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Quantitative Trait Loci Mapping for Egg Production in Layer Hens

Hongbo Liang, Jia Xuan
Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China
Corresponding author: jia.xuan@jicat.org

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Abstract Quantitative Trait Loci (QTL) mapping is a powerful tool for identifying genetic regions associated with economically important traits in poultry, such as egg production in layer hens. This study provides a comprehensive analysis of recent advancements in QTL mapping for egg production traits, including egg number, egg weight, and eggshell quality. Through the integration of high-density SNP genotyping, genome-wide association studies (GWAS), and functional genomics, key QTLs influencing these traits have been identified, offering valuable insights into the genetic architecture underlying egg production. This study highlights the potential of marker-assisted selection (MAS) and genomic selection to accelerate genetic improvement in layer hens, allowing for more precise and efficient breeding strategies. Furthermore, the integration of QTL mapping with functional genomics holds promise for uncovering the molecular mechanisms driving complex traits, such as environmental adaptability and disease resistance. Future research directions focus on refining QTL mapping through advanced sequencing technologies and expanding its application to non-traditional traits, aiming to meet the challenges of climate change and sustainable poultry production.

Keywords QTL Mapping; Egg Production; Layer Hens; Marker-Assisted Selection; Genomic Selection

1 Introduction

Egg production traits in layer hens are complex, influenced by various genetic and environmental factors. Key traits include egg number, egg weight, eggshell quality, and age at first egg, all of which have significant impacts on productivity and economic profitability in the poultry industry. Genetic markers and quantitative trait loci (QTL) analysis play a crucial role in understanding the genetic basis of these traits. For example, chromosomes 1, 2, 4, and Z have been identified as key QTL regions associated with egg production traits across multiple studies (Sasaki et al., 2004).

Traditionally, genetic improvement in poultry breeding has been achieved through selective breeding, but the introduction of marker-assisted selection (MAS) has greatly accelerated the process. MAS uses genetic markers linked to desirable traits to select breeding individuals at an early stage, significantly reducing the generation interval and enhancing breeding efficiency. In recent years, genetic improvement techniques based on QTL mapping and genome-wide association studies (GWAS) have further refined the precision and efficiency of poultry breeding (Lien et al., 2020).

This study explores the genetic architecture of egg production traits in layer hens by identifying and mapping QTL, using GWAS and high-throughput sequencing to analyze historical and current data, thereby uncovering the genetic basis of egg production traits and providing new insights for the application of marker-assisted selection and genomic tools in layer breeding to improve production performance.

2 Egg Production Traits in Layer Hens

2.1 Key traits associated with egg production

Egg production in layer hens is influenced by several key traits, which are economically significant for the poultry industry. The most important traits include total egg number (EN), egg weight, and age at first egg (AFE). Total egg number represents the number of eggs laid over a specific period, making it a crucial measure of production performance and a common selection criterion for breeding. Egg weight affects the market value of the eggs, as heavier eggs are generally more desirable for consumers and thus, impact the pricing (Liu et al., 2019).

Additionally, traits such as laying rate and clutch behavior are critical in free-range or cage-free systems, where hens must lay eggs in nests rather than on the floor. Research indicates that selecting for nest acceptance (NAL) and laying frequency in these systems can improve efficiency. These behavioral traits can be improved through selective breeding to reduce the occurrence of floor eggs, thus enhancing production (Becot et al., 2021).

Moreover, eggshell quality is another key trait impacting egg production performance. Eggshell strength is essential for the storage and transportation of eggs, reducing breakage. By using QTL mapping, researchers have identified genetic loci that contribute to stronger eggshells, which can be leveraged in breeding programs to improve shell thickness, strength, and consistency (John-Jaja et al., 2017).

2.2 Heritability and genetic basis of egg production traits

The heritability of egg production traits varies based on the specific trait and chicken breed. Studies indicate that traits such as egg weight, AFE, and body weight have moderate to high heritability, meaning these traits can be effectively improved through selective breeding. Heritability estimates for egg weight typically range between 0.3 and 0.5, allowing for significant improvements over a short period. AFE, with heritability estimates of 0.2 to 0.4, is also a key target for improving early egg production performance (Das et al., 2016).

Genetic correlations between traits play an essential role in poultry breeding. For instance, there is a positive genetic correlation between egg weight and body weight, indicating that selecting hens for larger eggs may also lead to heavier body weight. However, increased body weight can delay the age of first egg, highlighting the need to balance trait selection. Simultaneous selection for traits such as egg weight and body weight ensures that the health and productivity of hens are maintained while improving egg quality (John-Jaja et al., 2017).

Behavioral traits like nest acceptance (NAL) also have moderate heritability in cage-free systems. Studies show that while behavioral traits tend to have lower heritability than physical traits, improvements through selective breeding are still possible. NAL has a heritability estimate of 0.13 to 0.26, indicating that it is feasible to reduce floor laying and improve productivity in non-cage environments through genetic selection (Becot et al., 2021).

2.3 Phenotypic variation and environmental influence

Egg production traits in hens are influenced not only by genetics but also by significant environmental factors. As shown in Figure 1, traits such as egg production, egg weight, body weight change, and feed conversion ratio exhibit noticeable individual variation, indicating the importance of environmental factors like housing systems, feed quality, temperature, and lighting. For example, differences in body weight (Figure 1e and 1f) and feed intake directly impact egg weight (Figure 1b) and laying rate (Figure 1a). Additionally, the distribution of feed conversion ratio (Figure 1g) and body weight change (Figure 1h) suggests varying feed efficiency under different environmental conditions. Proper management of feeding, especially adjusting nutrition at different production stages, can optimize egg weight, eggshell quality, and overall production efficiency. (Anene et al., 2020).

In free-range or cage-free systems, hens may exhibit greater behavioral diversity, affecting egg-laying patterns and clutch size. In these systems, environmental management, such as optimizing nest design, can help reduce floor laying and improve productivity. Environmental conditions, including temperature and lighting, also play a crucial role in determining egg-laying performance. High temperatures or improper lighting can lead to lower egg production, decreased eggshell quality, and health issues in hens. Therefore, maintaining optimal environmental conditions is essential for improving both egg production and hen welfare (Becot et al., 2021).

Temperature and lighting also influence the phenotypic expression of egg production traits. For instance, excessively high temperatures can reduce the number of eggs laid and weaken eggshell quality. Adequate control of environmental factors, such as maintaining a consistent temperature and proper lighting schedules, can help improve both the quantity and quality of eggs produced.

3 QTL Mapping for Egg Production

3.1 Historical perspectives and early studies

Quantitative Trait Loci (QTL) mapping for egg production in layer hens has been a critical research area since the 1990s. Early studies primarily used microsatellite markers to map QTLs associated with egg production traits such as egg number, egg weight, and age at first egg. These early efforts were constrained by the relatively low marker density and limited mapping populations, which resulted in low-resolution maps. Despite these challenges, the identification of QTLs in these early studies provided a foundational understanding of the genetic basis of economically important traits in poultry. Key discoveries include the identification of major QTLs on several chromosomes that affect egg weight and production rate, setting the stage for more advanced genetic analyses using modern techniques (Goto and Tsudzuki, 2017).

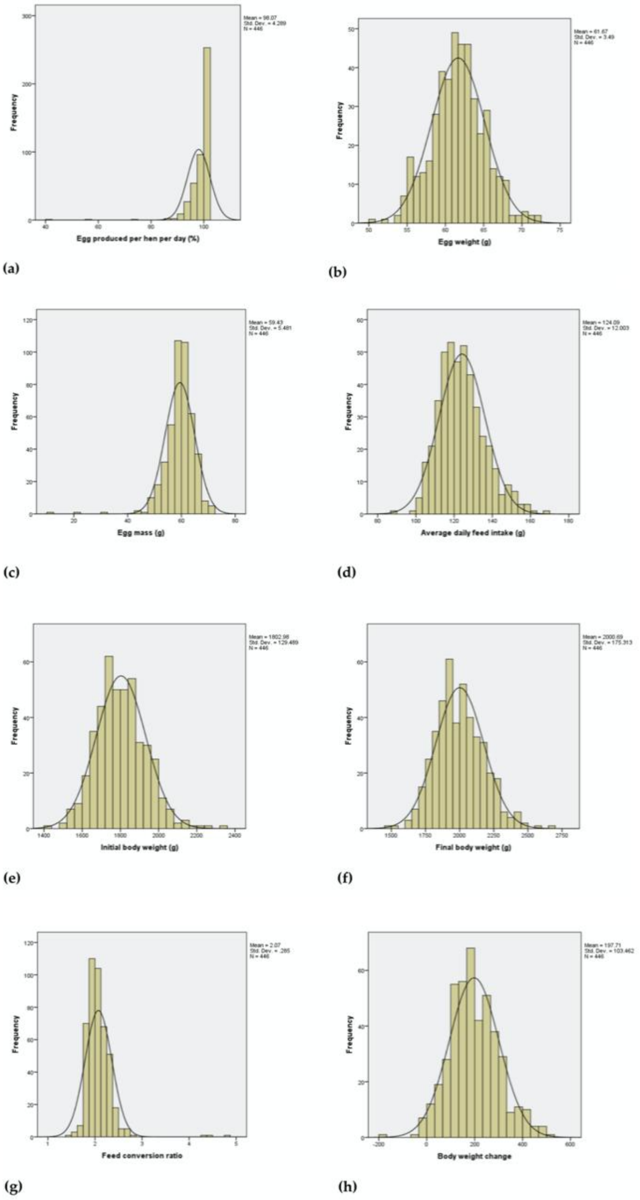

Figure 1 Histogram of performance traits showing distributions of 446 individually caged ISA Brown hens aged between 25 and 30 weeks for (a) egg produced per hen per day, (b) egg weight, (c) egg mass, (d) average daily feed intake, (e) initial body weight, (f) final body weight, (g) feed conversion ratio, and (h) body weight change (Adapted from Anene et al., 2020)

Image caption: Histograms illustrate various performance traits in a population of ISA Brown hens. Traits such as egg weight, egg mass, and body weight exhibit a normal distribution, indicating consistent performance among the flock. However, traits like daily egg production and feed conversion ratio show a skewed distribution, reflecting individual differences within the population. (Adapted from Anene et al., 2020)

The introduction of linkage mapping in the early 2000s significantly enhanced the precision of QTL mapping. These early linkage studies utilized F2 crosses between different chicken breeds, allowing researchers to track the inheritance of genetic markers along with phenotypic traits. This approach led to the discovery of multiple QTLs for egg production-related traits, including laying performance and egg quality. For example, a major QTL associated with egg number was identified on chromosome 1, providing insights into the genetic regulation of egg production (Lien et al., 2020).

3.2 Current approaches in QTL mapping for egg production

Current approaches to QTL mapping have greatly benefited from the rapid advancements in high-throughput genotyping technologies, particularly genome-wide association studies (GWAS) and SNP array technologies. These tools enable the simultaneous analysis of thousands of genetic markers, providing a deeper understanding of the genetic architecture underlying egg production traits. GWAS has proven especially effective in identifying genetic loci associated with egg production traits, such as age at first egg, egg number, and egg weight. For instance, Figure 2 illustrates a linkage disequilibrium (LD) analysis of significant SNP regions on GGA1 associated with egg number during the third laying period (EN3), revealing high LD among multiple SNPs between 117.87 Mb and 118.36 Mb. This suggests that this region may contain key QTLs influencing egg number. Such analytical methods help researchers precisely locate candidate genes related to egg production and provide valuable targets for marker-assisted selection (MAS) and genomic selection. Recent studies have also identified significant SNPs on multiple chromosomes linked to egg number across different laying stages, offering accurate genetic targets and strategies for breeding improvement (Liu et al., 2019).

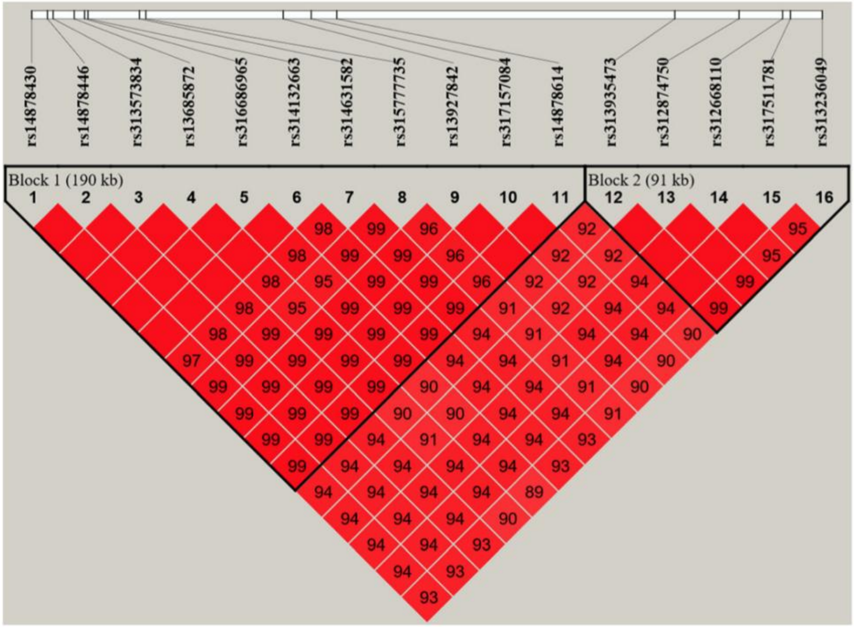

Figure 2 Linkage Disequilibrium (LD) analyses of SNPs in the significant region (0.49 Mb) for egg number in period 3 (EN3). LD plot of significant SNPs on GGA1 from 117.87 Mb to 118.36 Mb. (Adapted from Liu et al., 2019)

Image caption: The linkage disequilibrium (LD) analysis of single nucleotide polymorphisms (SNPs) in the significant region (0.49 Mb) for egg number during the third laying period (EN3). The LD matrix in the figure shows the associations between SNPs located on the GGA1 chromosome within the region from 117.87 Mb to 118.36 Mb. (Adapted from Liu et al., 2019)

Additionally, modern QTL mapping has incorporated more refined statistical models, such as mixed linear models, that account for both fixed effects and random population structure, increasing the accuracy of QTL detection. These models are particularly useful in overcoming confounding factors like environmental effects and genetic background noise. Advanced studies have also begun combining QTL mapping with other genomic tools, such as transcriptome analysis, to identify candidate genes responsible for regulating egg production traits. These integrative approaches are enhancing our understanding of the molecular mechanisms underlying QTLs and their functional roles in egg production (Haqani et al., 2021).

3.3 Recent advances in high-throughput genotyping and phenotyping

Recent advances in high-throughput genotyping and phenotyping have revolutionized QTL mapping for egg production traits. Technologies like Restriction-site Associated DNA sequencing (RAD-seq) and genotyping-by-sequencing (GBS) have made it possible to rapidly genotype large populations at a fraction of the cost of traditional methods. These high-throughput methods allow for the identification of thousands of SNPs across the genome, leading to more precise and fine-scale mapping of QTLs. For example, a 2021 study used RAD-seq to identify nine QTLs associated with egg-related traits in Japanese quail, including egg weight, shell strength, and yolk size (Haqani et al., 2021).

High-throughput phenotyping technologies have also become integral to modern QTL mapping efforts. These platforms, which include non-invasive imaging, robotics, and advanced sensor systems, allow for the rapid collection of detailed phenotypic data from large populations. For example, high-throughput imaging can track growth and egg production parameters across entire populations, significantly improving the accuracy and efficiency of phenotyping efforts. The integration of these technologies with genotyping has led to the identification of previously undetectable QTLs, particularly those associated with complex traits such as clutch size and egg quality (Jamann et al., 2015).

The combination of high-throughput genotyping and phenotyping has enabled the development of high-density genetic maps that provide unprecedented resolution in QTL mapping. These maps facilitate the fine-mapping of QTLs and the identification of candidate genes with greater precision, which is essential for marker-assisted selection (MAS) in breeding programs. As a result, breeders can now apply MAS more effectively to improve traits such as egg number, egg weight, and shell quality in layer hens(Wang et al., 2020).

4 Case Study: QTL Mapping in Layer Hens

4.1 Study design and sample population

In QTL (Quantitative Trait Loci) mapping studies for egg production traits in layer hens, researchers often employ crossbreeding strategies using breeds with different genetic backgrounds to create a diverse population. A notable example is the cross between Taiwanese L2 chickens and Rhode Island Red hens, which generates an F2 population suitable for studying adaptability to various climatic conditions and egg production traits. This study population consisted of 844 chickens, and their genotypes were analyzed using a 60K SNP (Single Nucleotide Polymorphism) chip, allowing researchers to investigate traits such as body weight, tibia length, and egg production rates (Lien et al., 2020).

The research employed both genome-wide association studies (GWAS) and linkage-based QTL mapping to analyze the genomic data of these chickens. This combination allows the identification of key QTLs associated with traits such as eggshell strength, egg weight, and overall production performance. By combining high-density genotype data with phenotypic data, researchers could identify important genetic regions associated with the traits of interest, laying the groundwork for future functional genomic studies and marker-assisted selection (MAS) (Liu et al., 2019).

To ensure accuracy in identifying QTLs, researchers maintained the F2 population in a controlled environment with consistent feeding and management practices. This minimized environmental influences on phenotypic variation, ensuring that the identified QTLs more accurately reflected genetic effects. This study design helped improve the precision of QTL mapping and provided valuable data for future breeding programs aimed at enhancing egg production traits (Stainton et al., 2015).

4.2 Identification of significant QTL for egg production

Through genome-wide analysis and QTL mapping of the sample population, researchers identified several significant QTLs associated with egg production traits. For example, QTLs were found on GGA1, GGA6, and GGA24 chromosomes, controlling traits such as egg number, egg weight, and age at first egg (AFE). These QTLs demonstrated their impact across different stages of egg production, with GGA1 showing a significant influence on egg number during early and mid-laying periods. This discovery provided insight into the genetic regulation of egg production at different life stages of the hens (Lien et al., 2020).

In addition to egg number, traits such as eggshell strength and egg weight were key focuses of the study. A QTL on GGA23 was identified to be strongly associated with both eggshell strength and egg weight, particularly under tropical climate conditions. This QTL helps explain the adaptability of chickens in high-temperature environments, enabling them to maintain high productivity in challenging conditions. These findings suggest potential genetic mechanisms that control egg production under environmental stress (Haqani et al., 2021).

Furthermore, by integrating whole-genome sequencing (WGS) with QTL analysis, researchers were able to validate the precision of these identified QTLs. Significant SNP variants were found on GGA1 and GGA6, pointing to candidate genes related to egg weight, eggshell quality, and egg production rate. These genes provide important targets for future functional studies and potential genetic editing to improve egg production in layer hens (Stainton et al., 2015).

4.3 Interpretation of results and application in breeding programs

The findings from QTL mapping offer significant potential for future breeding programs. Marker-assisted selection (MAS) can be applied using the identified QTLs to select chickens with favorable genetic traits, such as higher egg production, increased egg weight, and stronger eggshells. In tropical climates, using these QTL markers will help breeders choose hens with better environmental adaptability, improving overall productivity and egg quality (Lien et al., 2020).

Moreover, the identification of these QTLs opens the door for functional validation through gene editing technologies such as CRISPR/Cas9. By targeting key genes associated with egg production traits, researchers can validate the roles these genes play in regulating egg weight, shell strength, and production rates. This not only enhances the precision of genetic improvement in breeding programs but also provides new opportunities for functional genomics research into layer hens (Goto and Tsudzuki, 2017).

In conclusion, these QTL discoveries pave the way for more targeted breeding strategies. By utilizing the identified genetic regions, breeders can achieve faster genetic progress in improving key egg production traits, reducing production costs and enhancing the overall economic efficiency of layer hen operations. These results provide a solid foundation for breeding chickens that are better adapted to environmental stresses while maintaining high productivity (Meng et al., 2015).

5 Challenges and Limitations in QTL Mapping

5.1 Genetic complexity of egg production traits

Egg production traits in layer hens are highly complex, controlled by multiple genes, each with a small effect. This polygenic nature complicates the identification of significant QTLs as they may interact with each other through additive, dominant, or epistatic effects. Furthermore, QTLs can exhibit age-specific effects, meaning that their influence on egg production traits might vary at different life stages. This genetic complexity requires sophisticated methods to accurately capture these interactions and account for the dynamic nature of gene expression throughout the hen's laying period (Goto and Tsudzuki, 2017).

Another significant challenge is the influence of environmental factors on the expression of egg production traits. Environmental factors such as temperature, feed quality, and housing conditions can mask the effects of QTLs, making it difficult to isolate the genetic contributions from phenotypic data. This is particularly problematic in traits with low heritability, where environmental variance plays a substantial role. Consequently, QTL mapping for egg production often requires well-controlled environments or large sample sizes to ensure statistical power (Lan et al., 2020).

Moreover, genetic heterogeneity across different chicken breeds can also complicate QTL discovery. Breeds adapted to different environments may possess unique genetic architectures that contribute to egg production.

Therefore, QTLs identified in one population may not be transferable to another. This necessitates further research across multiple populations and environments to identify broadly applicable QTLs (Teh et al., 2020).

5.2 Statistical and computational challenges

The large volume of data generated from high-throughput genotyping and phenotyping technologies presents significant statistical and computational challenges in QTL mapping. For instance, analyzing thousands of molecular phenotypes while controlling for multiple testing is computationally intensive. To address this, tools like FastQTL have been developed, which apply efficient permutation-based methods to control for multiple testing. Despite improvements, the computational cost of large-scale QTL studies remains a limitation for many researchers (Ongen et al., 2015).

Additionally, the statistical power of QTL mapping is often limited by the sample size. In small or narrowly bred populations, recombination events are infrequent, making it difficult to accurately detect QTLs. This issue is exacerbated in traits controlled by many small-effect loci, where large samples are needed to achieve sufficient statistical power. New statistical models, such as mixed linear models (MLMs) and Bayesian methods, attempt to overcome these limitations by better modeling the genetic architecture and population structure (Wang et al., 2015).

Moreover, handling the correlations among individuals due to family structure or shared environments can introduce bias into QTL mapping. This is particularly problematic in structured populations or multiparent crosses. Tools such as lme4qtl, which extend mixed-model approaches to account for complex covariance structures, have been developed to address these issues, though these require significant computational resources (Ziyatdinov et al., 2017).

5.3 Integration with genomic selection and other molecular tools

While QTL mapping has been a useful tool for identifying regions of the genome associated with complex traits, integrating these findings into genomic selection programs presents another set of challenges. Genomic selection relies on the use of dense marker maps, but the incorporation of QTL markers into these models can introduce statistical biases or overfitting. This has led to the development of new statistical frameworks that balance the contributions of both genome-wide markers and QTLs (Lan et al., 2020).

Another challenge is the integration of genomic data with transcriptomics and proteomics. Emerging molecular tools such as eQTL mapping provide insights into gene expression patterns, yet combining these data with QTL mapping can be computationally demanding. Tools like TORUS are being developed to integrate genomic annotations into QTL discovery, providing a more comprehensive understanding of gene regulation in complex traits (Wen, 2016).

Finally, practical challenges remain in applying QTL discoveries to breeding programs. While marker-assisted selection (MAS) can leverage QTL information, the full potential of QTLs in breeding is often limited by difficulties in functional validation. This is especially true for QTLs with small effects or those influenced by epistatic interactions, requiring further research to translate genomic insights into breeding improvements (Khalil et al., 2021).

6 Future Directions and Applications

6.1 Enhancing breeding efficiency through qtl mapping

One of the main future directions for QTL mapping is its integration into breeding programs to enhance the efficiency of genetic selection. QTL mapping allows breeders to identify specific chromosomal regions associated with key traits, such as egg production in layer hens. This provides breeders with genetic markers that can accelerate the selection of individuals with superior traits, reducing the time needed for genetic improvement compared to traditional methods. Studies have shown that high-density SNP chips and advanced genotyping techniques can significantly improve the precision of QTL mapping, thus enhancing the overall breeding process (Lien et al., 2020).

As high-throughput genotyping becomes more accessible, the integration of QTL data into genome-wide selection strategies will become more widespread. This will allow breeders to simultaneously select for multiple traits, improving both productivity and adaptability in different environments. For instance, genomic selection techniques that include QTL information can increase selection accuracy and lead to faster genetic gains (Cockram and Mackay, 2018). Additionally, the continuous improvement in statistical tools and computing power will make it easier to identify QTLs with small effects, thereby contributing to a more complete understanding of the genetic architecture of complex traits like egg production.

6.2 Potential for marker-assisted selection (MAS) in egg production

Marker-assisted selection (MAS) is a key application of QTL mapping in breeding programs. MAS utilizes genetic markers identified through QTL mapping to select individuals carrying favorable alleles, thereby improving specific traits such as egg production or egg quality. With the identification of significant QTLs associated with egg production traits, breeders can employ MAS to enhance traits like egg number, size, and shell strength in layer hens. Recent advancements have improved the reliability and efficiency of MAS, especially with the introduction of high-density linkage maps and genome-wide association studies (GWAS), making the process more precise and cost-effective (Khalil et al., 2021).

Furthermore, MAS is particularly advantageous for traits with low heritability, where traditional selection methods are less effective. For example, traits such as disease resistance and environmental adaptability, which are critical for egg production, can be improved through MAS by targeting specific QTLs related to these traits. In the future, the development of more comprehensive genomic resources and advanced mapping techniques will further refine MAS, making it an indispensable tool for genetic improvement in poultry breeding (Yang et al., 2020).

6.3 Role of functional genomics in understanding QTL

The integration of functional genomics with QTL mapping offers significant potential for uncovering the biological mechanisms underlying complex traits. Functional genomics aims to link gene function with phenotypic traits by investigating gene expression, protein interactions, and metabolic pathways. By combining QTL data with transcriptomics, proteomics, and epigenetics, researchers can identify the genes and molecular pathways that regulate egg production traits, providing deeper insights into the genetic control of these traits (Robledo et al., 2016).

For example, expression quantitative trait loci (eQTL) mapping, which identifies genetic variants that influence gene expression levels, can be used in conjunction with traditional QTL mapping to pinpoint causal genes for egg production traits. This approach not only helps in identifying candidate genes but also in understanding how genetic variations affect gene expression and, ultimately, the phenotype. As more genomic and transcriptomic data become available, functional genomics will play a crucial role in validating the effects of QTLs and translating them into practical breeding applications (Ocaña-Moral et al., 2017).

In conclusion, the integration of functional genomics with QTL mapping represents a powerful tool for advancing poultry breeding. By understanding the molecular basis of important traits, breeders can develop more targeted breeding strategies that improve egg production and other economically valuable traits more efficiently (Mengesha et al., 2022).

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Conflict of Interest Disclosure

Authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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