 1) small herd sizes (Kosgey & Okeyo 2007); 2) the farmers often selling their best animals when in need of cash, leading to negative selection (Kosgey & Okeyo 2007); 3) absence of pedigree and phenotypic data (Gizaw et al. 2009; Haile et al. 2023); and 4) lack of experts to run genetic evaluation and provide farmers with guidance about genetic improvement (Gizaw et al. 2014c).

To address these challenges, nucleus breeding programs have been proposed (Galal 1986; Kosgey 2004). These programs aim to genetically improve merit for productivity traits within a small population of animals, often on research stations or government farms. However, these programs are difficult to implement in smallholder systems as they require a long-term commitment from sponsors and active participation from farmers (Kosgey 2004). Developing breeding programs tailored to smallholder systems is complex. These programs must balance genetic gain in the short term with maintaining genetic diversity and avoiding inbreeding in the long term (van der Werf 2000).

Several studies have explored different breeding strategies for smallholder systems, including cooperative village or village-based breeding programs (CBBP), centralized nucleus breeding programs at research stations (CNBP), and combined nucleus-village breeding programs (CNVBP). The CBBPs are a new approach to genetic improvement programs proposed for the low-input traditional smallholder farming system (Sölkner et al. 1998; Kahi et al. 2005; Gizaw et al. 2014a). In these programs, farmers within specific geographical boundaries collaborate to improve livestock through community participation and decentralized selection directly in local herds (Sölkner et al. 1998; Gizaw et al. 2009). This involves the exchange of bucks between herds within CBBP. The CNBPs are conducted at research stations, where high-quality nucleus herds are managed under controlled conditions and undergo intensive selective breeding. In CNBPs, breeding bucks are exclusively selected from nucleus herds, and superior animals are then disseminated to farmers. While the CNBP approach requires significant resources and infrastructure, it allows for more intensive selection (Hodges 1990; Kosgey 2004). The

CNVBPs integrate both the nucleus at the research station and village herds, facilitating a continuous gene flow between them. Superior animals were selected from both sources (Mueller & James 1984a; Gizaw et al. 2011). These breeding programs could prevent the genetic lag between nucleus and village populations and support the conservation of local genetic resources (Gizaw et al. 2009). Each breeding program has its pros and cons. In low-input settings with limited infrastructure, the CBBPs are widely implemented in smallholder systems for goats and sheep in Africa (Gizaw et al. 2009; Tesema et al. 2021), dairy goats in Mexico (Wurzinger et al. 2013), indigenous pigs in Vietnam (Herold et al. 2010).

Among these breeding strategies, the CBBPs closely align with the observed management practices in Laos. Our previous studies (Chapter Five) observed that goats in Laos graze on communal lands or are kept on private property, with males used either from their herd or exchanged with other herds. Some gene flow was detected between herds both within villages and across districts (Le et al. 2023; Le et al. 2024a). Additionally, Lao goats in smallholder systems are low input and use limited infrastructure. Currently, no formal breeding program has been introduced or implemented for Lao native goats in smallholder systems and farmers lack systematic evaluation of productivity (Gray et al., 2019). There is also limited awareness of inbreeding and its potential negative impact on animal performance (Liehn et al., 2024a). To assess the potential of CBBPs in this context, we simulated various breeding scenarios in which sires and dams were selected either randomly or based on an observed phenotype for body weight. These sires were used either within their herds or exchanged with other herds within and between villages, or between districts. When sires are selected from the same herd or different herds, females could be mated with siblings or relatives, which would increase the inbreeding rate. In breeding programs, inbreeding should be managed and preferably kept at a low level (van der Werf 2000). Given the different selection methods and levels of sire exchange, we evaluated and compared the body weight improvement and the rate of inbreeding across these breeding scenarios to identify the most effective approach for sustainable genetic gain.

This study was a simulation study that evaluated different breeding strategies to improve the body weight and manage inbreeding levels for Lao native goats at herd, village, and district levels. The objective was to identify the most effective breeding programs for improving body weight while maintaining genetic diversity in smallholder systems, providing recommendations to Lao farmers on sustainable breeding practices.

6.3. Materials and methods

The simulation of alternative breeding programs was conducted using code developed in R. The simulation used breeding program designs applicable to the goat production systems in Central Laos, with particular attention to smallholder farmers in the region. Since no live animals were involved in this study, animal ethics approval was not necessary.

6.3.1. Breeding objectives

In this study, adult body weight was identified as the key breeding objective trait for Lao native goats. Lao farmers reported that local goats give birth to their first kid at 12 to 18 months of age (Xayalath et al. 2021). On average, does produce 1.4 litter/year with 1.5 kids per litter, ranging from 1 to 3 kids/litter (Windsor et al. 2018; Xayalath et al. 2021; Walkden-Brown et al. 2024). At birth, kids weigh between 1.1 to 1.5 kg and reach an average of 9.7kg by weaning. It takes 6 to 8 months for them to attain a body weight of 15kg (Xayalath et al. 2021), and they typically require an average of 13.4 months to reach 20kg (Gray et al. 2019). Selecting for high mature weight may increase the time taken, where consumers prefer a live weight of approximately 25kg at slaughter. Traders, abattoirs, and restaurant owners offered higher prices to Lao farmers when their goats reached this target weight at around a year old (Bui et al., 2022). As a result, Lao farmers are increasingly motivated to improve the productivity of their goats by enhancing their body weight to meet the growing demand from traders exporting to Vietnam (Liehr et al. 2024a).

6.3.2. Breeding scenarios

Eight breeding scenarios were simulated in this study at three different levels: herd, village and districts. The simulation started with a base population for each herd containing 22 unrelated animals (20 females and 2 males) and 20 females were mated to one of two males in the two mating rounds thereafter, with an average of two progeny per female per mating, ranging from 1 to 3 offspring. Each village had just three herds and there were three villages per district. The simulation ran for 20 mating cycles, assuming a 0.5 sex ratio among offspring. The total number of animals simulated for one breeding program at herd, village and district level was therefore 822, 2,466, and 7,398, respectively.

For each mating cycle, females over 12 months and under 8 years of age were selected candidates to be mated, while selected males were able to randomly mate with different females. The herd of the offspring was assigned based on the herd of their dams. Starting from the third mating cycle, the mating strategy varied depending on the specific breeding scenario. Each breeding scenario was replicated 1000 times to track patterns of genetic gain and inbreeding.

Heritability (h^2) for body weight was set at 0.2, with offspring survival from birth to mating age at 0.8 and dam survival after each mating round at 0.9. Phenotypes were sampled as the sum of the breeding value and a random residual effect, with variance equal to h^2 and $(1-h^2)$, respectively. Therefore, the phenotypic variance was assumed to be 1 and $\sigma_a^2 = h^2$. Breeding values in the base population were sampled randomly for $N(0, \sigma_a^2)$, whereas breeding values in subsequent generations were simulated as a parental average breeding value with an additional Mendelian sampling term. The variance due to Mendelian sampling decreased with increased inbreeding (van der Werf and de Boer, 1990), and can be written as follows:

$$\text{var}(\Phi) = \frac{1}{2} \left[1 - \frac{1}{2} (F_s + F_d) \right] \sigma_a^2$$

where $\text{var}(\Phi)$ is a variance of the trait; F_s and F_d are inbreeding coefficients for sire and dam, respectively; σ_a^2 is the additive genetic variance before selection. The inbreeding coefficient was calculated from pedigree using the method of Meuwissen and Luo (1992), and the code for calculating inbreeding coefficients is provided in Appendix C.

From the third mating cycle onward, dams and sires were selected either randomly or based on their phenotype, depending on the breeding scenario. For each herd, two male offspring from the $(i - 2)$ mating cycle were selected, while 20 dams were selected from the dams of the $(i - 1)$ mating cycle and the female offspring from the $(i - 2)$ mating cycle (Figure 6.1). Mating occurred either randomly or in a rotational system, depending on the scenario.

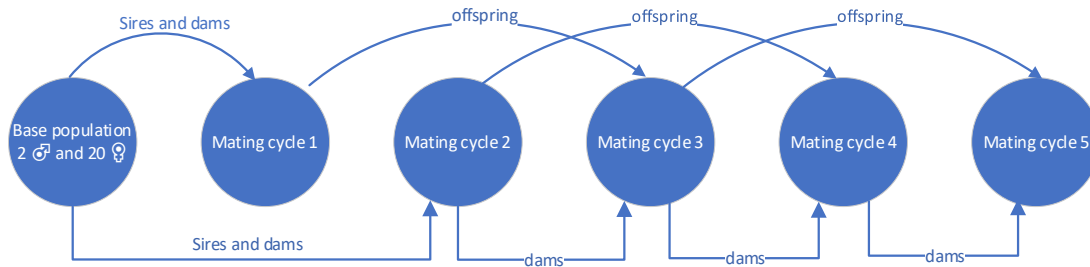


Figure 6. 1. The diagram of the first five mating cycles for herd mating breeding scenarios

Definition of the breeding scenarios

Herd random mating breeding scheme (Herd-random): This simulation was for a single herd and sires and dams were randomly selected. Each of the selected females was mated randomly to one of the selected males.

Herd random mating with the selection of males and females on phenotypic (Herd-rank): This was similar to the herd-random scenario but sires and dams were selected based on their phenotype. The two heaviest sires and 20 heaviest dams of the selection candidates were selected from within the herd.

Village-random breeding scheme (Village-random): This was a simulation of three herds within a village. In each herd, sires and dams were randomly selected. From the third mating cycle, two sires and 20 dams were selected randomly from each herd and these six sires were randomly allocated to these 60 females.

Village-random mating of the phenotypic ranked animal breeding scheme (Village-rank): This was a similar simulation in the Village-random, but the sires and dams were selected based on their phenotype.

Village-rotational mating of phenotypic ranked animal breeding scheme (Village-rotation): This breeding scheme was similar to village-ranked. Instead of random mating, a mating rotation was applied in this scenario, where selected males from herd 1 were mated with selected females in herd 2, selected males from herd 2 were mated with selected females from herd 3 and selected males from herd 3 were mated with selected females from herd 1 (Figure 6.2A).

District-random breeding scheme (District-random): This was a simulation for three villages, each with three herds. From the third mating cycle, in each village and herd, two males and 20 females were randomly selected, similar to herd-random. In total, at each mating cycle, 18 males and 180 females were randomly selected and these 18 sires were randomly allocated to these 180 females.

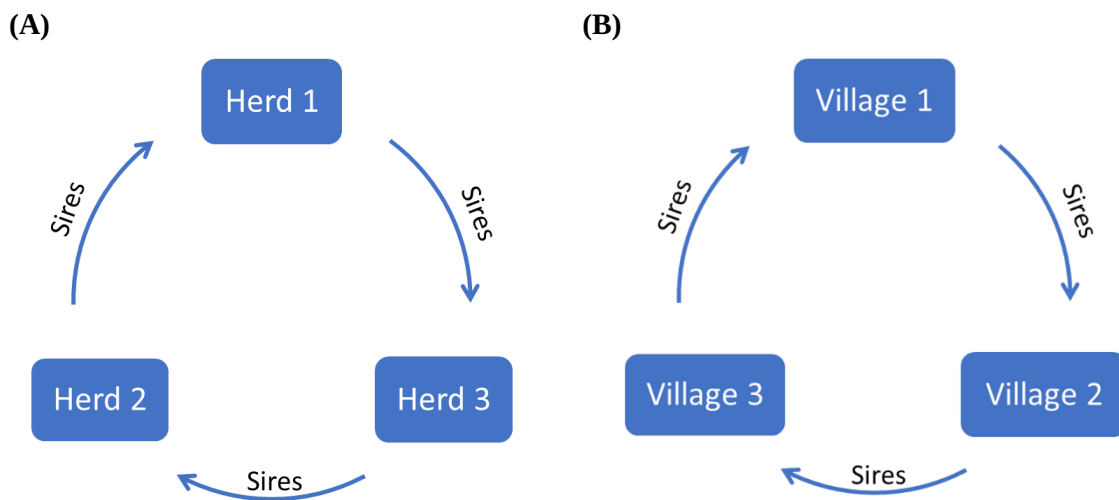


Figure 6. 2. Diagram of rotational mating: rotation of sires between herds within a village (A) and rotation between villages (B)

Random mating at district level of males and females selected based on phenotype (District-rank): This breeding scheme was similar to District-random and Village-rank. In each herd, two males and 20 females were selected based on their phenotypic ranking. In total, the 18 heaviest males and 180 heaviest females, were equally distributed over 9 herds, and 18 sires were each randomly allocated to 180 females, with 10 females allocated to each sire

District-rotational mating of phenotypic ranked animal breeding scheme (District-rotation): This simulation was similar to District-ranked, where animals were selected based on their phenotype for each herd. In the rotational mating scheme, selected males from Village 1 were mated with selected females from Village 2, selected males from Village 2 were mated with females from Village 3 and selected males from Village 3 were mated with selected females from Village 1 (Figure 6.2B).

6.3.5. Data analysis

In each breeding scenario, the body weight improvement was calculated as the average body weight across all the animals born from each mating cycle and then averaged across 1000 replicates. Similarly, the inbreeding coefficient was averaged over all progeny born in each mating cycle, averaging the averaged across 1000 replicates.

The results were visualized with *ggplot2* packages in R (Wickham 2011)

6.4. Results

6.4.1. Body weight improvement and inbreeding for herd-based program

The changes in body weight and inbreeding level of Lao native goats over 20 mating cycles are shown in Figure 6.3A and Figure 6.3B, respectively. In both scenarios, average body weight shows a consistent increase over the mating cycles. However, the rate of improvement was faster in the herd-rank scenario, while the herd-random scenario showed a very small increase. Beyond these initial cycles, body weight in the herd-rank scenario was consistently higher than in the herd-random scenario, reflecting a stronger impact of selection based on the phenotype of both sires and dams. Over 20 mating cycles, the maximum body weight in herd-rank scenarios could increase by 0.69 PSD units while the improvement in the herd-random scenario was 0.26 PSD units.

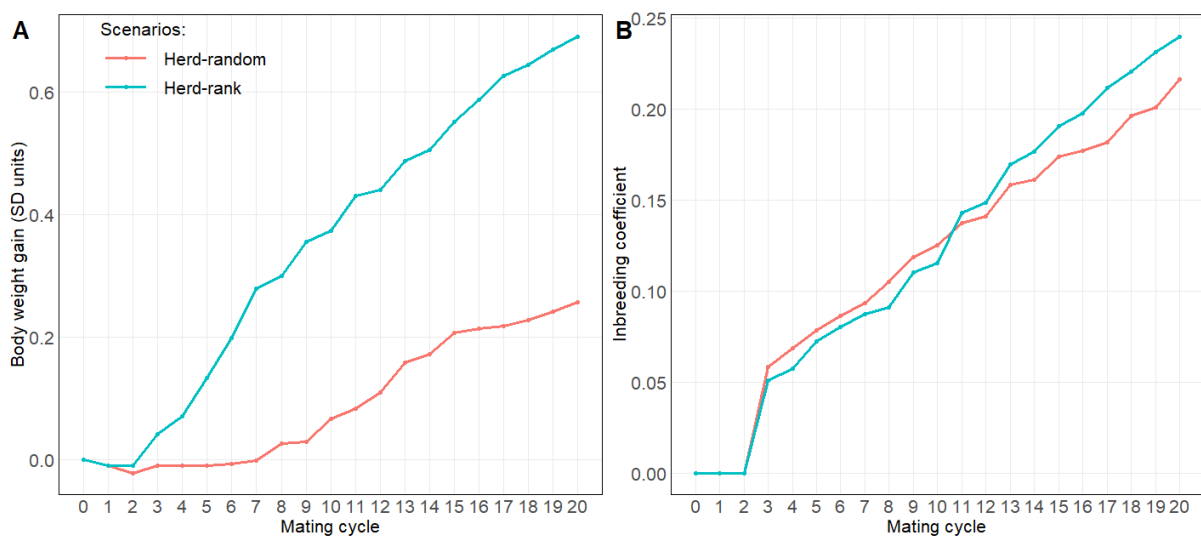


Figure 6. 3. Changes in average body weight (A) and inbreeding level (B) across mating cycles of herd-based scenarios

The inbreeding coefficient also increased across both scenarios. Starting from the third mating cycle, the inbreeding levels began to increase, with the inbreeding rate slightly higher under random mating compared to the herd-rank scenario. However, after the 11th mating cycle, the inbreeding rate in herd-rank surpassed that of random selection. By the 20th mating cycle (~ 13 years), the inbreeding coefficients reached 0.240 for the herd-rank scenario and 0.216 for the herd-random scenario.

Results in Figure 6.3 suggest that while phenotype-ranked mating at the herd level could improve body weight, it also led to a higher rate of inbreeding compared to random mating. It reflected a trade-off between genetic improvement and inbreeding risk in herd management strategies.

6.4.2. Body weight improvement and inbreeding for village-based program

The changes in body weight and inbreeding levels of Lao native goats under three village scenarios are shown in Figure 6.4A and Figure 6.4B, respectively. In all three village breeding scenarios, village-random, village-rank and village-rotation, the trends in body weight and inbreeding varied between scenarios.

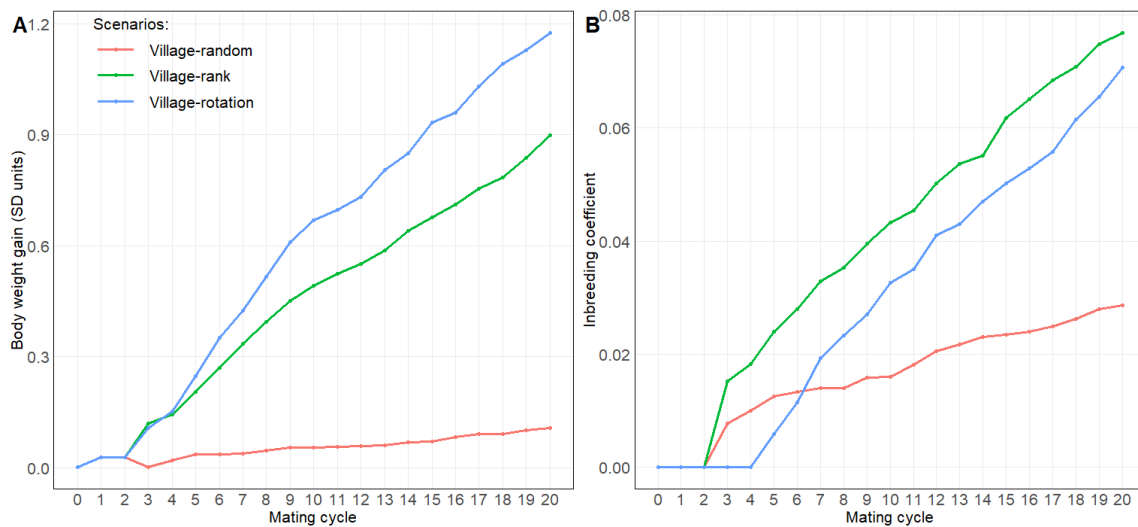


Figure 6. 4. Changes in average body weight (A) and inbreeding level (B) across 20 mating cycles of village-based scenarios

The results in Figure 6.4A illustrate a steady increase in body weight over all mating cycles in two Village scenarios where there was a selection on phenotype. The change under the random selection scenario was very small. The highest body weight improvement was observed in the village-rotation scenario, with phenotypic change in body weight reaching approximately 1.2 PSD units at the 20th mating cycle. The village-rank scenario also demonstrated a significant increase in body weight, though it was less than in the village-rotation scenario. After 20 mating cycles, the village-rank scenario could improve weight gain by 0.9 PSD units. In contrast, the village-random scenario showed a small increase in body weight, remaining under 0.108 PSD units throughout the mating cycles.

The inbreeding coefficient in three village scenarios increased over 20 mating cycles. The village-rank scenario showed the highest inbreeding level, reaching just over 0.077 at the 20th mating cycle. The village-rotation scenario followed closely, with the inbreeding level increasing starting from the fifth mating cycle and approaching 0.071 – approximately 7.8% lower than the village-rank scenario. The village-random scenarios had the lowest inbreeding level at 0.029, which was 62.3% lower than the village-rank scenario and 59.2% lower than the village-rotation scenario.

The results in Figure 6.4 show that, among the three village scenarios, body weight improvement was greater in the village-rank and village-rotation scenarios compared to the village-random scenario, though it also resulted in a higher rate of inbreeding. Additionally, the village-rotation scenario achieved greater body improvement while maintaining a lower inbreeding rate than the village-rank scenario.

6.4.3. Body weight improvement and inbreeding for district-based program

The body weight improvement and inbreeding levels across different district scenarios are presented in Figure 6.5. The district-rotation scenario achieved the highest body weight improvement, reaching approximately 1.488 PSD units after 20 mating cycles. The district-rank scenario followed, with a steady increase throughout the mating cycles, resulting in a bodyweight improvement of around 1.131 PSD units. In contrast, no substantial body weight improvement was observed in the random mating scenarios at the district level.

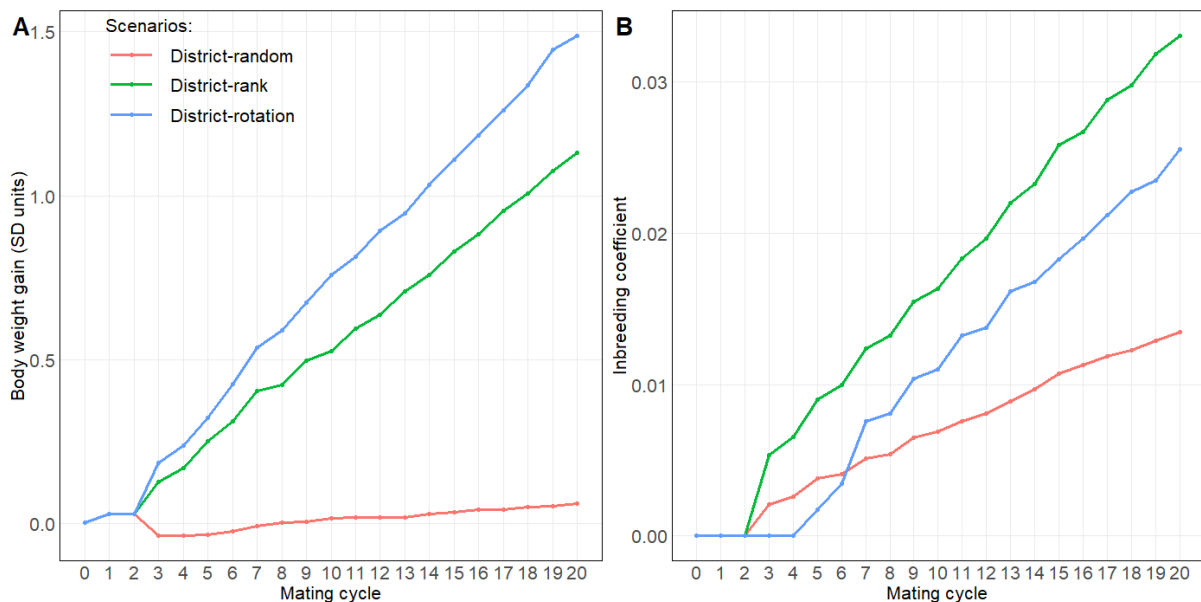


Figure 6. 5. Changes in average body weight (A) and inbreeding level (B) across mating cycles of district-based scenarios

The inbreeding coefficient increased across all district breeding scenarios. After 20 mating cycles, the inbreeding coefficients were 0.114, 0.101, and 0.061 for rank, rotation and random scenarios, respectively, at the district level.

The results in Figure 6.5 suggest the district-rotation scenario achieved greater body improvement while maintaining a lower inbreeding rate than the ranked scenario.

6.4.4. Assessment of body weight and inbreeding across breeding scenarios

On average, in terms of breeding strategy, the rotation approach consistently led to the greatest improvement, followed by rank scenarios, while random mating showed little effect on body weight.

For the same schemes, the district scenarios always showed more body weight improvement than the village scenarios, with the herd scenarios achieving the least gains.

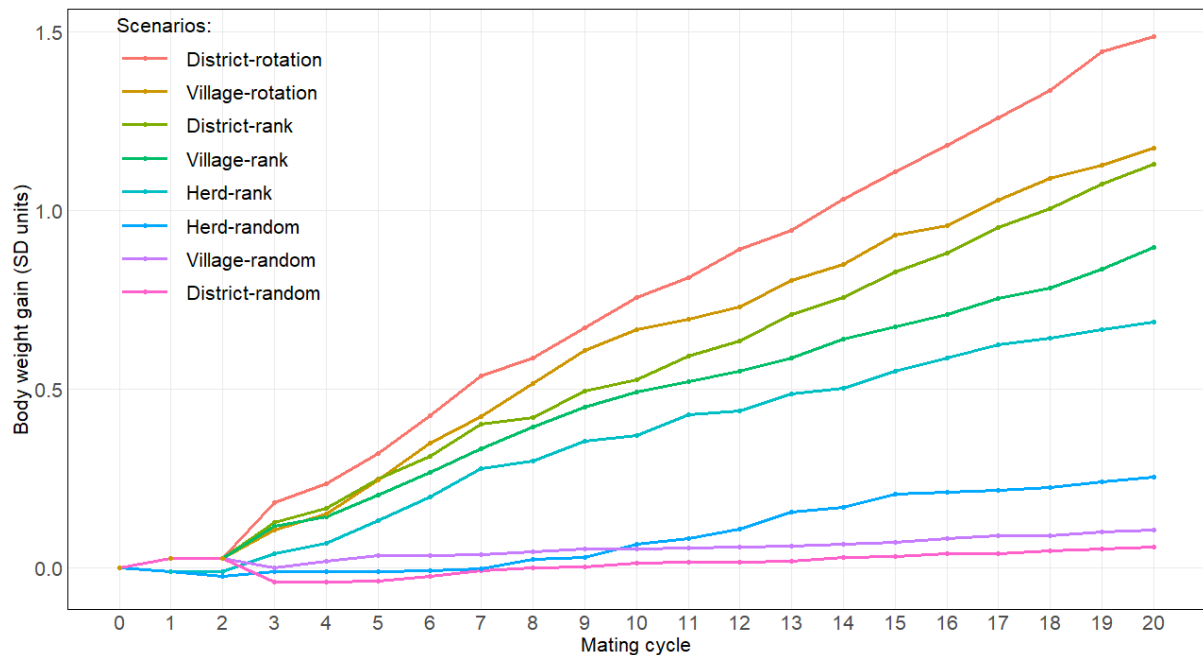


Figure 6. 6. Average body weight gain across mating cycles under all breeding scenarios

Combining these factors, the district-rotation scenario achieved the highest body weight improvement over 20 mating cycles, which was 26.6% higher than the improvement of the next best scenario, the village-rotation approach (1.488 vs 1.175 PSD units). Following this, rank scenarios across district, village, and herd levels achieved 1.131, 0.899, and 0.69 PSD units, respectively. Results in Figure 6.6 suggested that the rotation strategy, especially at the district level, was the most effective for improving the body weight in goats.

The inbreeding coefficients at the district, village, and herd levels across different mating cycles are displayed in Figure 6.7. Although inbreeding levels increased in all breeding scenarios, they could be classified into three groups. The first group, the herd breeding scenarios, showed the highest inbreeding levels across mating cycles. By the 20th mating cycle, the inbreeding for both herd breeding scenarios was over 0.2.

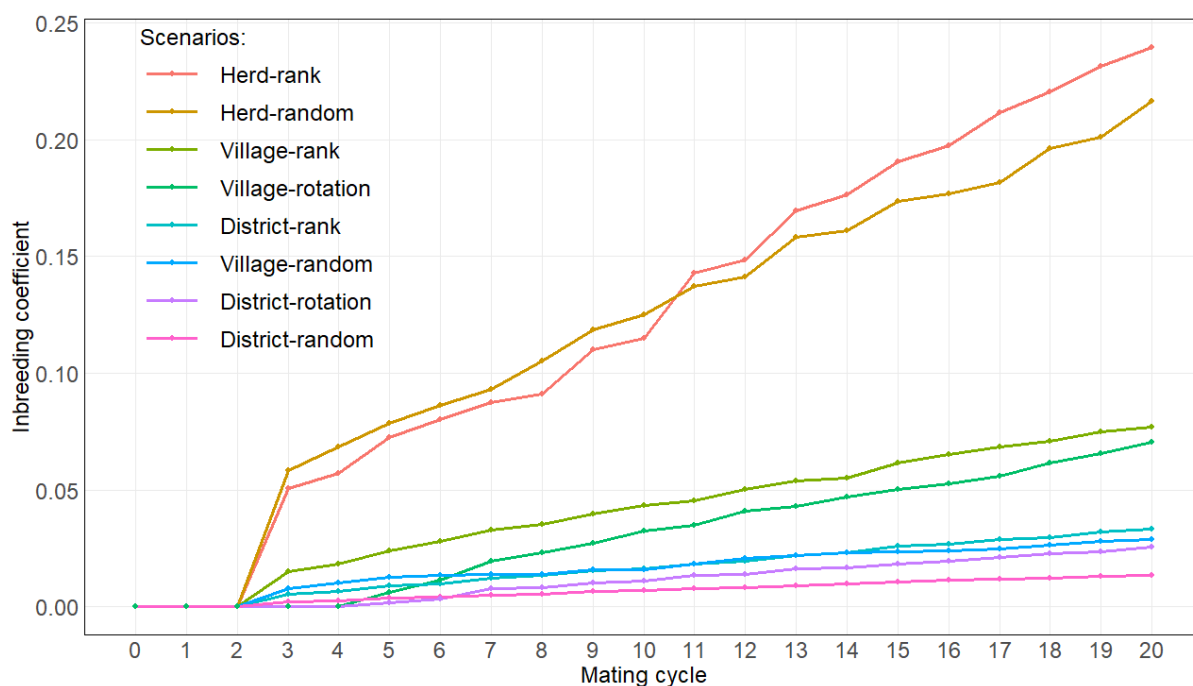


Figure 6. 7. Average inbreeding level across mating cycles under all breeding scenarios

The second group, with moderate inbreeding levels, included village-rank and village-rotation scenarios. In this group, the inbreeding gradually increased over the mating cycles, reaching 0.077 in the village-rank scenario and 0.071 for the village-rotation scenario at the 20th mating cycle.

The third group, with the lowest inbreeding level, included village-random and all district level breeding strategies. The inbreeding level in this group increased slightly, staying relatively low. At the 20th mating cycle, the inbreeding rate for this group ranged from 0.014 to 0.033, in the order district-rank, village-random, district-rotation, and district-random.

6.5. Discussion

The various breeding scenarios simulated in this study reflect both current breeding practices in smallholder systems in Central Laos and alternative breeding programs potentially suitable to these systems. Most goats in Laos are raised in smallholder systems (Xayalath et al. 2021), typically kept on private property or in shared grazing areas (Xaypha 2005). Additionally, our previous study (Chapter Five) found that goats in Nhonnhang and Nhonsomphou villages were kept in isolated grazing areas without interaction with other herds, as was reflected in the herd breeding scenarios simulated for these villages. The village breeding scenarios were simulated for Xaloi, Kanglouang, and Sebanghiang villages, where goats shared grazing areas to varying extents. Additionally, some Lao farmers occasionally borrowed bucks from other herds for mating (Liehr et al. 2024a), or trade goats at local markets in districts such as Phin and Songkhone (Le et al. 2024a). The practice of exchanging bucks between villages has been successfully implemented in other low-input systems in parts of Eastern and Southern Africa (Gizaw et al. 2009; Haile et al. 2023), similarly to the simulated district breeding

scenarios. Traditional management in Laos involved largely uncontrolled breeding (Gray et al. 2019), though a small proportion of Lao farmers selected goats based on their appearance (Liehr et al. 2024a). While the rotation mating strategy is not yet systematically practised in Lao goat production, it has been recommended for smallholder systems for goat (Getachew et al. 2022), sheep (Gizaw et al. 2014c), and cattle (Omer et al. 2022).

The results of this study indicate that strategies differed in their impact on genetic gain for growth of Lao native goats. Across three levels (herd, village, and district), structured selection and rotational mating offered substantial body weight improvement compared to random mating. In particular, the district-rotation scenario achieved the greatest body weight improvement, followed by the village-rotation scenario. It emphasises the importance of deliberate and controlled selection for maximizing body weight improvement. The rank scenarios at the district and village levels also showed steady body weight increases over mating cycles, though at a lower rate than the rotational mating strategy.

These findings align with previous studies. Haile et al. (2020) found that in Ethiopian community-based breeding programs (CBBPs) which reflected the district-rotation scenarios in our study, sheep body weight at six months increased by 18-31% compared to station-managed conditions, which is comparable to the village-rotation scenario. Additionally, Haile et al. (2020) noted growth levels of lambs from CBBPs were 3.7kg higher than those reported in station management. The improved growth and carcass traits of goats have also been reported in Malawi and Ethiopia under CBBPs (Getachew et al. 2022; Haile et al. 2023). In Ethiopia, Gizaw et al. (2014a) observed genetic improvement in Menz sheep under village breeding programs, with birth weight, three-month and six-month weights increasing by 0.49 to 2.46kg after three generations. In Sudan, Omer et al. (2022) found the highest genetic gain in milk yield performance of Butana cattle under the rotational use of bulls between villages compared to the use of farm bulls.

In traditional breeding practices, common in smallholder systems, production trait improvements tend to stagnate or reduce (Gizaw et al. 2014a; Mueller et al. 2015). In this study, the random mating scenarios at herd, village, and district levels, reflected Laos' current traditional breeding practice and showed negligible body weight improvement. Walkden-Brown et al. (2024) observed that Lao native goats in the smallholder systems had a slight weight increase during the dry season, followed by a decrease in the rainy season, with no significant year-to-year gains. This aligns with our findings and those of other studies, such as Omer et al. (2022), where no genetic gain in milk yield for Butana cattle was achieved. Similarly, stagnating body weight in Ethiopian sheep breeds under random mating was noted by Gizaw et al. (2014a). Even negative trends in genetic gain in production traits may result from unintentional negative selection by farmers, where superior bucks or does are sold for higher prices instead of being retained for breeding (Kosgey & Okeyo 2007).

While body weight gains are desirable, they must be balanced against increasing inbreeding risk. In this study, the herd rank scenario showed moderate improvement in body weight but consistently high inbreeding levels, reaching over 0.2 by the 20th mating cycle. In the rank scenarios, animals selected for breeding were more closely related, which elevates inbreeding risk, particularly in small populations. This aligned with Gizaw et al. (2014a), who reported that restricted genetic pools under high selection intensity can lead to higher inbreeding. In contrast, rotational mating scenarios at a larger scale (district or village) achieved a better balance in our study between improvement of body weight and maintaining genetic diversity. This finding was consistent with the outcomes of CBBPs for goats and sheep in Ethiopia, and cattle in Sudan (Gizaw et al. 2014a; Gizaw et al. 2014c; Getachew et al. 2022; Omer et al. 2022).

Our findings underscore the potential of district or village-rotational scenarios as optimal approaches for maximizing body weight improvement against slight trade-offs in inbreeding in the Lao native goat population. For practical implementation, rotational breeding within a village or between villages could form a foundation for genetic improvement. However, program design should also consider local conditions. For example, in more isolated populations like those in Kanglouang village, the village-rotational scenario may be optimal, while in regions with accessible trade and minimal geographical boundaries like villages in Phin and Songkhone districts, the district-rotational scenarios would be ideal. These two approaches could be adapted for other regions in Lao, depending on specific local conditions.

An important factor in these programs is the establishment of effective recording and training systems for participating farmers. Accurate pedigree and performance records are important for identifying high-performing animals and selecting suitable breeding candidates (Gizaw et al. 2014b). Haile et al. (2023) emphasized that successful CBBPs implementation for goats and sheep in Tanzania, Malawi, and Ethiopia relied on animal performance and pedigree records, along with active farmer involvement. However, both pedigree and phenotype data are currently not recorded in smallholder systems in Laos (Gray et al. 2019). Therefore, Lao farmers will need training in basic animal husbandry and selection practices. With these records, farmers could begin selecting animals based on the phenotype ranking, followed by rotational mating as suggested in this study.

Further study could explore the use of Best Linear Unbiased Prediction (BLUP) to estimate the breeding value of economic traits for Lao goats. With pedigree records, the breeding value can be estimated accurately using relatives in the numerator relationship matrix (Henderson 1988). Selection based on the estimated breeding value (EBV) provided higher genetic gains and greater accuracy than phenotypic selection alone (Omer et al. 2022). For instance, Kahi et al. (2004) demonstrated better genetic improvement in cattle breeds through EBV. Additionally, genomic markers for goats, available since 2014, have enabled genomic selection studies, showing that genomic selection offers even greater accuracy than EBV-based selection (Gorjanc et al. 2015). The genomic selection allows to pre-select

animals at younger ages and parents with higher accuracy than BLUP (VanRaden et al. 2009; Patry & Ducrocq 2011; van der Werf 2013). However, at this stage this method is not practical for Lao farmers yet, requiring significant investment and capacity-building efforts.

In Laos, goats typically graze on communal lands for 6 to 8 hours daily and are housed together for 16 to 18 hours (Walkden-Brown et al., 2024). To implement ranking and rotational mating strategies for Lao farmers, it is recommended that the breeding bucks be kept separate, with other bucks castrated to prevent undesired mating. Experiences from implementing CBBPs in other countries provide possible arrangements for managing male candidates. For example, in Argentina, breeding goat males were kept in specialized ‘male flocks’ during the off-season (Mueller et al, 2013). In Bolivia, llama males were herded separately from females until needed (Mueller 2013). Similarly, in Vietnam, individual farmers took on the responsibility of managing boars for their community (Roessler et al., 2012).

Feed availability is an issue in Laos and genetic improvement in adequate feed management must be addressed alongside genetic improvement for weight gain. Lao farmers mainly rely on local grass and fodder to feed their goats (Gray et al, 2019). However, the feed availability was characterized by seasonal shortage, low nutrition content and limited energy and protein (Phengsavanh 2003; Phengsavanh et al. 2017; Phengvilaysouk et al. 2022). Supplementation is rarely practised in smallholder systems (Phengsavanh 2003). Recently, some farmers practice supplementary forage feeding during the rainy season using a cut-and-carry approach (Gray et al., 2019; Liehn et al., 2024a). Walkden-Brown et al. (2024) reported that goats receiving supplementary feed in experimental settings had an average daily gain of 67.5 g/day, compared to 20.8 g/day for free-grazing goats. Therefore, to improve the genetic potential for weight gain in Lao native goats must be accompanied by forage growing interventions and supplementary feed.

Genetic improvement for indigenous breeds can be achieved through within-breed selection or by crossbreeding with exotic breeds (FAO 2010). This study focused on simulating breeding strategies to improve the body weight of Lao goats through within-breed selection. An alternative approach, not simulated in this study, involves introducing superior bucks to the native population. Several studies have illustrated the improvement of genetics for local breeds through the incorporation of exotic germplasm. For example, the Boer goat breed has been used to improve the body weight of Central Highland goats in Ethiopia (Tesema et al. 2021), and the Huai goat breed in China (Barry & Godke 1991; Yao et al. 2023). In Vietnam, Co goat was crossbred with bucks from India and New Zealand to improve body size and carcass traits (Binh & Lin 2005; Norton et al. 2009). However, crossbreeding programs face significant challenges, including the poor adaptability of exotic breeds to the local environment, lack of infrastructure, and limited farmer motivation (Kosgey et al. 2006; Haile et al. 2023). Dessie et al. (2014) reported that after 27 years of crossbreeding programs supported by NGOs and the Ethiopian government, Boer x Konso crossbreeds were reported to be less productive than the

indigenous goats. In Laos, Back Thao bucks from Vietnam were introduced to mate with Lao native goats, resulting in crossbred with body weights at 12 months that were 0.94 and 1.95kg higher than female and male native goats, respectively (Trach & Phiovankham 2011). Boer goats imported from Thailand are also present in Northern Laos (Wilson 2007). Unfortunately, until today there are no further documents that cover those breeds and their development in Laos. Further studies may be considering the effectiveness of crossbreeding to Lao native goats. Additionally, using genetic evaluation tools to compare the local breeds, imported breeds and their crossbreds is essential to identify the best-performing animals. Such evaluations should also assess the adaptability of imported breeds to the tropical monsoon climate of Laos and the smallholder farming systems prevalent in the country.

In this study, we proposed a breeding program targeting body weight as a single trait. Once a basic breeding program has been established, expansion a breeding objective with multiple traits should be considered. In a further breeding program, multiple economic traits should be considered. Given that over 90% of Lao goat populations are exported to Vietnam to meet the high meat demand, traits related to meat quantity and quality should be included in future breeding programs for Lao native goats.

6.6. Conclusions

In this study, we simulated various breeding scenarios that reflect both current breeding practices in Laos and alternative breeding strategies for goat production in smallholder systems. The results indicated that traditional breeding practices in Laos, represented by random mating scenarios, failed to improve body weight and still lead to substantial increases in inbreeding over time, especially at the herd level. Rotational mating strategies at the village and district levels offer potential alternative breeding programs for goat production, with applicability depending on local conditions.

In isolated villages, the village-rotational mating strategy provides a much greater balance between body weight improvement that may outweigh increases in inbreeding, while district-rotational programs could be more beneficial in regions with accessible trade networks. These rotational breeding approaches not only improve the body weight of Lao native goats but also have lower rates of inbreeding and therefore maintain genetic diversity within the population, which supports the long-term sustainability of breeding programs. Implementing rotational mating strategies could bring economic and productivity benefits to Lao farmers. However, they require infrastructure for pedigree and performance recording, along with the active involvement of farmers.

6.7. Author contributions

SL and JvdW conceived the study. SL developed the code, conducted the statistical analysis and drafted the manuscript. JvdW wrote the inbreeding function, supervised the statistical analysis and contributed to manuscript writing. SdlHS and PA supervised the statistical analysis and provided guidance on manuscript preparation. All authors have read and approved the final manuscript.

6.8. Acknowledgements

The authors sincerely thank Prof. Stephen Walken-Brown and Dr. Luisa Olmo School of Environmental & Rural Science, University of New England for their inspiration and collaboration on Lao native goats under the ACIAR Project LS/2017/034 in Laos. The first author gratefully acknowledges financial support from the Australian Commonwealth Government through the Research Training Program stipend scholarship at the University of New England, Armidale, NSW, Australia.

6.9. Funding information

Not applicable

6.10. Declarations

The authors declare no conflict of interest.

Higher Degree Research Thesis by Publication
University of New England

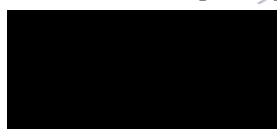
STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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26/11/2024

Date



/ Principal Supervisor

26/11/2024

Date

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We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
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Chapter Seven: General discussion and conclusions

7.1. Aims and summary of main findings

Genetic improvement of indigenous livestock provides an important pathway to improve the living standard of farmers in developing countries. This potential is apparent in Laos where native goats contribute up to 46% of annual household income in goat raising households (Walkden-Brown et al. 2024). Like other indigenous breeds, Lao native goats have small body sizes and a slow growth rate but they are adapted to local environments and management practices. Therefore, it is important to understand their genetic characteristics for sustainable breeding and conservation.

This thesis aimed to evaluate the genetic diversity and population structure of Lao native goats, identify the candidate regions and potential genes in the Lao goat genome that are associated with production traits and adaptation to the local environment, estimate animal movement patterns of goats in different seasons and the degree of mixing between herds within and between villages, and evaluate designs for effective breeding programs for the goat population in a smallholder system.

The first experimental chapter of this thesis (Chapter Three) investigated the genetic diversity and population structure of Lao native goats by using 50K genomic data from samples collected in Central Laos and from 163 goat breeds from other countries available in the public domain. This is the first detailed analysis of Lao native goats using a medium-density SNP Chip. It showed that there was moderate genetic diversity and low levels of inbreeding in the native goat population in Laos with some differences between surveyed villages potentially linked to geography and culture. The results also showed that Lao native goats have a close genetic relationship with goats from China, Mongolia and Pakistan, and possibly share a common ancestor with Guangfen, Jining Grey and Luoping Yellow breeds of China and Teddi goats of Pakistan.

In Chapter Four, we investigated the signature of selection for Lao native goats using the DCMS approach, incorporating the p-values from the nine statistical tests within Lao native goats and their co-ancestors from Chinese and Pakistani goat breeds. There were 68 unique coding genes from 24 genomic regions identified in Lao native goats. These genes may be linked to adaptation to the tropical monsoon climate in Laos and economic traits such as carcass characteristics, growth, reproduction and milk production traits in that environment.

Chapter Five used GPS data over a 12-month period combined with genomic data to examine the animal movement patterns, home range, gene flow and genetic relatedness of Lao goats between herds within and between villages. There was variation in home range size between villages and males tended to cover larger areas than females, overall a larger home range was occupied in the dry season compared to the rainy season. Home ranges were compared with patterns of gene flow, derived from genomic

data from animals of diverse villages. There was low to moderate gene flow between villages, also reflected by minimal home range overlap between villages. Within each village, the home range overlap between herds was consistent with gene flow patterns and genetic relatedness. The results in Chapter Five illustrated differences in goat management and mating patterns between villages.

In Chapter Six, a simulation study was conducted to evaluate breeding strategies to assess bodyweight improvement and inbreeding in Lao native goats in smallholder systems. The simulation compared random mating with ranking and selection on phenotype, and systems of rotational mating at herd, village and district levels. These strategies reflected both traditional breeding practices in Lao and alternative breeding strategies. The results showed that random selection and mating showed minimal body weight change and a significant increase in inbreeding over time when breeding at the herd level. In contrast, a rotational mating strategy could offer a significant body weight improvement while maintaining a low inbreeding rate. The village-rotational mating strategy could be implemented for isolated villages, while the district-rotational strategy could benefit areas which are accessible to trade networks and have minimal geographical boundaries.

The results from Chapters Three, Four, and Five provide a detailed picture of Lao native goats, highlighting various aspects of their genetic structure, mating patterns, and breeding potential. Native goats in Central Laos were classified into two groups: Sepon and the combined group of Phin and Songkhone, both exhibiting moderate genetic diversity and low inbreeding levels. The effective population sizes in both groups are large enough to support selection and the implementation of an effective breeding program (Chapter Three). Additionally, I investigated the potential genes associated with adaptation to the local environment and regional management practices, as well as economic traits such as growth, reproduction, and meat quality (Chapter Four). These genes could be incorporated into selective breeding programs by selecting animals with favourable alleles for these traits. Chapter Five examined movement patterns and home range size, which varies with management practices (isolated, seasonal free grazing and completed free grazing), and explored how geography and management influence gene flow between herds. The findings show the importance of considering spatial and genetic factors when designing breeding programs. Based on this understanding of Lao native goats' genetic resources and environmental context, various breeding strategies were proposed to align with both traditional practices and alternative methods (Chapter Six). The results showed the potential benefit of exchanging selected bucks between herds.

Given the findings in this thesis, this general discussion will focus on three main points. These are 1) sustainable improvement and conservation of local goat breeds, 2) the design and implementation of breeding programs for indigenous breeds, including alternative breeding strategies and the use of genetic evaluation tools, and 3) research limitation and future consideration.

7.2. Sustainable improvement and conservation of local goat breeds

The genetic merit of indigenous goat breeds can improve through selective breeding within the breed or by introducing other breeds through crossbreeding and combining this with selective breeding. One of the aims of this thesis was to identify effective strategies to boost goat productivity in smallholder systems in Laos. The most sustainable approach to preserving local livestock breeds is to enhance their value through targeted improvement for unique characteristics and those that are economically valuable. Through careful selection within native breeds, it is possible to achieve steady, long-term genetic gains. Selecting high-performance animals over multiple generations could enhance the productivity of the local goat populations. However, the selection of higher-performing animals can also lead to an increased rate of inbreeding. In Chapter Six, it was shown that body weight in Lao native goats could be effectively improved by selection based on individual phenotypes. Combining this with exchanging bucks within and across herds at village and district levels could help control the rate of inbreeding. An alternative approach to mitigate inbreeding would be to involve a greater number of herds, with superior bucks selected from a broader regional pool. Haile et al. (2023) observed the benefit of gathering around 100 goat herds for each breeding program and around 130 CBBPs existed in Ethiopia. Additionally, using native breeds for local production helps to sustain genetic diversity and avoid genetic introgression from exotic breeds. Conservation efforts here include the preservation, selective improvement, and sustainable use of these breeds (FAO, 1986). Similar approaches to both conserve and improve the local goat breeds have been implemented in countries like China (Liu et al, 2019), Vietnam (Norton et al. 2009) and Mexico (Sánchez-Gutiérrez et al. 2021). Implementing these strategies in Laos is achievable but will require the establishment of a network of herds and ensuring consistent selection and breeding practices remain in place.

While crossbreeding was not investigated in the thesis, it is highly relevant to improve the genetic potential of Lao native goats. While pure breeds offer significant benefits, crossbreeding with exotic breeds is often promoted as a faster and more economical way to enhance breeding performance (Kingham 1987). Introducing exotic breeds to improve local goat breeds has been done in various areas such as South America (Lôbo et al. 2010), Europe (Pérez-Baena et al. 2021), Africa (Tesema et al. 2020; Tesema et al. 2021), and Asia (Guizhi 2007; Norton et al. 2009; Trach & Phiovankham 2011). The Boer goat, a well-known meat breed, has been widely used in crossbreeding programs in both commercial farms and smallholder systems (Skinner 1972; Barry & Godke 1991; Norton et al. 2009; Tesema et al. 2020). For example, Boer goats have been crossbred with local goat breeds since 2007 to improve goat yield in Ethiopia (Tesema et al. 2020). In China, Boer goats were crossbred with local breeds to produce the BoHuai goats, which has significantly improved meat production, reproduction, and meat quality traits (Guizhi 2007). Although the Boer breed is present in Laos, there is no evidence of crossbreeding with local goats. However, the Vietnamese Back Thao goat was introduced to enhance body weight in native goats in Laos (Trach & Phiovankham 2011). Nevertheless, crossbreeding with

exotic breeds has not always achieved the expected productivity improvements. In some studies, crossbred performance was lower than the indigenous goats (Onzima et al. 2014; Argyriadou et al. 2020). This was due to local conditions not supporting the crossbreeding with exogenous breeds (Onzima et al. 2014). Challenges in regions such as Sub-Saharan Africa illustrate that crossbreeding programs often require higher input, which can limit their effectiveness in smallholder settings where resources are limited (Onzima 2019). Further studies may be considering the effectiveness of crossbreeding to Lao native goats. Phenotype recording and genetic evaluation could help assess the performance of local vs crossbred or imported breeds.

7.3. Breeding programs for indigenous breeds

Breeding programs for local breeds, such as Lao native goats, offer an opportunity to enhance goat productivity leading to improved economic resilience in rural communities. However, establishing these programs in smallholder settings demands increased labour inputs and a commitment to long-term development. These programs must balance short-term genetic gains with maintaining genetic diversity to prevent inbreeding depression over time (van der Werf 2000). Many developing countries face challenges in implementing these programs due to infrastructure limitations, resource constraints, a lack of systematic data collection, a shortage of skilled personnel, and minimal institutional support (Kosgey & Okeyo 2007). Smallholder farmers often rely on traditional breeding practices involving selecting animals based on observable traits like size or colour, without the support of systematic recording or pedigree tracking (Gizaw et al. 2014b; Gray et al. 2019; Haile et al. 2023). In Laos, as in many developing countries, structured genetic improvement programs are rare. Therefore, designing breeding programs suited to smallholders could overcome these challenges and support sustainable long-term improvement.

7.3.1. Alternative breeding programs

In the scientific literature, examples of various breeding programs have been described designed for indigenous breeds in smallholder systems. While some have succeeded, others failed to achieve genetic improvement. Among these, Community-based breeding programs (CBBPs) have been proven effective, particularly with indigenous sheep, goats, and cattle in Africa (Haile et al, 2018; Omer et al, 2019; Gizaw et al 2014). These programs are tailored for low-input systems, using farmers within limited geographic areas who share a common interest in preserving and enhancing their livestock's genetic resources (Mueller et al. 2015). CBBPs prioritize indigenous stock and emphasize farmers' active involvement, from program design to implementation, making for a participatory, bottom-up approach (Mueller et al. 2015). Their success is based on aligning with farmers' breeding goals and ensuring infrastructure, participation, and ownership of the program (Sölkner et al. 1998; Gizaw et al. 2009; Mueller et al. 2015; Haile et al. 2023). In Chapter Six, it was shown that pooling selected males and females from across herds within and between villages could improve the body weight of Lao native

goats while inbreeding was significantly lower than with within-herd mating. Rotating breeding bucks among herds across villages can further enhance genetic improvement while managing inbreeding levels. Depending on geographic boundaries, the optimal scope of CBBPs may vary: for isolated villages like Sepon, a village-level CBBP would be optimal, whereas district or province-level programs may suit areas with accessible trade networks.

The open nucleus breeding program (ONBP) is another viable model for indigenous breeds. In ONBPs, high-performance animals are grouped in nucleus herds at research stations for genetic improvement, with top animals from local herds introduced into the nucleus, and superior animals shared back into the general population (James 1977; Mueller & James 1984b). These nucleus herds can be managed by external organizations, such as government bodies or universities (Mueller et al. 2015). ONBPs have been successfully implemented in various species, including Iranian cashmere goats (Mueller 2013), Kenyan dairy goats (Ojango et al. 2010), Peruvian wool sheep (Mueller et al. 2002), and Vietnamese indigenous pigs (Herold et al. 2010). This open nucleus approach could increase the rate of genetic gain, it might enhance farmer engagement and support the conservation of local genetic resources (Gizaw et al. 2009). In Laos, ONBPs could be established at Livestock Research Stations or larger farms, with 93 large goat farms available across provinces (Xayalath et al. 2021), these could serve as potential open nucleus farms.

7.3.2. Utilizing genetic evaluation tools

Accurate data recording is the foundation for evaluating the effectiveness of a breeding program. Pedigree information is essential for controlling inbreeding, while records of phenotypic traits are necessary for selection to achieve genetic progress. One of the main challenges to implementing breeding programs for indigenous breeds is the lack of structured data recording (Haile, et al. 2023). Under (semi) free-grazing conditions, comprehensive pedigree tracking or sire identification is often impractical; however, dam-offspring recording is feasible. With rotational mating strategies, complete pedigree records could be maintained as farmers know both sires and dams of offspring within their herds. For phenotypic recording, households can start with simple metrics, such as recording body weight at birth, weaning, and maturity. Haile et al. (2023) recommend starting with key economic traits that align with routine practices to ensure that data collection remains simple and sustainable. As farmers become accustomed to the process, additional economic traits, like reproductive metrics, can be incorporated at the household level, while more complex traits, like carcass and meat quality, may require specialized assessment by trained personnel.

After data collection, genetic evaluation methods can be used to calculate the selection merit of animals and response to selection over time, as well as inbreeding levels for individual animals. The most basic evaluation method is based on individual performance or selection by phenotype. Farmers can select their animal based on the phenotypic ranking, and select the best males and females in their herds.

However, this approach could deliver biased ranking when comparing phenotypes across herds, seasons, or years. Additionally, the BLUP method uses both phenotypic records and information on relatives and can account for fixed effects of herds, seasons, and years to estimate breeding values of animals (Henderson 1986; van der Werf 2000). Information from the pedigree is then used to build the numerator relationship matrix (Wright 1922) and can be used to use information on relatives.

With advancements in genomic technology, genomic selection (GS) has become a powerful breeding tool in advanced breeding programs. GS can use genomic data alone or in combination with pedigree data to estimate an animal's genetic potential. This method enables to selection of animals at a younger age, which shortens the general interval, providing higher accuracy of the prediction, and then faster genetic progress (Hayes et al. 2009a; van der Werf 2013; Meuwissen et al. 2016; Le et al. 2024b). GS has been widely applied in breeding programs for animals and plants (Hayes et al. 2009a; van der Werf 2013; Mrode et al. 2018). GS does not require pedigree records (Meuwissen et al. 2001), as pedigree relationships can be replaced by genomic relationships. Therefore, GS could be convenient for breeding programs where pedigree recording is problematic, such as in indigenous breed studies. However, implementing GS in smallholder systems remains challenging due to cost and limited infrastructure or access to genotyping services. Moreover, GS requires the establishment of a reference population with a significant cohort of animals recording for phenotypes as well as having genotype information. The opportunities and limitations of applying GS in both smallholder and intensive systems have been thoroughly reviewed by Burrow et al. (2021), Mrode et al. (2018), and Mrode et al. (2019). They concluded that the feasibility of applying GS in smallholder systems requires significant investment and capacity-building efforts.

GS holds substantial potential to improve genetic traits in smallholder systems, its practical implementation requires addressing critical challenges, including cost-effective genotyping, establishing robust reference populations, and tailoring programs to fit local socioeconomic and logistical conditions. Before using any genetic evaluation tools, at least a basic breeding program should be implemented first with simple recording phenotype, pedigree and awareness of farmers on improvement and recording.

7.3.3. Implementation of breeding programs for indigenous breeds in smallholder systems

Implementing any breeding programs for indigenous breeds in smallholder systems requires a carefully structured approach that aligns with local resources, farmer engagement, and sustainable practices. Below are the main step-by-step suggestions for effective implementation.

1. Engage interested farmers and assess current production: Gathering the community to recruit committed participants. Farmers should volunteer and commit to participating in the breeding

program, and agree to a common breeding objective. Identify the current breeding structure, animal performance and the primary challenges in husbandry.

2. **Defining breeding objectives:** With the farmers, creating clear breeding objectives. Which traits need to be improved and how important are different traits in relation to each other? Beginning with simple traits (e.g. growth, reproduction, and health), progressing to more complex traits (e.g. carcass traits, and meat quality). These objectives should be alignment with farmers' needs, perspectives and preferences (Mueller et al. 2015; Haile et al. 2023). Farmers' involvement in deciding which traits to improve is important for the program's success.
3. **Establish breeding structures:** Decide on an appropriate breeding structure, such as CBBPs, ONBPs, and CNBPs. Each structure enables farmers' participation and sharing of genetic resources among farmers or between farmers and nucleus herds managed by breeding organizations.
4. **Provide training for farmers:** Provide training to farmers on basic livestock husbandry, health management and breeding practices such as control matings. Instruction on record-keeping and the long-term benefits of breeding programs should be included.
5. **Data recording and collection:** Farmers can record animal performance and pedigree on notebooks or mobile apps. Local enumerators or extension staff could assist with data recording, and ensure continuous data collection over time. If GS is applied, trained staff should record sample information.
6. **Create mating arrangements:** The principle is selecting the best males to mate with the best females. Depending on the breeding strategy, rotational bucks may be chosen from nucleus herds or other herds in the CBBPs. These rotations should be carefully coordinated and monitored by both farmers and extension staff.
7. **Develop selection criteria and procedure:** Based on breeding objectives, develop clear selection criteria for males and females. Local enumerators or extension staff may initially demonstrate how to select animals based on agreed-upon selection criteria. Farmers should then be encouraged to make selections independently.
8. **Evaluation and monitor the breeding programs:** The collected data from step 5 should be handled by trained staff or researchers to calculate genetic parameters, EBV, selection responses and genetic trends for single traits or selection indices for multiple traits selection. Farmers should receive feedback to guide selection for future mating cycles. Regular feedback from farmers is also important to ensure alignment with their expectations and to make necessary adjustments.

9. Secure institutional support and funding: Long-term developments require support from local and national agriculture research institutions, such as the Department of Livestock and Fisheries in Laos, local universities, and international Non-Governmental Organizations. These partners can provide technical support, training, funding, data collection and genetic evaluations. Institutional involvement is also important for setting up infrastructure, such as data management systems or nucleus farms across provinces.
10. Plan for sustainability, marketing and scaling: Encourage to development of a trademark for indigenous breeds, such as “Lao mountain goat”, to enhance market appeal and increase value. Efforts should also focus on training a new generation of farmers, building infrastructure, and scaling up breeding programs across regions.

7.4. Research limitations and future consideration

The DNA samples used in this study were collected from one province in Central Laos, Savannakhet and only three districts in Savannakhet province were sampled, with just one village represented in Sepon district. While Savannakhet contained the highest proportion of Laos’s goats (15.6% or 103,000 goats) in 2019 (MAF 2020), to accurately capture genetic diversity and population structure of native goat breeds in Laos future studies should broaden the sampling to include other regions of Laos. Priority should be given to areas near the national borders as Bui et al. (2023) noted that goat trade occurs between Vietnam and Laos, and Xaypha (2005) and Xayalath et al. (2021) reported the presence of goat breeds imported from Thailand and Vietnam. In recent research, large farms in the Phin district were found to import Boer bucks from Thailand to improve herd performance (Walkden-Brown et al. 2024), though no official records are tracking this breed development in Laos. Expanding sampling across Laos would provide a comprehensive picture of all Lao goat breeds and allow for an assessment of gene flow among the Northern, Central and Southern regions, and between Laos and neighbouring countries.

This study was the first to use using SNP arrays for a genetic analysis of a goat population in Southeast Asia. For a more complete assessment of there is gene flow and migration patterns between goat populations in Southeast Asian countries, future studies should consider samples from neighbouring countries. Especially, samples from Vietnam and Thailand, where goat imports to Laos were documented, would be valuable. Additionally, using whole-genome sequencing (WGS) or higher-density SNP arrays may provide more powerful analyses in population studies. WGS offers greater insight into genetic diversity, population structure, demographic processes, and potential genes associated with economic traits (Ng & Kirkness 2010; Friedenberg et al. 2016; Benjelloun et al. 2019). The availability of WGS data has also facilitated comparative genomics studies in goats. For example, Wang et al. (2016) used WGS to identify genes under positive selection for economic traits such as cashmere traits, environmental adaptation, and coat colours of eight goat populations in China. Other studies have used WGS to examine genetic diversity, population structure and genes linked with

important economic traits in different goat breeds (Guo et al. 2018; An et al. 2024; HuangFu et al. 2024). Therefore, future studies should expand sampling to neighbouring Southeast Asian populations and incorporate higher-density SNP array or WGS genotype data.

Most of the population genetic software was developed for human populations (Falush et al. 2003; Alexander et al. 2009). These methods assume a large effective population size and individuals are unrelated, therefore, marker loci are usually in linkage equilibrium. Livestock populations, however, often include half-sibling or full-sibling relationships, creating high levels of LD. Thus, for livestock, samples should be collected ideally from unrelated animals. During data collection, as described in Chapter Three, field staff were instructed to avoid sampling full-sibling animals when they were possible to be verified by goat owners. However, in free grazing systems where there is a lack of pedigree recording, farmers may not recall the exact relationship between all animals. To ensure unrelated samples, animals of similar ages can be selected, as this may help farmers identify whether they share a dam. Additionally, since household herd sizes were small in this study with only three DNA samples collected per household, larger herds should be used where possible to increase sample size for better genetic analysis.

7.5. Conclusions

Identifying and understanding local genetic resources is an important step in developing and implementing effective breeding programs. Lao native goats play important roles in the livelihoods of smallholder farmers in Lao; however, their productivity is limited and requires improvement. This thesis demonstrated moderate genetic diversity with low inbreeding among Lao native goats in Central areas and revealed close genetic relationships with breeds from China, Mongolia, and Pakistan. Our findings identified 68 unique coding genes in the genome of Lao goats linked to adaptation, and economic traits (e.g. growth, meat quality and reproduction traits). Although Lao goats typically graze in communal areas, the degree of home range overlap between herds varied between villages, ranging from isolated grazing areas to fully shared spaces. Analyses of gene flow and genetic relatedness indicated limited interaction between villages but higher genetic mixing within villages, reflecting differences in local management practices. Furthermore, we demonstrated the benefits of the rotational mating strategy at village and district levels over the traditional random mating, which improved the body weight of Lao native goats while maintaining low inbreeding levels. Several areas for future research were discussed, including expanding sampling across regions in Laos and Southeast Asia, considering sustainable methods to conserve and enhance local goat breeds, evaluating alternative breeding programs for indigenous goats in smallholder systems and implementing genetic evaluation tools to maximize genetic gain. A step-by-step approach to developing and implementing breeding programs for smallholder farmers is also recommended to ensure successful adoption and long-term impact.

Chapter 8. Consolidated Reference List

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Appendices

Appendix A

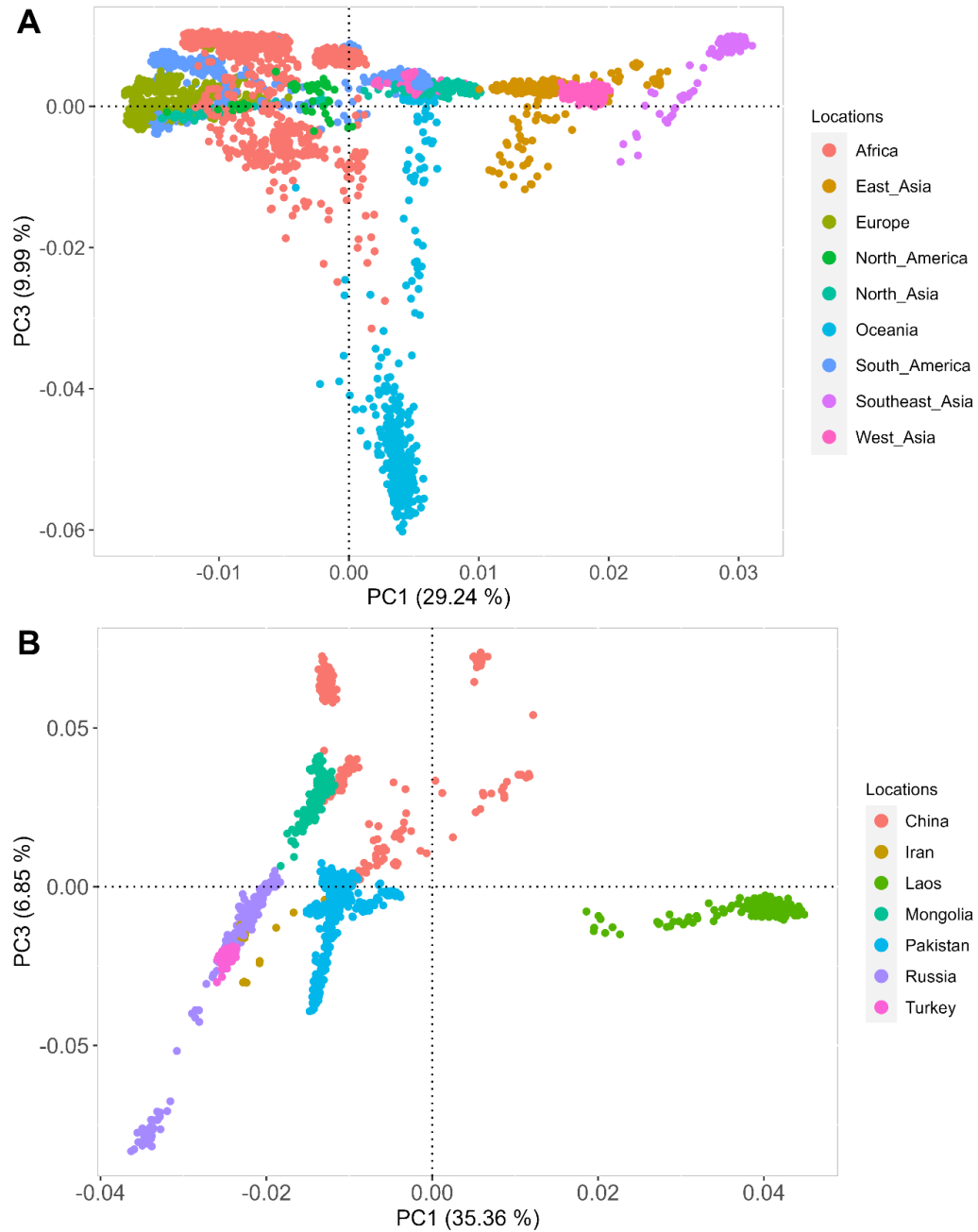


Figure S3. 1. Principle component analysis at the global level (A) and Asian (B). One dot represented an individual, and colours represented populations.

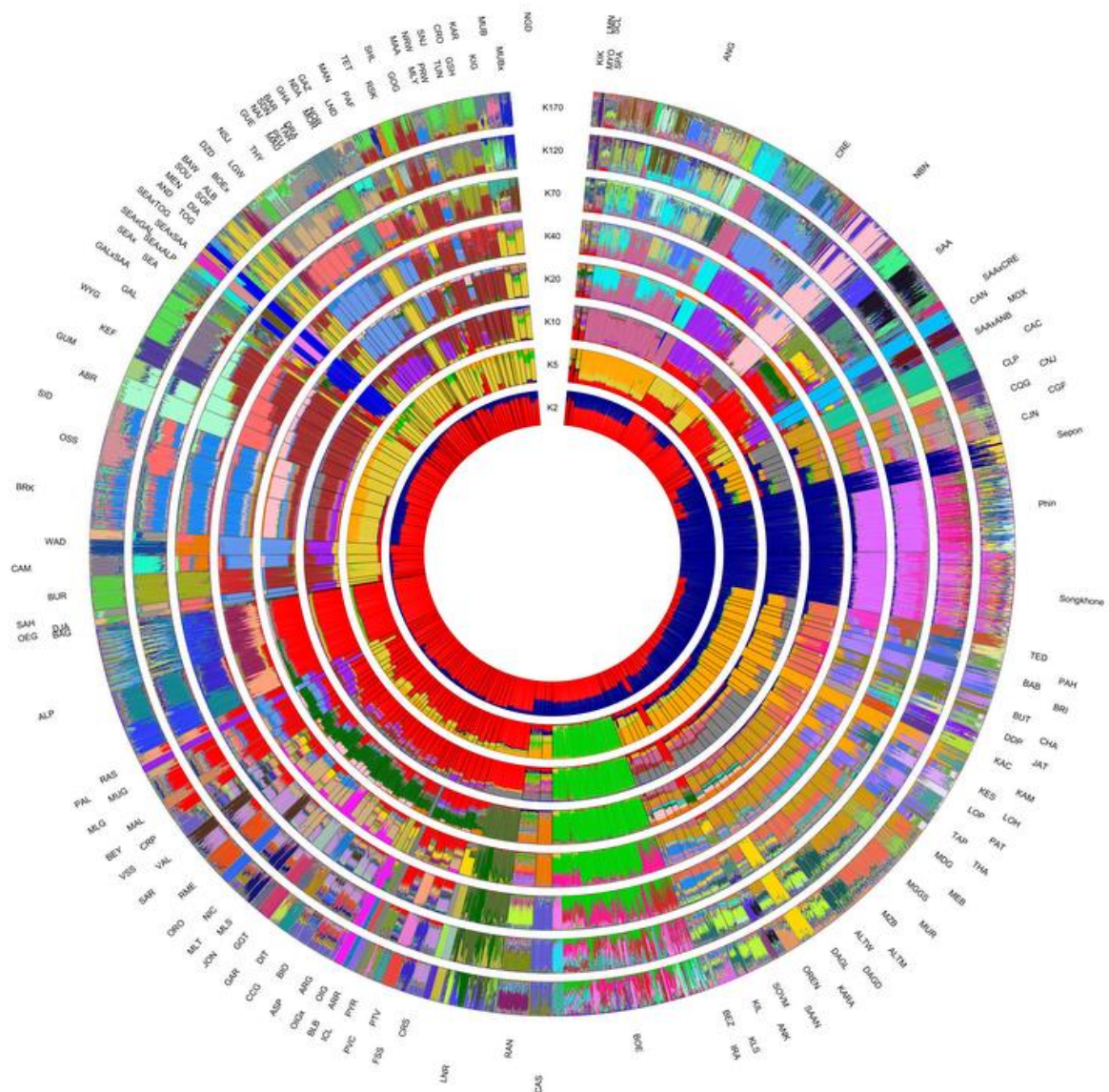


Figure S3. 2. Admixture analysis of 5574 individuals from the 166 goat populations at the global level. Results for number of clusters (K) = 2, 5, 10, 20, 40, 70, 120 and 170 are shown. Goats are grouped by population and each individual is represented as a single vertical line. The proportion of the coloured segment in each of K represents their estimated ancestry deriving from different populations. For a description of the goat breeds, see Table S3.3.1.

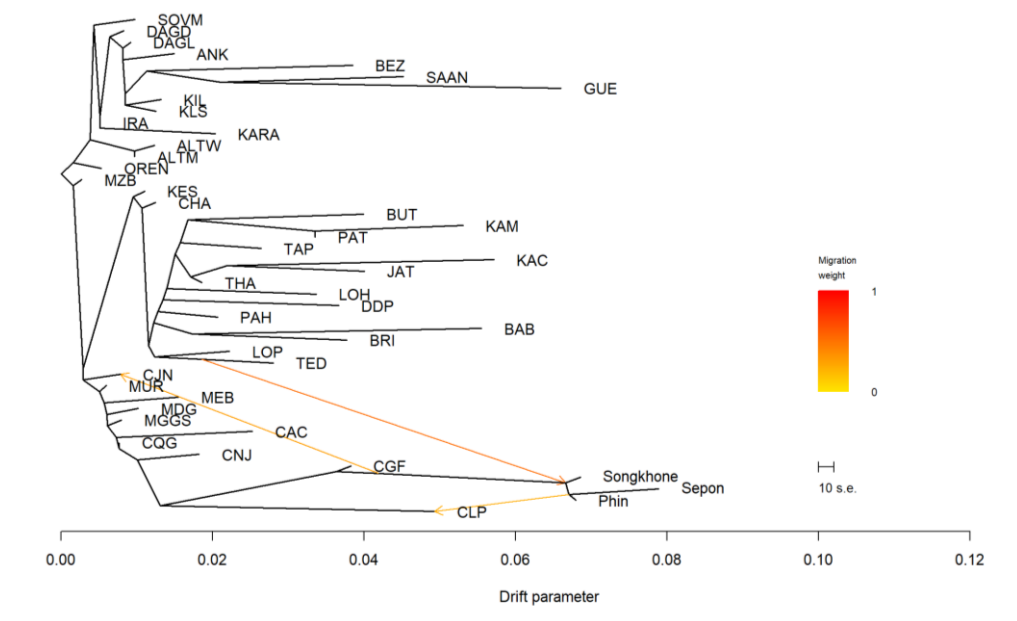


Figure S3. 3. Maximum likelihood tree with 3 migration events between 43 goat breeds in Asian regions. Migration edges are coloured according to their migration weight. For a description of the goat breeds, see Table S3.3.1.

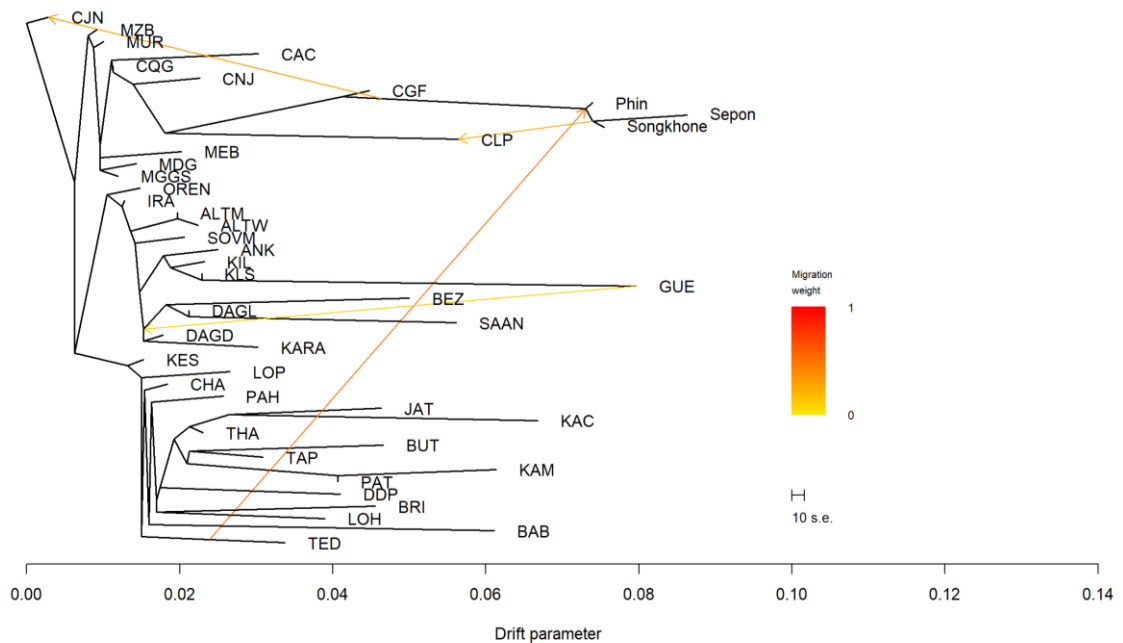


Figure S3. 4. Maximum likelihood tree with 4 migration events between 43 goat breeds in Asian regions. Migration edges are coloured according to their migration weight. For a description of the goat breeds, see Table S3.3.1.

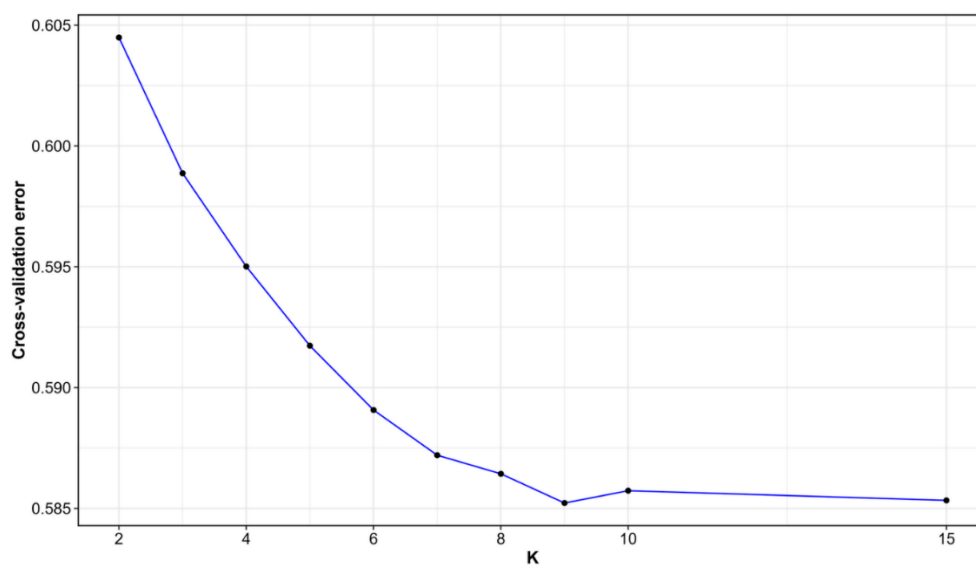


Figure S3. 5. Cross-validation plot for the different number of assumed ancestors (K=1-15) in Laos dataset indicating the choice of the appropriate K = 9 for Lao goats.

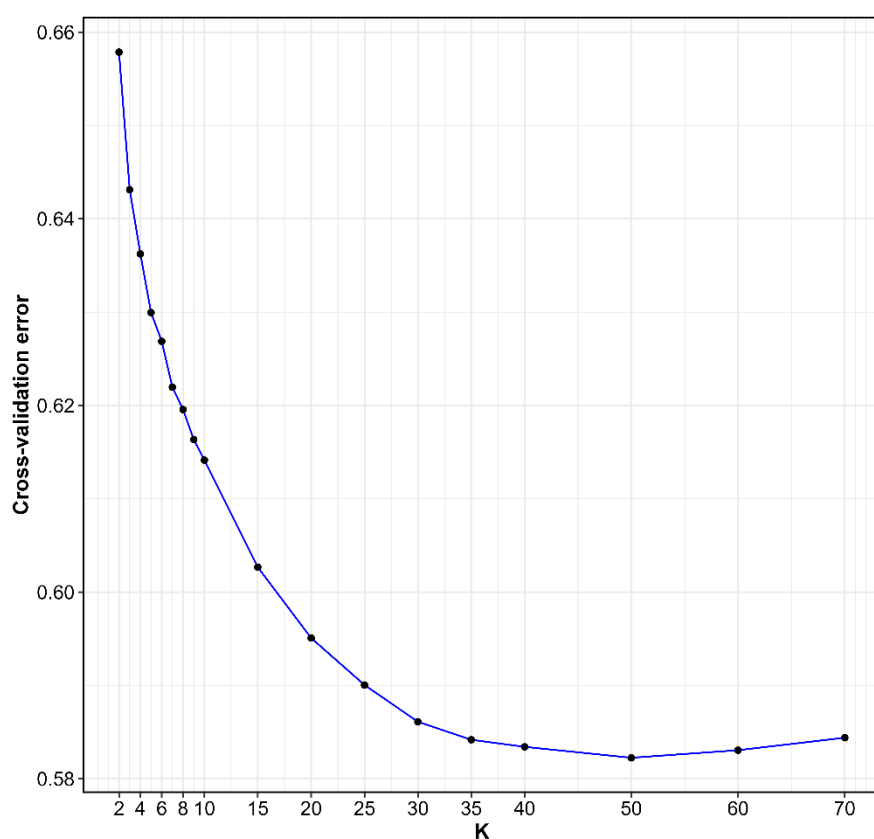


Figure S3. 6. Cross-validation plot for the different number of assumed ancestors (K=1-70) in the Asian dataset indicating the choice of the appropriate K = 50 for Asian goats.

Table S3. 1. Description of the working datasets for Laos, Asian and Global

Breed code 1	Breed code 2	Breed	Continent	Country	N individuals	Global dataset	Asian dataset	Lao dataset	Reference
LAO PHI	Phin	Lao native goats	Southeast.Asia	Laos	184	+	+	+	Present study
LAO_SEP	Sepon	Lao native goats	Southeast.Asia	Laos	59	+	+	+	Present study
LAO SON	Songkhone	Lao native goats	Southeast.Asia	Laos	177	+	+	+	Present study
CHN_AC	CAC	Aarbas Cashmere	Asian	China	59	+	+		Berihulay et al., 2019
CHN_GF	CGF	Guangfeng	Asian	China	24	+	+		Berihulay et al., 2019
CHN_JN	CJN	Jining Grey	Asian	China	39	+	+		Berihulay et al., 2019
CHN_LP	CLP	Luoping Yellow	Asian	China	24	+	+		Berihulay et al., 2019
CHN_NJ	CNJ	Nanjiang	Asian	China	23	+	+		Berihulay et al., 2019
CHN_QG	CQG	Quinggeda	Asian	China	24	+	+		Berihulay et al., 2019
IRN_BEZ	IEZ	Bezoar	West.Asia	Iran	7	+	+		Colli et al. 2018
IRN_IRA	IRA	Iranian goat	West.Asia	Iran	9	+	+		Colli et al. 2018
MNG_DG	MDG	Dorgon	Asian	Mongolia	37	+	+		Mukhina et al., 2022
MNG_EB	MEB	Erchim	Asian	Mongolia	37	+	+		Mukhina et al., 2022
MNG_GGS	MGGS	Gob Gurvan Saikhan	Asian	Mongolia	37	+	+		Mukhina et al., 2022
MNG_UR	MUR	Ulgii Red	Asian	Mongolia	37	+	+		Mukhina et al., 2022
MNG_ZB	MZB	Buural	Asian	Mongolia	36	+	+		Mukhina et al., 2022
PAK_BAB	PAB	Barbari	West.Asia	Pakistan	17	+	+		Colli et al. 2018
PAK_BRI	PRI	Bari	West.Asia	Pakistan	34	+	+		Colli et al. 2018
PAK_BUT	PUT	Bugituri	West.Asia	Pakistan	40	+	+		Colli et al. 2018
PAK_CHA	PHA	Chappar	West.Asia	Pakistan	10	+	+		Colli et al. 2018
PAK_DDP	PDP	Dera.Din.Panah	West.Asia	Pakistan	22	+	+		Colli et al. 2018
PAK_JAT	PAT	Jattan	West.Asia	Pakistan	24	+	+		Colli et al. 2018
PAK_KAC	PAC	Kachan	West.Asia	Pakistan	24	+	+		Colli et al. 2018
PAK_KAM	PAM	Kamori	West.Asia	Pakistan	42	+	+		Colli et al. 2018
PAK_KES	PES	Koh-e-sulmani	West.Asia	Pakistan	14	+	+		Colli et al. 2018
PAK_LOH	POH	Lohri	West.Asia	Pakistan	25	+	+		Colli et al. 2018
PAK_LOP	POP	Local.Pothohari	West.Asia	Pakistan	16	+	+		Colli et al. 2018
PAK_PAH	PAH	Pahari	West.Asia	Pakistan	19	+	+		Colli et al. 2018
PAK_PAT	PAT	Pateri	West.Asia	Pakistan	35	+	+		Colli et al. 2018

Breed code 1	Breed code 2	Breed	Continent	Country	N individuals	Global dataset	Asian dataset	Lao dataset	Reference
PAK_TAP	PAP	Tapri	West.Asia	Pakistan	24	+	+		Colli et al. 2018
PAK_TED	PED	Teddi	West.Asia	Pakistan	49	+	+		Colli et al. 2018
PAK_THA	PHA	Thari	West.Asia	Pakistan	16	+	+		Colli et al. 2018
RUS_ALTM	ALTM	Altai Mountain	Asian	Russia	33	+	+		Deniskova et al., 2021
RUS_ALTW	ALTW	Altai White Downy	Asian	Russia	20	+	+		Deniskova et al., 2021
RUS_DAGD	DAGD	Dagestan Downy	Asian	Russia	34	+	+		Deniskova et al., 2021
RUS_DAGL	DAGL	Dagestan Local	Asian	Russia	20	+	+		Deniskova et al., 2021
RUS_KARA	KARA	Karachayev	Asian	Russia	36	+	+		Deniskova et al., 2021
RUS_OREN	OREN	Orenburg	Asian	Russia	32	+	+		Deniskova et al., 2021
RUS_SAA	SAAN	Saanen	Asian	Russia	33	+	+		Deniskova et al., 2021
RUS_SOVM	SOVM	Soviet Mohair	Asian	Russia	29	+	+		Deniskova et al., 2021
TUR_ANK	TNK	Ankara	West.Asia	Turkey	20	+	+		Colli et al. 2018
TUR_KIL	TIL	Kil	West.Asia	Turkey	25	+	+		Colli et al. 2018
TUR_KLS	TLS	Kilis	West.Asia	Turkey	40	+	+		Colli et al. 2018
ANG		Angora	South.America	Argentina	369	+			Colli et al. 2018
CRE		Creole	South.America	Argentina	174	+			Colli et al. 2018
NBN		Nubian	South.America	Argentina	99	+			Colli et al. 2018
SAA		Saanen	South.America	Argentina	165	+			Colli et al. 2018
SAAxCRE		Saanen x Creole	South.America	Argentina	17	+			Colli et al. 2018
BOE		Boer	Oceania	Australia	332	+			Colli et al. 2018
CAS		Cashmere	Oceania	Australia	48	+			Colli et al. 2018
RAN		Rangeland	Oceania	Australia	65	+			Colli et al. 2018
CAN		Caninde'	South.America	Brazil	31	+			Colli et al. 2018
MOX		Moxoto'	South.America	Brazil	30	+			Colli et al. 2018
SAAxANB		Saanen x Anglo Nubian	South.America	Brazil	14	+			Colli et al. 2018
DJA		Djallonke	Africa	Burkina.Faso	12	+			Colli et al. 2018
SAH		Sahel	Africa	Burkina.Faso	15	+			Colli et al. 2018
BUR		Burundi goat	Africa	Burundi	70	+			Colli et al. 2018
CAM		Cameroon Goat	Africa	Cameroon	40	+			Colli et al. 2018
WAD		West African Dwarf	Africa	Cameroon	55	+			Colli et al. 2018
LNR		Landrace.Goat	Europe	Denmark	155	+			Colli et al. 2018

Breed code 1	Breed code 2	Breed	Continent	Country	N individuals	Global dataset	Asian dataset	Lao dataset	Reference
BRK		Barki	Africa	Egypt	134	+			Colli et al. 2018
OSS		Oasis	Africa	Egypt	72	+			Colli et al. 2018
SID		Saidi	Africa	Egypt	60	+			Colli et al. 2018
ABR		Abergelle	Africa	Ethiopia	53	+			Colli et al. 2018
GUM		Gumez	Africa	Ethiopia	41	+			Colli et al. 2018
KEF		Keffa	Africa	Ethiopia	49	+			Colli et al. 2018
WYG		Woyito.Guji	Africa	Ethiopia	46	+			Colli et al. 2018
CRS		Corse	Europe	France	30	+			Colli et al. 2018
FSS		Fosses	Europe	France	26	+			Colli et al. 2018
PTV		Poitevine	Europe	France	29	+			Colli et al. 2018
PVC		Provencale	Europe	France	18	+			Colli et al. 2018
PYR		Pyrenean	Europe	France	27	+			Colli et al. 2018
ICL		Icelandic.Goat	Europe	Iceland	13	+			Colli et al. 2018
ARR		Traditional.Arran	Europe	Ireland	10	+			Colli et al. 2018
BLB		Bilberry	Europe	Ireland	10	+			Colli et al. 2018
OIG		Old.Irish.Goat	Europe	Ireland	19	+			Colli et al. 2018
OIGx		Old.Irish.goat.cross	Europe	Ireland	10	+			Colli et al. 2018
ARG		Argentata	Europe	Italy	24	+			Colli et al. 2018
ASP		Aspromontana	Europe	Italy	24	+			Colli et al. 2018
BIO		Bionda.dell'Adamello	Europe	Italy	24	+			Colli et al. 2018
CCG		Ciociara.Grigia	Europe	Italy	19	+			Colli et al. 2018
DIT		Di.Teramo	Europe	Italy	24	+			Colli et al. 2018
GAR		Garganica	Europe	Italy	20	+			Colli et al. 2018
GGT		Girgentana	Europe	Italy	30	+			Colli et al. 2018
JON		Jonica	Europe	Italy	16	+			Colli et al. 2018
MLS		Maltese.sarda	Europe	Italy	15	+			Colli et al. 2018
MLT		Maltese	Europe	Italy	16	+			Colli et al. 2018
NIC		Nicastrese	Europe	Italy	24	+			Colli et al. 2018
ORO		Orobica	Europe	Italy	23	+			Colli et al. 2018
RME		Rossa.Mediterranea	Europe	Italy	45	+			Colli et al. 2018
SAR		Sarda	Europe	Italy	33	+			Colli et al. 2018

Breed code 1	Breed code 2	Breed	Continent	Country	N individuals	Global dataset	Asian dataset	Lao dataset	Reference
VAL		Valdostana	Europe	Italy	24	+			Colli et al. 2018
VSS		Valpassiria	Europe	Italy	24	+			Colli et al. 2018
GAL		Galla	Africa	Kenya	23	+			Colli et al. 2018
GALxSAA		Galla.x.Saanen	Africa	Kenya	1	+			Colli et al. 2018
SEA		Small.East.African	Africa	Kenya	55	+			Colli et al. 2018
SEAx		Admixed.Small.East.African	Africa	Kenya	2	+			Colli et al. 2018
SEAxALP		Small.East.African.x.Alpine	Africa	Kenya	3	+			Colli et al. 2018
SEAxGAL		Small.East.African.x.Galla	Africa	Kenya	18	+			Colli et al. 2018
SEAxSAA		Small.East.African.x.Saanen	Africa	Kenya	2	+			Colli et al. 2018
SEAxTOG		Small.East.African.x.Toggenburg	Africa	Kenya	5	+			Colli et al. 2018
TOG		Toggenburg	Africa	Kenya	23	+			Colli et al. 2018
AND		Androy	Africa	Madagascar	7	+			Colli et al. 2018
DIA		Diana	Africa	Madagascar	17	+			Colli et al. 2018
MEN		Menabe	Africa	Madagascar	21	+			Colli et al. 2018
SOF		Sofia	Africa	Madagascar	24	+			Colli et al. 2018
SOU		Sud.Ouest	Africa	Madagascar	10	+			Colli et al. 2018
ALB		Alpine.x.Boer	Africa	Malawi	7	+			Colli et al. 2018
BAW		Balaka-Ulongwe	Africa	Malawi	12	+			Colli et al. 2018
BOEx		Admixed.Boer	Africa	Malawi	7	+			Colli et al. 2018
DZD		Dedza	Africa	Malawi	15	+			Colli et al. 2018
LGW		Lilongwe	Africa	Malawi	4	+			Colli et al. 2018
NSJ		Nsanje	Africa	Malawi	7	+			Colli et al. 2018
THY		Thyolo	Africa	Malawi	9	+			Colli et al. 2018
GUE		Guera	Africa	Mali	25	+			Colli et al. 2018
MAU		Maure	Africa	Mali	14	+			Colli et al. 2018
NAI		Naine	Africa	Mali	17	+			Colli et al. 2018
PEU		Peulh	Africa	Mali	25	+			Colli et al. 2018
SDN		Soudanaise	Africa	Mali	24	+			Colli et al. 2018
TAR		Targui	Africa	Mali	22	+			Colli et al. 2018
BAR		Barcha	Africa	Morocco	4	+			Colli et al. 2018
DRA		Draa	Africa	Morocco	4	+			Colli et al. 2018

Breed code 1	Breed code 2	Breed	Continent	Country	N individuals	Global dataset	Asian dataset	Lao dataset	Reference
GHA		Ghazalia	Africa	Morocco	4	+			Colli et al. 2018
MOR		Moroccan.goat	Africa	Morocco	10	+			Colli et al. 2018
NDA		Noire.de.l'Atlas	Africa	Morocco	4	+			Colli et al. 2018
NOR		Nord	Africa	Morocco	4	+			Colli et al. 2018
GAZ		Gaza	Africa	Mozambique	4	+			Colli et al. 2018
LND		Landin	Africa	Mozambique	33	+			Colli et al. 2018
MAN		Manica	Africa	Mozambique	3	+			Colli et al. 2018
PAF		Pafuri	Africa	Mozambique	4	+			Colli et al. 2018
TET		Tete	Africa	Mozambique	2	+			Colli et al. 2018
RSK		Red.Sokoto	Africa	Nigeria	21	+			Colli et al. 2018
SHL		Sahel	Africa	Nigeria	21	+			Colli et al. 2018
CRP		Carpatian.goat	Europe	Romania	14	+			Colli et al. 2018
BEY		Bermeya	Europe	Spain	24	+			Colli et al. 2018
MAL		Mallorquina	Europe	Spain	20	+			Colli et al. 2018
MLG		Malaguena	Europe	Spain	42	+			Colli et al. 2018
MUG		Murciano-Granadina	Europe	Spain	20	+			Colli et al. 2018
PAL		Palmera.(Canaria.island.breed)	Europe	Spain	15	+			Colli et al. 2018
RAS		Blanca.de.Rasquera	Europe	Spain	20	+			Colli et al. 2018
ALP		Alpine	Europe	Switzerland	277	+			Colli et al. 2018
GOG		Gogo	Africa	Tanzania	12	+			Colli et al. 2018
MAA		Maasai	Africa	Tanzania	20	+			Colli et al. 2018
MLY		Malya	Africa	Tanzania	25	+			Colli et al. 2018
NRW		Norwegian	Africa	Tanzania	18	+			Colli et al. 2018
PRW		Pare.White	Africa	Tanzania	22	+			Colli et al. 2018
SNJ		Sonjo	Africa	Tanzania	22	+			Colli et al. 2018
TUN		Tunisian	Africa	Tunisia	23	+			Colli et al. 2018
CRO		Local.Cross	Africa	Uganda	5	+			Colli et al. 2018
GSH		Gishu	Africa	Uganda	3	+			Colli et al. 2018
KAR		Karamonja	Africa	Uganda	20	+			Colli et al. 2018
KIG		Kigezi	Africa	Uganda	5	+			Colli et al. 2018
MUB		Mubende	Africa	Uganda	23	+			Colli et al. 2018

Breed code 1	Breed code 2	Breed	Continent	Country	N individuals	Global dataset	Asian dataset	Lao dataset	Reference
MUBx		Admixed.Mubende	Africa	Uganda	3	+			Colli et al. 2018
NGD		Nganda	Africa	Uganda	11	+			Colli et al. 2018
SEB		Sebei	Africa	Uganda	24	+			Colli et al. 2018
BAG		Bagot	Europe	UK	1	+			Colli et al. 2018
OEG		Old.English	Europe	UK	2	+			Colli et al. 2018
KIK		Kiko	North.America	USA	11	+			Colli et al. 2018
LMN		LaMancha	North.America	USA	10	+			Colli et al. 2018
MYO		Myotonic	North.America	USA	1	+			Colli et al. 2018
SCL		San.Clemente	North.America	USA	2	+			Colli et al. 2018
SPA		Spanish	North.America	USA	20	+			Colli et al. 2018
MSH		Mashona	Africa	Zimbabwe	23	+			Colli et al. 2018
MTB		Matebele	Africa	Zimbabwe	26	+			Colli et al. 2018
MTBx		Matabele.cross	Africa	Zimbabwe	24	+			Colli et al. 2018

Note: Breed code 1 was used for all analyses, except for the migration analysis, where breed code 2 was applied.

Table S3. 2. Pairwise fixation index (FST) among 43 populations in Asia regions.

	CHN_ AC	CHN_ GF	CHN_ JN	CHN_ LP	CHN_ NJ	CHN_ QG	IRN_ BEZ	IRN_ IRA	LAO_ PHI	LAO_ SEP	LAO_ SON	MNG_ DG	MNG_ EB	MNG_ GGS
CHN_AC	-													
CHN_GF	0.117	-												
CHN_JN	0.069	0.064	-											
CHN_LP	0.128	0.153	0.106	-										
CHN_NJ	0.073	0.098	0.047	0.117	-									
CHN_QG	0.047	0.076	0.026	0.093	0.020	-								
IRN_BEZ	0.139	0.160	0.101	0.199	0.124	0.094	-							
IRN_IRA	0.069	0.094	0.037	0.129	0.053	0.023	0.078	-						
LAO PHI	0.091	0.096	0.060	0.124	0.077	0.054	0.133	0.067	-					
LAO SEP	0.116	0.124	0.085	0.153	0.104	0.080	0.165	0.095	0.038	-				
LAO SON	0.093	0.098	0.063	0.127	0.078	0.056	0.136	0.068	0.011	0.040	-			
MNG DG	0.058	0.087	0.037	0.101	0.043	0.016	0.104	0.034	0.064	0.089	0.066	-		
MNG EB	0.071	0.101	0.050	0.115	0.056	0.030	0.117	0.047	0.077	0.102	0.079	0.038	-	
MNG_GGS	0.051	0.078	0.029	0.096	0.036	0.009	0.088	0.020	0.057	0.081	0.059	0.017	0.030	-
MNG UR	0.052	0.081	0.032	0.095	0.037	0.010	0.098	0.028	0.059	0.083	0.060	0.018	0.031	0.011
MNG_ZB	0.051	0.079	0.030	0.095	0.037	0.009	0.092	0.023	0.057	0.081	0.059	0.016	0.031	0.009
PAK_BAB	0.159	0.189	0.134	0.221	0.153	0.124	0.209	0.132	0.145	0.175	0.147	0.130	0.143	0.120
PAK_BRI	0.123	0.148	0.099	0.173	0.112	0.086	0.164	0.087	0.111	0.137	0.112	0.093	0.105	0.084
PAK_BUT	0.127	0.154	0.104	0.180	0.116	0.091	0.174	0.096	0.109	0.138	0.111	0.099	0.111	0.089
PAK_CHA	0.073	0.100	0.047	0.128	0.058	0.029	0.105	0.027	0.062	0.092	0.064	0.039	0.053	0.029
PAK_DDP	0.119	0.148	0.095	0.173	0.108	0.081	0.160	0.086	0.107	0.136	0.109	0.089	0.101	0.079
PAK_JAT	0.124	0.152	0.100	0.178	0.113	0.087	0.169	0.092	0.108	0.137	0.109	0.095	0.109	0.085

	CHN_ AC	CHN_ GF	CHN_ JN	CHN_ LP	CHN_ NJ	CHN_ QG	IRN_ BEZ	IRN_ IRA	LAO_ PHI	LAO_ SEP	LAO_ SON	MNG_ DG	MNG_ EB	MNG_ GGS
PAK_KAC	0.159	0.191	0.136	0.216	0.153	0.126	0.215	0.138	0.142	0.175	0.144	0.131	0.145	0.122
PAK_KAM	0.150	0.178	0.127	0.205	0.143	0.117	0.203	0.125	0.130	0.160	0.132	0.122	0.135	0.114
PAK_KES	0.069	0.097	0.045	0.124	0.054	0.026	0.103	0.025	0.060	0.088	0.062	0.036	0.050	0.027
PAK_LOH	0.115	0.143	0.091	0.168	0.104	0.078	0.159	0.083	0.102	0.129	0.104	0.086	0.099	0.076
PAK_LOP	0.091	0.118	0.065	0.143	0.077	0.049	0.129	0.051	0.077	0.106	0.079	0.059	0.072	0.050
PAK_PAH	0.089	0.115	0.063	0.141	0.075	0.047	0.126	0.049	0.075	0.102	0.076	0.057	0.070	0.047
PAK_PAT	0.105	0.129	0.081	0.155	0.093	0.066	0.147	0.069	0.088	0.115	0.089	0.075	0.087	0.065
PAK_TAP	0.098	0.122	0.073	0.149	0.086	0.058	0.137	0.059	0.083	0.111	0.086	0.068	0.080	0.058
PAK_TED	0.103	0.125	0.077	0.151	0.090	0.065	0.140	0.066	0.082	0.108	0.083	0.072	0.085	0.064
PAK_THA	0.080	0.106	0.055	0.132	0.066	0.038	0.117	0.041	0.065	0.093	0.067	0.048	0.062	0.039
RUS_ALTM	0.072	0.095	0.044	0.123	0.057	0.031	0.091	0.024	0.073	0.097	0.076	0.039	0.051	0.024
RUS_ALTW	0.079	0.104	0.051	0.133	0.065	0.038	0.099	0.032	0.081	0.107	0.084	0.047	0.059	0.030
RUS_DAGD	0.071	0.093	0.041	0.123	0.055	0.029	0.081	0.013	0.071	0.095	0.073	0.038	0.049	0.024
RUS_DAGL	0.073	0.094	0.040	0.130	0.057	0.030	0.073	0.012	0.074	0.101	0.077	0.039	0.051	0.023
RUS_KARA	0.095	0.119	0.066	0.150	0.081	0.055	0.109	0.044	0.095	0.120	0.097	0.063	0.075	0.049
RUS_OREN	0.067	0.092	0.041	0.117	0.052	0.026	0.091	0.023	0.069	0.094	0.071	0.034	0.047	0.021
RUS_SAAAN	0.136	0.148	0.092	0.189	0.119	0.095	0.113	0.076	0.140	0.163	0.143	0.103	0.113	0.086
RUS_SOVM	0.076	0.101	0.049	0.128	0.062	0.035	0.096	0.024	0.076	0.102	0.079	0.044	0.055	0.031
TUR_ANK	0.088	0.111	0.056	0.143	0.072	0.045	0.094	0.023	0.086	0.112	0.088	0.054	0.067	0.040
TUR_KIL	0.084	0.106	0.053	0.138	0.068	0.041	0.090	0.018	0.082	0.108	0.085	0.050	0.062	0.037
TUR_KLS	0.080	0.102	0.050	0.133	0.065	0.040	0.089	0.014	0.080	0.103	0.083	0.048	0.060	0.034

	MNG UR	MNG_ ZB	PAK BAB	PAK_ BRI	PAK_ BUT	PAK_ CHA	PAK_ DDP	PAK_ JAT	PAK_ KAC	PAK_ KAM	PAK KES	PAK LOH	PAK_ LOP	PAK_ PAH
CHN_AC														
CHN_GF														
CHN_JN														
CHN_LP														
CHN_NJ														
CHN_QG														
IRN_BEZ														
IRN_IRA														
LAO PHI														
LAO SEP														
LAO SON														
MNG DG														
MNG EB														
MNG_GGS														
MNG UR	-													
MNG_ZB	0.009	-												
PAK_BAB	0.124	0.121	-											
PAK_BRI	0.088	0.085	0.147	-										
PAK_BUT	0.093	0.090	0.171	0.127	-									
PAK_CHA	0.033	0.030	0.126	0.077	0.080	-								
PAK_DDP	0.083	0.080	0.164	0.124	0.125	0.071	-							
PAK_JAT	0.089	0.086	0.172	0.125	0.115	0.076	0.122	-						
PAK_KAC	0.126	0.122	0.216	0.167	0.160	0.122	0.163	0.139	-					
PAK_KAM	0.117	0.115	0.202	0.157	0.144	0.110	0.157	0.155	0.195	-				

	MNG UR	MNG_ ZB	PAK BAB	PAK_ BRI	PAK_ BUT	PAK_ CHA	PAK_ DDP	PAK_ JAT	PAK_ KAC	PAK_ KAM	PAK KES	PAK LOH	PAK_ LOP	PAK_ PAH
PAK_KES	0.030	0.028	0.121	0.077	0.083	0.015	0.068	0.076	0.121	0.113	-			
PAK_LOH	0.079	0.077	0.163	0.117	0.121	0.069	0.112	0.119	0.161	0.141	0.067	-		
PAK_LOP	0.052	0.051	0.140	0.096	0.100	0.042	0.088	0.096	0.138	0.130	0.038	0.086	-	
PAK_PAH	0.050	0.048	0.130	0.090	0.092	0.035	0.072	0.089	0.131	0.124	0.033	0.080	0.053	-
PAK_PAT	0.069	0.067	0.148	0.105	0.097	0.053	0.102	0.102	0.142	0.038	0.057	0.090	0.075	0.070
PAK_TAP	0.061	0.059	0.138	0.088	0.086	0.046	0.094	0.085	0.131	0.121	0.047	0.090	0.067	0.061
PAK_TED	0.067	0.065	0.146	0.104	0.111	0.059	0.103	0.105	0.146	0.139	0.057	0.100	0.069	0.067
PAK_THA	0.042	0.040	0.124	0.079	0.075	0.023	0.070	0.064	0.107	0.112	0.023	0.070	0.042	0.037
RUS ALTM	0.033	0.026	0.134	0.098	0.104	0.044	0.094	0.100	0.136	0.129	0.042	0.091	0.064	0.062
RUS ALT W	0.041	0.033	0.146	0.107	0.114	0.051	0.104	0.110	0.148	0.140	0.049	0.101	0.073	0.070
RUS DAG D	0.032	0.027	0.127	0.092	0.099	0.038	0.089	0.095	0.132	0.123	0.036	0.086	0.059	0.057
RUS DAGL	0.033	0.027	0.131	0.097	0.105	0.040	0.092	0.100	0.139	0.130	0.038	0.091	0.062	0.059
RUS KARA	0.058	0.053	0.154	0.118	0.126	0.066	0.116	0.122	0.157	0.149	0.063	0.113	0.085	0.084
RUS_OREN	0.029	0.025	0.130	0.094	0.100	0.038	0.087	0.095	0.132	0.123	0.035	0.086	0.059	0.055
RUS_SAAAN	0.098	0.091	0.185	0.158	0.166	0.107	0.153	0.160	0.194	0.189	0.106	0.152	0.127	0.124
RUS SOV M	0.038	0.034	0.135	0.100	0.105	0.045	0.096	0.102	0.140	0.132	0.043	0.093	0.065	0.063
TUR_ANK	0.049	0.043	0.146	0.109	0.116	0.054	0.106	0.112	0.153	0.142	0.051	0.104	0.075	0.073
TUR_KIL	0.045	0.040	0.139	0.104	0.111	0.048	0.100	0.107	0.146	0.136	0.046	0.098	0.070	0.067
TUR_KLS	0.043	0.037	0.131	0.097	0.106	0.044	0.096	0.101	0.139	0.129	0.043	0.092	0.066	0.064

	PAK_ PAT	PAK_ TAP	PAK_ TED	PAK_ THA	RUS ALTM	RUS_ ALTW	RUS DAGD	RUS DAGL	RUS KARA	RUS OREN	RUS_ SAAN	RUS SOVM	TUR_ ANK	TUR_ KIL	TUR KLS
CHN_AC															
CHN_GF															
CHN_JN															
CHN_LP															
CHN_NJ															
CHN_QG															
IRN_BEZ															
IRN_IRA															
LAO PHI															
LAO SEP															
LAO SON															
MNG DG															
MNG EB															
MNG_GGS															
MNG UR															
MNG_ZB															
PAK_BAB															
PAK_BRI															
PAK_BUT															
PAK_CHA															
PAK_DDP															
PAK_JAT															
PAK_KAC															
PAK_KAM															

	PAK_ PAT	PAK_ TAP	PAK_ TED	PAK_ THA	RUS ALT M	RUS_ ALTW	RUS DAGD	RUS DAGL	RUS KARA	RUS OREN	RUS_ SAAN	RUS SOVM	TUR_ ANK	TUR_ KIL	TUR KLS
PAK_KES															
PAK_LOH															
PAK_LOP															
PAK_PAH															
PAK_PAT	-														
PAK_TAP	0.068	-													
PAK_TED	0.090	0.079	-												
PAK_THA	0.055	0.044	0.059	-											
RUS ALT M	0.081	0.072	0.077	0.055	-										
RUS ALT W	0.090	0.081	0.085	0.062	0.003	-									
RUS DAGD	0.076	0.067	0.072	0.050	0.023	0.029	-								
RUS DAGL	0.080	0.070	0.075	0.053	0.022	0.028	0.010	-							
RUS KARA	0.102	0.094	0.097	0.076	0.050	0.058	0.041	0.037	-						
RUS OREN	0.075	0.067	0.072	0.049	0.028	0.035	0.025	0.023	0.051	-					
RUS SAAN	0.143	0.132	0.138	0.118	0.079	0.084	0.071	0.050	0.095	0.081	-				
RUS SOVM	0.082	0.074	0.078	0.056	0.033	0.040	0.017	0.026	0.053	0.036	0.088	-			
TUR_ANK	0.092	0.083	0.087	0.065	0.039	0.046	0.028	0.027	0.058	0.041	0.084	0.035	-		
TUR_KIL	0.087	0.077	0.083	0.061	0.037	0.044	0.027	0.025	0.054	0.037	0.081	0.037	0.034	-	
TUR_KLS	0.083	0.074	0.079	0.057	0.036	0.043	0.025	0.024	0.053	0.036	0.082	0.035	0.031	0.026	-

Appendix B

Table S4. 1. List of genomic regions under putative selection (q-value < 0.05) identified using DCMS for Lao native breeds

CHR	SNP	Position	ROH	XP (Lao- Ted)	XP (Lao- GF)	XP (Lao- JN)	XP (Lao- LP)	F _{ST} (Lao- Ted)	F _{ST} (Lao- GF)	F _{ST} (Lao- JN)	F _{ST} (Lao- LP)	DCMS pvalue	DCMS qvalue
1	snp42348-scaffold559-372721	10480653	0.9715	0.2526	0.0713	0.0134	0.0022	0.0117	0.0376	0.0152	0.0326	0.0001	0.0339
1	snp42350-scaffold559-452798	10562733	0.9715	0.2536	0.0529	0.0057	0.0010	0.0378	0.0376	0.0332	0.0326	0.0001	0.0441
1	snp42351-scaffold559-520734	10632303	0.9715	0.2982	0.0381	0.0040	0.0030	0.0117	0.0276	0.0152	0.0312	0.0000	0.0204
1	snp42354-scaffold559-621023	10733021	0.9715	0.3536	0.0582	0.0055	0.0175	0.0117	0.0276	0.0051	0.0209	0.0001	0.0318
1	snp48946-scaffold699-196577	1.36E+08	0.8844	0.2168	0.1063	0.0048	0.0494	0.0878	0.0025	0.0027	0.0074	0.0000	0.0204
1	snp48945-scaffold699-162286	1.36E+08	0.8844	0.2935	0.1458	0.0044	0.1204	0.0878	0.0025	0.0027	0.0074	0.0001	0.0352
1	snp48944-scaffold699-124602	1.36E+08	0.8844	0.2226	0.0418	0.0078	0.1040	0.0878	0.0090	0.0080	0.0088	0.0001	0.0446
1	snp37478-scaffold458-160742	1.36E+08	0.8107	0.2367	0.1665	0.0559	0.0211	0.0470	0.0025	0.0027	0.0074	0.0000	0.0206
2	snp12717-scaffold1489-164913	59551834	0.9571	0.6577	0.1436	0.0057	0.0010	0.1089	0.0055	0.0069	0.0047	0.0001	0.0358
2	snp12716-scaffold1489-127937	59588829	0.9571	0.6975	0.1492	0.0021	0.0006	0.1565	0.0055	0.0069	0.0047	0.0001	0.0338
2	snp12715-scaffold1489-82636	59634164	0.9571	0.6962	0.1569	0.0020	0.0013	0.1565	0.0055	0.0069	0.0047	0.0001	0.0408
2	snp12714-scaffold1489-43980	59672826	0.9571	0.6913	0.1921	0.0022	0.0024	0.0827	0.0055	0.0069	0.0047	0.0001	0.0362
2	snp5750-scaffold1200-1150845	59732329	0.9571	0.7371	0.0238	0.0023	0.0014	0.1565	0.0055	0.0069	0.0047	0.0000	0.0232
4	snp38988-scaffold494-4504824	41868638	0.8718	0.0605	0.0012	0.0059	0.0389	0.3792	0.0430	0.0141	0.0396	0.0001	0.0429
4	snp38989-scaffold494-4540261	41904084	0.8718	0.0431	0.0005	0.0084	0.0475	0.2500	0.0355	0.0085	0.0166	0.0000	0.0166
4	snp38990-scaffold494-4569522	41933245	0.8718	0.0808	0.0011	0.0087	0.0723	0.2255	0.0355	0.0085	0.0166	0.0001	0.0274
4	snp38991-scaffold494-4622352	41986300	0.8718	0.1409	0.0039	0.0065	0.0627	0.1509	0.0355	0.0085	0.0166	0.0001	0.0341
4	snp49209-scaffold701-2633497	72541454	0.5361	0.0404	0.0469	0.0623	0.0488	0.0051	0.1997	0.0372	0.1125	0.0001	0.0281

CHR	SNP	Position	ROH	XP (Lao- Ted)	XP (Lao- GF)	XP (Lao- JN)	XP (Lao- LP)	F _{ST} (Lao- Ted)	F _{ST} (Lao- GF)	F _{ST} (Lao- JN)	F _{ST} (Lao- LP)	DCMS pvalue	DCMS qvalue
4	snp49208-scaffold701-2600343	72585446	0.5361	0.0065	0.0578	0.0949	0.0199	0.0051	0.1997	0.0372	0.1125	0.0000	0.0155
4	snp49207-scaffold701-2565765	72619696	0.5014	0.0101	0.0598	0.0523	0.0256	0.0086	0.1997	0.0372	0.1125	0.0000	0.0182
4	snp49206-scaffold701-2506608	72680277	0.5014	0.0200	0.0760	0.1656	0.0340	0.0051	0.1997	0.0372	0.1125	0.0001	0.0294
4	snp49204-scaffold701-2399096	72789884	0.5361	0.0512	0.0347	0.0690	0.0391	0.0051	0.0886	0.0555	0.0645	0.0000	0.0183
4	snp49199-scaffold701-2159744	73027129	0.5361	0.0145	0.0758	0.4310	0.0437	0.0040	0.0886	0.0555	0.0645	0.0001	0.0274
4	snp58452-scaffold950-1241231	79179764	0.9846	0.0040	0.0011	0.0007	0.0023	0.0358	0.6552	0.2949	0.5558	0.0001	0.0427
4	snp49389-scaffold704-388851	86132620	0.7693	0.0394	0.0051	0.0028	0.0056	0.0529	0.1252	0.0303	0.0946	0.0000	0.0149
4	snp49388-scaffold704-328231	86193863	0.7900	0.0192	0.0027	0.0023	0.0146	0.0340	0.1252	0.0303	0.0946	0.0000	0.0082
4	snp49387-scaffold704-286906	86233773	0.7900	0.0332	0.0009	0.0036	0.0256	0.0340	0.1199	0.0303	0.0875	0.0000	0.0092
4	snp49386-scaffold704-253747	86266862	0.7900	0.0211	0.0007	0.0066	0.0148	0.0340	0.1199	0.0303	0.0875	0.0000	0.0073
4	snp49385-scaffold704-186891	86334401	0.7900	0.0409	0.0107	0.0185	0.0906	0.0340	0.1199	0.0303	0.0875	0.0002	0.0496
6	snp30882-scaffold340-3646604	11733550	0.6692	0.0440	0.1347	0.1008	0.1061	0.0143	0.0067	0.0568	0.0062	0.0000	0.0232
6	snp30880-scaffold340-3553070	11828141	0.6692	0.0444	0.1023	0.1405	0.0769	0.0688	0.0035	0.0504	0.0045	0.0001	0.0362
6	snp30879-scaffold340-3499544	11882255	0.6361	0.0472	0.0703	0.0904	0.0689	0.1362	0.0035	0.0568	0.0062	0.0001	0.0441
6	snp30873-scaffold340-3222318	12160039	0.6998	0.0541	0.0361	0.1294	0.0490	0.2143	0.0022	0.0504	0.0045	0.0001	0.0431
7	snp56920-scaffold902-577883	79787284	0.7458	0.1750	0.0921	0.1579	0.1180	0.0053	0.0173	0.0380	0.0244	0.0002	0.0461
7	snp56919-scaffold902-547182	79817948	0.7458	0.1437	0.1152	0.0717	0.1174	0.0071	0.0173	0.0380	0.0244	0.0001	0.0431
7	snp56911-scaffold902-230163	80136724	0.7226	0.1799	0.0260	0.0837	0.3763	0.0048	0.0066	0.0073	0.0090	0.0000	0.0149
8	snp13914-scaffold1543-240075	7540204	0.5361	0.0411	0.0485	0.0287	0.0283	0.1003	0.0236	0.0078	0.0573	0.0001	0.0274
8	snp13916-scaffold1543-339272	7634445	0.5361	0.0858	0.0164	0.0302	0.0272	0.1003	0.0325	0.0196	0.0683	0.0001	0.0362
8	snp13917-scaffold1543-379882	7675032	0.5361	0.0866	0.0140	0.0694	0.0260	0.1003	0.0236	0.0196	0.0573	0.0001	0.0367

CHR	SNP	Position	ROH	XP (Lao- Ted)	XP (Lao- GF)	XP (Lao- JN)	XP (Lao- LP)	F _{ST} (Lao- Ted)	F _{ST} (Lao- GF)	F _{ST} (Lao- JN)	F _{ST} (Lao- LP)	DCMS pvalue	DCMS qvalue
8	snp13918-scaffold1543-410162	7705281	0.5361	0.0269	0.0091	0.0078	0.0216	0.1003	0.0325	0.0457	0.0683	0.0000	0.0169
8	snp13919-scaffold1543-441154	7736082	0.5361	0.0255	0.0067	0.0065	0.0396	0.1003	0.0325	0.0457	0.0683	0.0000	0.0169
8	snp13920-scaffold1543-471423	7765900	0.5014	0.0788	0.0172	0.0096	0.0228	0.1003	0.0325	0.0457	0.0683	0.0001	0.0306
8	snp14911-scaffold16-2932535	7844837	0.5706	0.0406	0.0172	0.0092	0.0063	0.0864	0.0325	0.0457	0.0573	0.0000	0.0166
8	snp14910-scaffold16-2888249	7889333	0.5014	0.1185	0.0059	0.0096	0.0079	0.0546	0.0236	0.0196	0.0306	0.0000	0.0073
8	snp14909-scaffold16-2835578	7940940	0.5014	0.0060	0.0002	0.0005	0.0022	0.0535	0.0236	0.0196	0.0306	0.0000	0.0000
8	snp14907-scaffold16-2745725	8031804	0.5014	0.0037	0.0003	0.0005	0.0011	0.0535	0.0325	0.0457	0.0573	0.0000	0.0000
8	snp14906-scaffold16-2699124	8078262	0.5014	0.0036	0.0001	0.0002	0.0016	0.0479	0.0325	0.0196	0.0573	0.0000	0.0000
8	snp14905-scaffold16-2661572	8115895	0.5014	0.0115	0.0006	0.0002	0.0003	0.0479	0.0236	0.0078	0.0306	0.0000	0.0000
8	snp14903-scaffold16-2567619	8207219	0.5014	0.0056	0.0006	0.0008	0.0019	0.0479	0.0184	0.0044	0.0152	0.0000	0.0000
8	snp14902-scaffold16-2538407	8236515	0.4649	0.0047	0.0005	0.0009	0.0008	0.0479	0.0184	0.0044	0.0152	0.0000	0.0000
8	snp14901-scaffold16-2504384	8270555	0.4266	0.0243	0.0014	0.0047	0.0016	0.0535	0.0184	0.0044	0.0152	0.0000	0.0000
8	snp14899-scaffold16-2433074	8340061	0.4266	0.0387	0.0109	0.0227	0.0039	0.0126	0.0184	0.0044	0.0152	0.0000	0.0002
8	snp14896-scaffold16-2296741	8475291	0.3456	0.2282	0.0666	0.0680	0.0129	0.0126	0.0106	0.0009	0.0147	0.0000	0.0027
8	snp14894-scaffold16-2229656	8542173	0.3067	0.3899	0.2766	0.1557	0.1927	0.0126	0.0106	0.0009	0.0147	0.0000	0.0232
8	snp14887-scaffold16-1940671	8834293	0.1985	0.2451	0.5161	0.3615	0.8038	0.0020	0.0083	0.0052	0.0130	0.0001	0.0354
8	snp14886-scaffold16-1879746	8893905	0.2322	0.1342	0.1321	0.1201	0.2864	0.0020	0.0184	0.0057	0.0152	0.0000	0.0073
9	snp35493-scaffold427-3534874	44127148	0.9516	0.0023	0.0210	0.0014	0.0061	0.0704	0.1854	0.2408	0.1432	0.0001	0.0389
9	snp35497-scaffold427-3723015	44316265	0.9446	0.0019	0.0390	0.0070	0.0035	0.0780	0.0313	0.0970	0.0387	0.0000	0.0169
9	snp35498-scaffold427-3753411	44346975	0.9361	0.0038	0.0181	0.0026	0.0318	0.0827	0.0313	0.0970	0.0387	0.0000	0.0232
9	snp35499-scaffold427-3801421	44394956	0.9404	0.0052	0.0150	0.0076	0.0119	0.0827	0.0265	0.0743	0.0120	0.0000	0.0166

CHR	SNP	Position	ROH	XP (Lao- Ted)	XP (Lao- GF)	XP (Lao- JN)	XP (Lao- LP)	F _{ST} (Lao- Ted)	F _{ST} (Lao- GF)	F _{ST} (Lao- JN)	F _{ST} (Lao- LP)	DCMS pvalue	DCMS qvalue
9	snp25074-scaffold2589-34416	44451584	0.9404	0.0152	0.0089	0.0026	0.0215	0.0780	0.0084	0.0631	0.0103	0.0000	0.0127
9	snp28687-scaffold31-274	44635759	0.9361	0.0281	0.0232	0.0094	0.1958	0.0780	0.0028	0.0111	0.0026	0.0000	0.0166
9	snp28689-scaffold31-93343	44727048	0.9309	0.0270	0.1561	0.0513	0.2109	0.0780	0.0028	0.0111	0.0026	0.0002	0.0461
9	snp28694-scaffold31-297232	44931940	0.8574	0.0446	0.1658	0.0596	0.7384	0.0796	0.0024	0.0010	0.0007	0.0001	0.0294
9	snp28695-scaffold31-328807	44963727	0.8718	0.0298	0.2538	0.0467	0.4080	0.0827	0.0010	0.0008	0.0006	0.0000	0.0155
9	snp28696-scaffold31-399209	45035151	0.8718	0.0667	0.3583	0.1609	0.5439	0.0827	0.0010	0.0001	0.0004	0.0000	0.0194
9	snp28697-scaffold31-454535	45093341	0.8718	0.2279	0.3507	0.3035	0.4248	0.0827	0.0010	0.0001	0.0004	0.0001	0.0341
9	snp36865-scaffold447-3152434	81390060	0.9891	0.0044	0.0402	0.0013	0.0163	0.0074	0.0297	0.0978	0.0511	0.0000	0.0155
9	snp36864-scaffold447-3122527	81419938	0.9891	0.0056	0.0441	0.0027	0.0081	0.0074	0.0297	0.0978	0.0511	0.0000	0.0166
9	snp36863-scaffold447-3068511	81473867	0.9896	0.0074	0.0055	0.0049	0.0034	0.0074	0.0297	0.0978	0.0511	0.0000	0.0073
9	snp36861-scaffold447-3008093	81534455	0.9896	0.0092	0.0032	0.0157	0.0028	0.0074	0.0365	0.3147	0.0569	0.0000	0.0162
9	snp36860-scaffold447-2977887	81564633	0.9896	0.0053	0.0038	0.0152	0.0013	0.0074	0.2884	0.3523	0.5338	0.0002	0.0461
14	snp22499-scaffold2226-181795	77607819	0.0540	0.1961	0.2516	0.0583	0.0499	0.1538	0.0246	0.0332	0.0152	0.0002	0.0493
17	snp5993-scaffold121-2283992	12016128	0.3456	0.3180	0.0588	0.0633	0.6058	0.1270	0.0055	0.0016	0.0031	0.0001	0.0385
17	snp5995-scaffold121-2360098	12092483	0.5014	0.4139	0.0404	0.0617	0.3480	0.1402	0.0052	0.0012	0.0031	0.0001	0.0358
17	snp6014-scaffold121-3130062	12865927	0.6998	0.3766	0.0507	0.1365	0.0641	0.0840	0.0048	0.0016	0.0024	0.0001	0.0270
17	snp6016-scaffold121-3220116	12955699	0.7226	0.4252	0.0730	0.1555	0.0350	0.0840	0.0052	0.0023	0.0030	0.0001	0.0351
17	snp21165-scaffold207-2503258	52903665	0.1658	0.0254	0.0174	0.0552	0.0525	0.1821	0.0416	0.1908	0.0546	0.0002	0.0493
17	snp21166-scaffold207-2532534	52935461	0.1658	0.0254	0.0100	0.0611	0.0258	0.1821	0.0386	0.1798	0.0473	0.0001	0.0318
19	snp16493-scaffold1738-470833	17341304	0.3456	0.0271	0.0302	0.0740	0.0846	0.0676	0.0180	0.0380	0.0102	0.0000	0.0182
19	snp16495-scaffold1738-537460	17408123	0.4649	0.0049	0.0365	0.0364	0.0119	0.0676	0.0149	0.0372	0.0097	0.0000	0.0053

CHR	SNP	Position	ROH	XP (Lao- Ted)	XP (Lao- GF)	XP (Lao- JN)	XP (Lao- LP)	F _{ST} (Lao- Ted)	F _{ST} (Lao- GF)	F _{ST} (Lao- JN)	F _{ST} (Lao- LP)	DCMS pvalue	DCMS qvalue
19	snp16496-scaffold1738-570744	17441258	0.3860	0.0291	0.0220	0.0258	0.0409	0.0423	0.0149	0.0372	0.0097	0.0000	0.0073
19	snp16500-scaffold1738-811773	17683289	0.4266	0.0173	0.0445	0.0600	0.0125	0.0423	0.0522	0.0695	0.0311	0.0000	0.0182
19	snp16501-scaffold1738-851028	17722582	0.4266	0.0689	0.0499	0.0738	0.0217	0.0395	0.0522	0.0695	0.0311	0.0001	0.0367
19	snp16502-scaffold1738-924755	17796436	0.4266	0.0399	0.0748	0.0389	0.0304	0.0198	0.0522	0.0695	0.0311	0.0000	0.0225
19	snp16503-scaffold1738-966035	17837581	0.3860	0.0441	0.0216	0.0358	0.0220	0.0198	0.0522	0.0695	0.0311	0.0000	0.0149
19	snp16504-scaffold1738-1012827	17884341	0.3860	0.0116	0.0192	0.0286	0.0234	0.0395	0.0544	0.1532	0.0555	0.0000	0.0169
19	snp16505-scaffold1738-1057576	17928782	0.3860	0.0300	0.0175	0.0214	0.0143	0.0395	0.0544	0.1532	0.0555	0.0000	0.0182
19	snp16506-scaffold1738-1098261	17969465	0.3860	0.0060	0.0911	0.0182	0.0256	0.0198	0.2101	0.1706	0.1422	0.0001	0.0306
19	snp16507-scaffold1738-1160273	18030277	0.4266	0.0011	0.0450	0.0154	0.0179	0.0198	0.2101	0.1706	0.1422	0.0000	0.0149
19	snp16508-scaffold1738-1196162	18066245	0.4266	0.0088	0.1989	0.0474	0.0099	0.0198	0.0544	0.1706	0.0555	0.0000	0.0232
19	snp16509-scaffold1738-1240011	18110358	0.3860	0.0130	0.1770	0.0433	0.0069	0.0198	0.0522	0.0695	0.0311	0.0000	0.0149
22	snp15313-scaffold163-1140420	40019989	0.8424	0.3154	0.2146	0.2203	0.1691	0.2765	0.0001	0.0015	0.0001	0.0001	0.0282
22	snp15310-scaffold163-1010990	40149074	0.8424	0.2368	0.0464	0.2300	0.0278	0.2084	0.0000	0.0010	0.0000	0.0000	0.0009
22	snp15307-scaffold163-888254	40272400	0.8265	0.2136	0.0230	0.1470	0.1366	0.2084	0.0000	0.0002	0.0000	0.0000	0.0004
22	snp15306-scaffold163-849464	40308951	0.8265	0.2711	0.1254	0.2201	0.0631	0.0700	0.0001	0.0010	0.0001	0.0000	0.0053
22	snp15304-scaffold163-741015	40417676	0.8265	0.2556	0.1339	0.1117	0.0775	0.0700	0.0011	0.0010	0.0008	0.0000	0.0166
22	snp15303-scaffold163-712180	40446596	0.8265	0.1448	0.0177	0.0338	0.0150	0.0301	0.0041	0.0056	0.0033	0.0000	0.0053
22	snp54165-scaffold827-589263	41747621	0.9105	0.1746	0.4475	0.2018	0.3145	0.0171	0.0011	0.0022	0.0008	0.0001	0.0356
22	snp54193-scaffold827-1817524	42978560	0.9361	0.2580	0.3291	0.1048	0.5439	0.0215	0.0008	0.0022	0.0003	0.0001	0.0341
22	snp54206-scaffold827-2468817	43632275	0.9404	0.1033	0.1804	0.1209	0.0852	0.0646	0.0019	0.0065	0.0009	0.0001	0.0406
24	snp35165-scaffold421-216725	30682572	0.3456	0.0108	0.0127	0.0200	0.0473	0.0007	0.4417	0.2717	0.4038	0.0000	0.0082

CHR	SNP	Position	ROH	XP (Lao- Ted)	XP (Lao- GF)	XP (Lao- JN)	XP (Lao- LP)	F _{ST} (Lao- Ted)	F _{ST} (Lao- GF)	F _{ST} (Lao- JN)	F _{ST} (Lao- LP)	DCMS pvalue	DCMS qvalue
24	snp35164-scaffold421-186960	30712159	0.3456	0.0297	0.0193	0.0459	0.0963	0.0007	0.4417	0.2717	0.4038	0.0000	0.0211
24	snp59277-scaffold974-734230	31386758	0.4266	0.0029	0.0101	0.1379	0.1814	0.0007	0.6987	0.4561	0.7046	0.0001	0.0371
28	snp10920-scaffold1390-648378	10586645	0.7458	0.0053	0.8181	0.0570	0.2370	0.2134	0.0002	0.0011	0.0019	0.0000	0.0182
28	snp39049-scaffold4955-48465	10604775	0.7458	0.0048	0.8516	0.0525	0.2928	0.2134	0.0002	0.0011	0.0019	0.0000	0.0204
28	snp39754-scaffold509-803733	11451884	0.6042	0.0236	0.1870	0.0541	0.0049	0.2864	0.0118	0.0268	0.0128	0.0001	0.0427

Appendix C

The R function to calculate the inbreeding:

```
INBRED=function(PED)
{
  k =nrow(PED)
  U=matrix(0,k,1)
  V=matrix(0,k,1)

  for (i in 1:k) {
    s=PED[i,2]
    d=PED[i,3]
    XX=1
    if (s > 0 ) { XX = XX - 0.25*U[s]}
    if (d > 0 ) { XX = XX - 0.25*U[d]}
    V[i]= sqrt(XX)      # V is column of L matrix
    U[i]= U[i]+ XX      # U accumulates

    if (i<k){
      for (j in (i+1):k)
      {
        s=PED[j,2]
        d=PED[j,3]
        XX=0
        if (s >= i) { XX= XX + 0.5*V[s]}
        if (d >= i) { XX= XX + 0.5*V[d]}
        V[j]=XX
        U[j]= U[j]+ XX*XX
      } # end of j
    } #end of if

  } # end of i

  return(list("U"=U,"V"=V))
}
```