

Research Report

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The Genetic Basis of Flocking Behavior in Sheep: Discoveries from Genome-Wide Association Studies

Jia Xuan ✉

Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China

✉ Corresponding email: cherryjxuan@gmail.com

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Abstract This study reviews the genetic basis of flocking behavior in sheep, with a focus on the contributions of genome-wide association studies (GWAS). Through GWAS, this study successfully identified genetic markers and regions closely associated with flocking behavior. These findings not only deepen our understanding of the genetics of sheep behavior but also optimize breeding and management strategies. The study also discusses the types and characteristics of sheep group behaviors, as well as the impact of environmental factors and human interventions on these behaviors. The results are significant in biotechnology and agricultural production, providing a scientific basis for improving the social adaptability and production efficiency of sheep. Looking forward, the research will continue to explore the functional validation of genetic markers and the genetic regulatory mechanisms of behavior, strengthen interdisciplinary cooperation and technological innovation, and promote further development in sheep genetics and agricultural science.

Keywords Sheep flocking behavior; Genetic markers; Genome-wide association study (GWAS); Breeding strategies; Behavioral genetics

Sheep, as important agricultural animals, have flocking behavior that is not only crucial for their own survival and reproduction but also has profound implications for human agricultural production. Research on sheep flocking behavior dates back decades, with many historical studies attempting to analyze the biological and environmental factors behind these behaviors. With advancements in science and technology, it has become apparent that sheep's social behaviors not only affect their health and welfare but also directly relate to breeding efficiency and the sustainability of agricultural production (Lama et al., 2019). In recent years, rapid developments in genetics have provided new tools and approaches for exploring the genetic basis of sheep flocking behavior, revealing connections between behavioral traits and specific genetic markers.

In modern breeding practices, understanding the genetic basis of sheep flocking behavior allows breeders to more precisely select individuals with desirable social traits, thereby enhancing the overall productivity and adaptability of the flock. Moreover, optimizing sheep's social interactions can improve the overall welfare of the flock, reduce stress and conflicts, and increase growth efficiency and production quality (Gootwine, 2020). Therefore, genetics plays an indispensable role in deciphering sheep flocking behavior, offering new perspectives and approaches for modern breeding and agricultural production.

Genome-wide association studies (GWAS) as a powerful genetic research tool, have been widely used in the field of animal behavioral genetics in recent years. GWAS can identify genetic markers associated with specific traits across the entire genome, offering unprecedented possibilities for understanding the genetic basis of sheep flocking behavior (Mohammadi et al., 2020). Through GWAS, researchers can reveal the complex genetic networks that influence sheep social behavior, further understanding how these behaviors are transmitted and varied through genetic mechanisms. Research into the genetic basis of sheep flocking behavior is not only significant for improving the welfare and production efficiency of sheep but also provides valuable genetic information for understanding social behaviors in other animals and even humans (Shi et al., 2024). Additionally, this research has general scientific value in revealing the genetic mechanisms of complex traits, helping to promote the integration and development of genetics, ethology, and agricultural science.

The main objective of this study is to review and summarize recent advancements in research on the genetic basis of sheep flocking behavior revealed through genome-wide association studies. By reviewing GWAS application cases in this field, the scientific significance and practical value of its findings are assessed. We hope that through this study, we can not only emphasize the unique contributions of GWAS in analyzing the genetic basis of sheep flocking behavior but also encourage further attention and investment in this field from both the academic and industrial communities. By synthesizing existing research findings, this study aims to provide scientific bases and new ideas for future genetic research, breeding practices, and the sustainable development of agricultural production.

1 The Genetic Basis of Flocking Behavior in Sheep

1.1 The role of genetic variation

Flocking behavior in sheep is one of the key characteristics essential for their survival and reproduction. This behavior not only helps protect sheep from predators but also enhances their efficiency in foraging and reproduction. Genetic variation plays a crucial role in the development of flocking behavior. Recent studies in behavioral genetics have shown that different genetic variations can significantly influence sheep's social interaction patterns, such as leadership, following behavior, and the distribution of social status within the group.

Research has found that certain specific gene variants are associated with stronger social connectivity and a tendency to flock in sheep. The identification of these genetic markers provides a new perspective on understanding the biological basis of sheep's flocking behavior. However, the expression of flocking behavior in sheep is influenced not only by genetic factors but also by environmental factors such as resource availability, group size, and external threats, which also play a significant role in their behavioral expression (Ozella et al., 2020). The complex interactions between genetic variations and environmental factors determine sheep's behavioral responses in different contexts, highlighting a major challenge in behavioral genetics—how to precisely distinguish and quantify the relative contributions of genetic and environmental factors to behavioral phenotypes.

1.2 Genetic regulation of flocking behavior

The genetic regulation of flocking behavior is a complex polygenic process, involving interactions among multiple genes and genomic regions. Scientists have identified several key genes and genomic regions that play significant roles in regulating flocking behavior in sheep. For example, certain gene variants may affect sheep's stress responses, social cognition abilities, or motor coordination, thereby indirectly influencing their flocking behavior. Wang et al. (2019) revealed through deep genome resequencing how artificial and natural selection have impacted visual degradation, high-altitude adaptability, and high fertility in domestic sheep in China, demonstrating how domestication has influenced genes related to sheep's vision, stress responses, and social cognition. This study provides insights into the genetic mechanisms behind phenotypic changes in sheep, including behavior (Figure 1).

Through the study of these genes and genomic regions, scientists are able to gain a deeper understanding of the genetic mechanisms behind flocking behavior, including the genetic diversity of behavioral phenotypes and the relationship between genotype and phenotype. This understanding is crucial for identifying key genetic factors that may affect sheep social interactions and group structure, providing the possibility to optimize the behavioral traits of sheep populations through genetic selection.

1.3 Progress in genome-wide association studies

Genome-wide association studies (GWAS) are a powerful genetic research tool that can identify genetic markers associated with specific behavioral traits across the entire genome of sheep (Kirichenko et al., 2022). The application of GWAS has greatly advanced the study of the genetic basis of sheep flocking behavior, revealing many previously unknown genes and genomic regions related to social behavior.

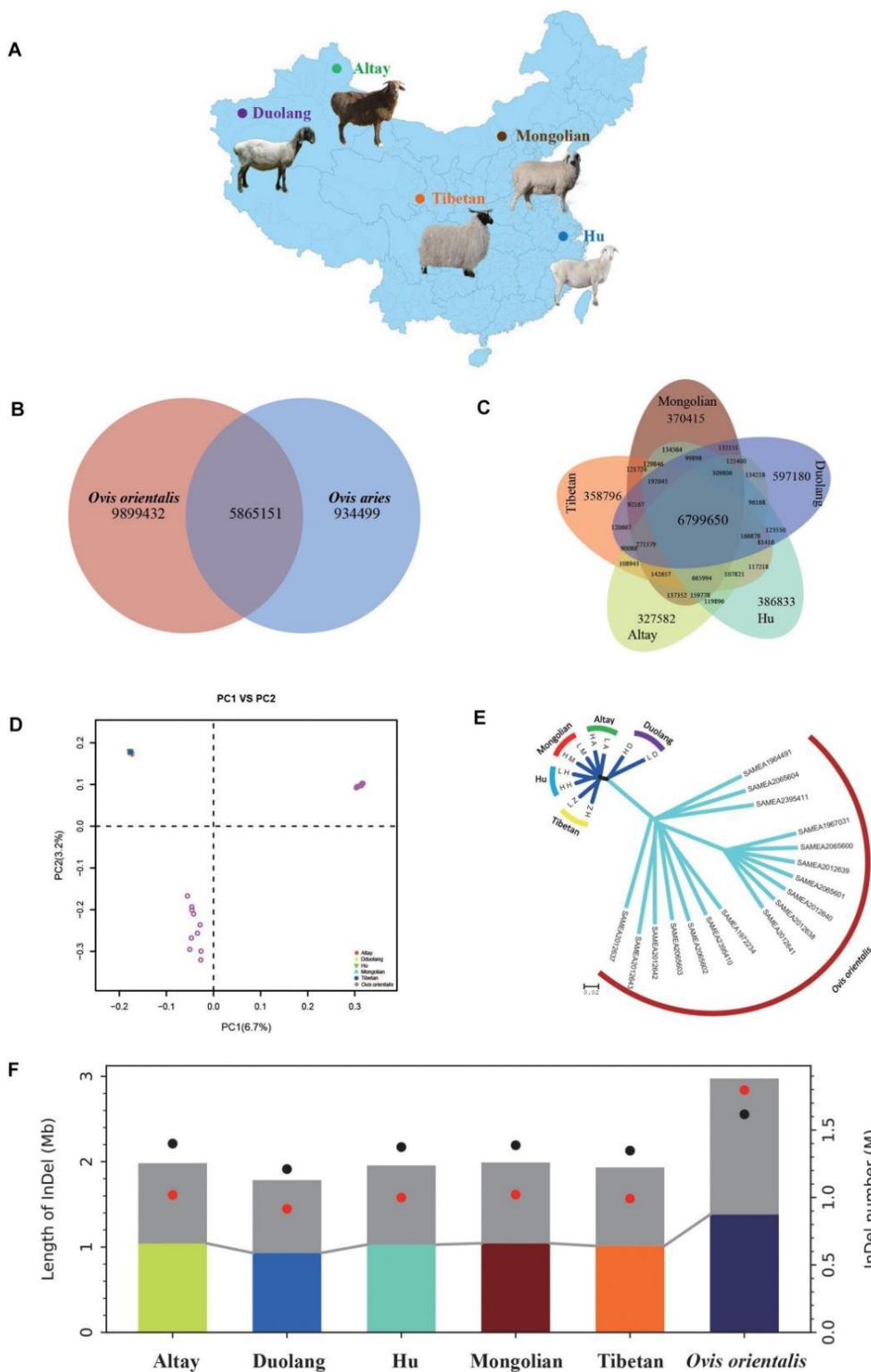


Figure 1 Geographic distribution and population genetics analyses of five indigenous Chinese sheep breeds (*Ovis aries*) and Asian Mouflon (*Ovis orientalis*) (Photo credit: Wang et al., 2019)

Note: (A) Geographic distribution of five indigenous Chinese sheep breeds (n=338 sheep). The map was generated using Adobe Illustrator CS6 software (<https://www.adobe.com/cn/products/illustrator.html>). (B) Venn diagram showing the shared single nucleotide polymorphisms (SNPs) between *Ovis aries* and *Ovis orientalis*. (C) Venn diagram showing the shared SNPs between the five indigenous Chinese sheep breeds. (D) Principal component (PC) analysis; PC 1 versus PC 2. (E) Neighbor-joining tree. (F) The length and number of indels in five indigenous Chinese sheep breeds and *Ovis orientalis*. Black and red dots represent the number of insertions and indels, respectively. Colored and gray pillars represent the length of insertions and indels, respectively (Adopted from Wang et al., 2019)

Through GWAS, researchers have successfully identified multiple genetic markers associated with sheep flocking behavior. These findings not only enrich our understanding of the genetic regulation of sheep flocking behavior but also provide new genetic resources for breeding. However, despite significant progress in uncovering the genetic basis of sheep flocking behavior, GWAS also faces some limitations and challenges. For instance, the reproducibility and interpretability of GWAS results are influenced by multiple factors such as sample size, genetic background, and environmental factors. Additionally, GWAS typically only identifies a small portion of genetic variations contributing to phenotypes, and many minor genetic effects may still be difficult to detect.

Despite these challenges, GWAS remains a powerful tool for revealing the genetic foundations of complex traits, including sheep flocking behavior. Future research needs to combine larger sample sizes, more comprehensive genetic information, and advanced statistical analysis methods to overcome current limitations and further unveil the genetic regulatory mechanisms of sheep flocking behavior.

2 Analysis of Flocking Behavior in Sheep

2.1 Types and characteristics of flocking behavior

Flocking behavior in sheep encompasses various patterns and characteristics that contribute to the overall dynamics of sheep herds. Sheep typically exhibit two primary types of flocking behavior: grazing and marching. Grazing behavior is characterized by the flock spreading out to forage, leading to an expansion and contraction pattern in their movement. In contrast, marching behavior involves the flock moving as a cohesive unit with higher polarization and lower angular momentum, often in response to threats or environmental stimuli (Welch et al., 2023).

2.2 Impact of flocking behavior on survival and reproduction

Flocking behavior significantly impacts sheep survival and reproduction. Coordinated movement within the flock enhances predator avoidance by diluting the risk of attack to individuals. This collective behavior provides a survival advantage, ensuring that sheep remain part of a cohesive group, which is crucial for their safety and well-being. Additionally, maternal behaviors, such as a ewe's proximity to her lamb, are heritable traits that can influence lamb survival. Ewes demonstrating better maternal behavior tend to have higher lamb survival rates, indicating a favorable genetic correlation between flocking behavior and reproductive success (Plush et al., 2016).

2.3 Observation and recording techniques

Accurate observation and recording of flocking behavior are essential for understanding its genetic basis. Techniques such as collar-mounted Real-Time Kinematic (RTK) satellite navigation receivers enable precise tracking of sheep movements. This technology, operating at high sample rates, provides detailed data on speed, direction, and group cohesion, allowing researchers to analyze flock dynamics comprehensively. The use of proximity sensors also aids in studying social interactions and the formation of subgroups within flocks, offering insights into individual and collective behaviors (Ozella et al., 2020; Welch et al., 2023).

2.4 Relationship between flocking behavior and environmental factors

Environmental factors play a crucial role in shaping flocking behavior. Variables such as weather conditions, predator presence, and resource availability influence how sheep move and interact within their flocks. For instance, flocks tend to form tighter groups in response to harsh weather conditions or predator threats. The presence of leadersheep, known for guiding the flock in times of danger, highlights the adaptive significance of specific behavioral traits under varying environmental pressures (Brunberg et al., 2020).

2.5 Impact of human intervention

Human intervention, including management practices and selective breeding, can significantly affect flocking behavior in sheep. Selective breeding for traits such as low agitation and favorable maternal behaviors can enhance flock cohesion and improve lamb survival rates. Moreover, management strategies that consider social structures and environmental factors can optimize flock welfare and productivity. Understanding the genetic underpinnings of flocking behavior allows for targeted interventions that align with both animal welfare and production goals (Plush et al., 2011; Ozella et al., 2020).

3 Key Findings from GWAS

3.1 Significant association loci

In recent years, genome-wide association studies (GWAS) have made significant progress in unveiling the genetic basis of flocking behavior in sheep. Through this technique, researchers have successfully identified multiple single nucleotide polymorphisms (SNPs) and gene regions significantly associated with sheep flocking behavior (Jiang et al., 2021). For instance, specific SNP loci have been found to be related to traits such as social tendencies, leadership behaviors, and the ability to respond to external stimuli in sheep. These loci are often located in or near genes controlling important biological pathways such as neural development, stress response, and social cognition.

The discovery of these significant association loci not only enriches our understanding of the genetic foundations of sheep flocking behavior but also provides potential genetic markers for future breeding programs. For example, variations in certain gene regions may make sheep more adaptable to group living, a trait that is significant for improving the overall welfare and productivity of the flock. By analyzing the biological functions of these loci in depth, researchers can better understand the genetic regulatory mechanisms of sheep flocking behavior, providing a scientific basis for precision breeding.

3.2 Revealing genetic architecture

The application of GWAS has not only revealed specific genetic markers related to sheep flocking behavior but has also helped us understand the genetic architecture of these behaviors. Studies have shown that sheep flocking behavior results from the interaction of multiple genes distributed across different chromosomes, involving various biological processes and pathways. This polygenic inheritance pattern illustrates the high complexity and genetic diversity of sheep flocking behavior. Mohammadi et al. (2020) found that GWAS identified genomic regions affecting growth and wool traits in Zandi sheep (Table 1). While focusing on physical traits, the identified genes and processes have broader implications for understanding complex behaviors such as group living.

Table 1 Descriptive statistics of 13 sheep growth traits and wool characteristics (Mohammadi et al., 2020)

Traits	Mean	Standard deviation	Minimum	Maximum	Standard error
Birth weight (kg)	4.10	0.77	2.10	6.28	0.068
Weaning weight (kg)	25.69	4.80	9.00	30.00	0.484
6-month weight (kg)	38.14	5.29	13.10	59.00	0.519
9-month weight (kg)	45.90	5.98	24.04	62.00	0.569
12-month weight (kg)	58.46	6.79	30.13	69.25	0.604
Prewaning average daily 0.12gain (kg)	0.197	0.04	0.08	0.34	0.004
Postweaning average daily gain (kg)	0.126	0.07	0.03	0.41	0.007
Mean Fiber diameter (µm)	29.85	3.25	22.40	39.04	0.032
Fiber diameter coefficient of variation (%)	43.12	7.84	19.00	68.35	0.764
Prickle factor (%)	27.04	10.42	12.04	43.10	0.998
Staple length (cm)	11.25	3.92	6.00	19.00	0.035
Kemp (%)	5.81	1.16	1.89	8.96	0.015
Outer coat fiber (%)	2.37	2.10	0.97	9.33	0.020

Additionally, genetic diversity plays a key role in the expression of flocking behavior. Sheep with different genetic backgrounds may exhibit different social behavior patterns under the same environmental conditions. This diversity not only reflects the sheep's ability to adapt to various ecological environments but also presents challenges and opportunities for breeding. By analyzing GWAS results, researchers can better understand the diversity and complexity of the genetic basis of flocking behavior, providing theoretical support for breeding sheep with superior social behavior traits.

3.3 Gene-environment interaction

Another important finding from GWAS is the role of gene-environment interactions in sheep flocking behavior. Studies have shown that the strength of association between certain genetic markers and flocking behavior can

vary under different environmental conditions, suggesting that environmental factors can influence the expression of genetic predispositions in behavioral phenotypes.

For example, the availability of resources, population density, and the presence of external threats can all affect the association between specific genetic markers and flocking behavior. The discovery of this gene-environment interaction is crucial for understanding how sheep adjust their social behavior in complex and changing natural conditions. It indicates that environmental factors must be considered in breeding and sheep management, requiring a comprehensive strategy to optimize the social structure and behavioral performance of the flock.

The study of gene-environment interactions not only increases the complexity of research on sheep flocking behavior but also presents new challenges and directions for future research. Exploring how to use genetic information to improve sheep's social behavior under different environmental conditions will be one of the important topics for future research.

4 Applications and Practical Significance

4.1 Impact on breeding strategies

The findings from Genome-Wide Association Studies (GWAS) have had a significant impact on sheep breeding programs and selection criteria. By identifying genetic markers associated with flocking behavior, GWAS provides breeders with a new tool for targeted selection and breeding based on genetic information. This marker-assisted selection method not only enhances the social adaptability and group coordination abilities of sheep but also optimizes the overall welfare and productivity of the flock.

Moghaddar et al. (2021) utilized priority genetic markers from whole-genome sequencing data for genomic prediction in smaller sheep populations. This study explored the accuracy of genomic predictions in a smaller flock, highlighting how priority genetic markers in GWAS can enhance breeding strategies. It compared different genomic selection methods and assessed their impact on the accuracy of trait prediction in sheep, demonstrating the practical application of GWAS in genomic prediction and selection.

García de Marina et al. (2021) showed the role of GWAS in identifying genomic regions associated with sheep milk production traits and their significance for breeding programs. By identifying potential candidate genes and their interactions, the study illustrated how GWAS findings can assist in selecting sheep with desirable production traits, thereby enhancing breeding efficiency.

Almasi et al. (2020) demonstrated through a GWAS on weaning traits in Lori-Bakhtiari sheep, identifying significant SNPs and candidate genes associated with these traits. It showcased the potential of GWAS in discovering genetic markers that could be used in selective breeding programs to enhance the growth performance of sheep.

In the process of achieving precision breeding, breeders face multiple challenges, including how to accurately identify genetic markers related to desired behavioral traits, and how to optimize these traits while maintaining genetic diversity. To overcome these challenges, breeding programs need to integrate high-throughput genotyping, advanced statistical analysis methods, and long-term breeding practices to effectively utilize beneficial genetic variations.

4.2 Sheep management and welfare

The application of GWAS in the genetic study of sheep flocking behavior has profound implications for improving sheep management and welfare. Understanding the genetic basis of flocking behavior can help farm managers better organize flocks, design breeding environments more suitable for animal welfare, reduce conflicts among sheep, and improve the overall health and productivity of the flock.

Using the findings from GWAS, genetic selection can be employed to cultivate sheep with better social behavior traits, thereby optimizing the social structure and interaction patterns of the flock. For example, by selecting individuals with stronger social connections and leadership abilities for breeding, a more harmonious and adaptable flock can be developed.

4.3 Public policy and education

Advancements in GWAS research on the genetic basis of sheep flocking behavior are crucial for formulating related animal welfare policies and educational strategies. With genetic information revealed by scientific research, policymakers can more accurately assess and establish animal welfare standards, promoting the improvement of animal protection laws and regulations.

Furthermore, integrating genetics and animal behavior knowledge into agricultural and biotechnological education can enhance the future farm managers' and breeders' awareness of the importance of animal welfare, cultivating their ability to guide practices using scientific findings. Additionally, the public's understanding of animal behavior and welfare will be improved, helping to establish a more humane and scientific animal management and breeding culture.

Through the research findings of GWAS, we can not only gain a deeper understanding of the genetic mechanisms behind sheep flocking behavior but also translate these scientific discoveries into practical applications, thereby generating positive social and economic impacts at multiple levels, including breeding strategies, animal management, public policy, and education.

5 Future Research Directions

5.1 Research gaps and challenges

Despite significant progress in uncovering the genetic basis of flocking behavior in sheep through genome-wide association studies (GWAS), current research still faces notable gaps and challenges. First, although some genetic markers associated with flocking behavior have been identified, little is known about how these markers influence behavior at the molecular level. Moreover, most studies focus on specific breeds or populations, limiting a comprehensive understanding of genetic diversity.

Potential approaches to address these challenges include expanding the scope of research to cover more populations and genetic backgrounds, and utilizing advanced bioinformatics and genomics techniques to delve deeper into the functions of genetic markers (Su et al., 2023). Additionally, conducting long-term population genetics studies and phenotypic tracking can provide a more comprehensive understanding of the relationship between genetic variation and behavioral phenotypes. Ongoing research is crucial for overcoming existing challenges, filling knowledge gaps, and is essential for advancing sheep genetics and breeding.

5.2 Potential of interdisciplinary collaboration

Collaboration across multiple disciplines such as bioinformatics, genetics, and ethology holds great potential in revealing the genetic basis of sheep flocking behavior. Interdisciplinary collaboration can provide a more comprehensive perspective and methodology for the research, enabling a deeper understanding of the genetic mechanisms of complex traits. For example, knowledge from ethology can help geneticists more accurately define and measure flocking behavior phenotypes, while bioinformatics technologies can support the analysis and interpretation of large-scale genomic data.

Furthermore, collaboration with fields such as computational science, statistics, and molecular biology can accelerate scientific discoveries and technological innovations, driving sheep genetic research towards more precise and dynamic directions. Interdisciplinary research not only improves research efficiency but also facilitates the exchange and integration of knowledge and technologies across different fields.

5.3 Development of technologies and methods

In the future, with the continuous emergence of new technologies and methods, genetic research on sheep flocking behavior will face new development opportunities. For instance, further refinement and application of gene-editing technologies like CRISPR/Cas9 will make functional validation experiments more efficient and precise. The development of single-cell sequencing technologies is expected to reveal genetic and expression heterogeneity at the cellular level, providing new perspectives for understanding complex traits.

The application of advanced computational technologies such as artificial intelligence and machine learning will greatly enhance the capability and accuracy of genetic data analysis, offering strong support for identifying and interpreting genetic variations. The development of these technologies will not only advance in-depth research on the genetics of sheep flocking behavior but also provide scientific bases for more precise breeding and management strategies, which are important for improving sheep productivity and welfare (Zhang et al., 2022). As technology continues to advance, we can look forward to achieving more significant results in the field of genetic research on sheep flocking behavior.

6 Conclusion and Outlook

This study, through a comprehensive review and analysis of recent research on the genetic basis of flocking behavior in sheep, especially the application of Genome-Wide Association Studies (GWAS), highlights the significant contributions of GWAS technology in revealing the genetic mechanisms of sheep social behavior. By identifying genetic markers and regions significantly associated with flocking behavior, these studies not only enrich our understanding of the genetics of sheep behavior but also provide a scientific basis for future breeding and management practices.

The findings of these studies have profound implications for biotechnology and agriculture. In biotechnology, the application of GWAS has facilitated innovation in genetic research methodologies and advancements in technology. In agriculture, a deeper understanding of the genetic foundations of sheep flocking behavior helps optimize breeding strategies, enhancing the social adaptability and productivity of sheep, thus advancing agricultural production towards more efficient and sustainable directions (Esmaeili-Fard et al., 2021).

Discoveries in the genetics of sheep flocking behavior have direct practical significance for breeding, sheep management, and the improvement of animal welfare. Utilizing genetic markers identified by GWAS, breeders can make more accurate genetic selections, developing sheep better suited for flocking life, thereby enhancing the overall performance and welfare levels of the flock (Barbosa et al., 2023). Additionally, these research outcomes offer new ideas and strategies for sheep management, such as improving breeding environments and adjusting group structures to promote harmonious interactions among sheep. The close connection between scientific research and practical application ensures that research outcomes can be transformed into tangible productivity, contributing to animal welfare, enhancing agricultural production efficiency, and supporting sustainable agricultural development.

Future research will continue to delve into the genetic basis of sheep flocking behavior, especially functional validation and mechanistic studies of genetic markers identified by GWAS, to more comprehensively understand the genetic regulation mechanisms of sheep social behavior (Wang et al., 2017). Moreover, with the development of new technologies and methods, it is expected that more genetic variations will be discovered, providing more genetic resources for breeding and management.

The importance of interdisciplinary collaboration is increasingly highlighted, and close cooperation among genetics, ethology, bioinformatics, and other fields will be key to future research. Additionally, technological innovations, such as CRISPR/Cas9 gene editing and single-cell sequencing technologies, will bring new breakthroughs to the study of sheep behavioral genetics. In summary, continuous exploration of the genetic basis of sheep flocking behavior, strengthening interdisciplinary cooperation and technological innovation, will provide strong support for addressing future challenges and promote further development in the fields of biotechnology and agriculture.

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