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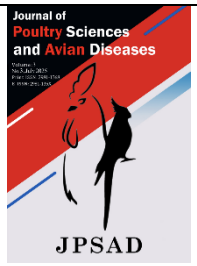

Immunogenetics Properties of Avian MHC Polymorphism and its Association with Diseases and Production Traits

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A B S T R A C T

Avian immunogenetics has emerged as a critical field in understanding the genetic basis of disease resistance and immune competence in poultry. Though structurally simpler than its mammalian counterpart, the Major Histocompatibility Complex (MHC) in chickens plays a pivotal role in pathogen defense due mainly to MHC's high polymorphism and dominant allelic expression patterns. Unlike mammals, where MHC class I and II molecules exhibit co-dominant expression, chickens predominantly express a single MHC class I molecule, leading to a binary resistance/susceptibility outcome against specific pathogens; their polymorphisms influence not only immunity but also economically valuable traits (i.e., growth and egg production). This unique feature has facilitated extensive research linking MHC alleles to disease outcomes, including resistance to infectious bursal disease virus (IBDV), Marek's disease (MD), and avian influenza. Beyond immunity, MHC polymorphisms correlate with economically significant traits such as egg production and growth rates, underscoring their dual role in health and production. However, modern poultry breeding programs often overlook genetic diversity, prioritizing production traits at the expense of immunocompetence. Integrating MHC-based marker-assisted breeding into poultry programs is essential to preserve genetic diversity and enhance immunocompetence. By leveraging advances in genomics and immunogenetics, future research can optimize poultry health, ensuring sustainable production in the face of evolving pathogen threats. This review highlights the importance of MHC polymorphism for both disease management and poultry economics; particularly, the study's strength lies in its presentation of allele-specific immunocompetence patterns across viral, bacterial, and parasitic pathogens, easing integrating MHC-based marker-assisted selection into breeding strategies to enhance disease resistance while maintaining genetic variability. These insights advance avian immunology and offer practical applications for improving global poultry welfare and food security.

Keywords: *Allelic polymorphism, MHC, Avian, Immunogenetics, Resistance, Production traits*

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1 Introduction

Genetic diversity is a common attribute found in individuals of all species. Previous research has demonstrated a significant association between genetic characteristics and susceptibility/resistance to pathogens in humans and animals. As one of the body's most complicated systems, the immune system consumes a large amount of body energy and is composed of various protein and non-protein components. These components are encoded by a substantial number of genes (1, 2). With molecular techniques and genomics advancements, researchers have unveiled the immune system's genetic basis. Understanding immunogenetics contributes to our knowledge of immunology and has practical applications in improving poultry health and welfare. By harnessing this knowledge, we can develop strategies for disease prevention, enhance immunocompetence, and ultimately mitigate the impact of infectious diseases on poultry production (3, 4).

Unfortunately, there is currently a lack of comprehensive research on immune genes in various bird species. Only a few studies have been conducted on mapping the genes of the immune system in a limited number of bird species, including chicken, duck, zebra finch, and turkey (5-8). These studies have shown that, similar to mammals, birds possess numerous genes responsible for encoding proteins that play a role in immune responses. However, it is worth noting that certain genes identified in mammals are absent in birds. For instance, TLR8, a specific Pattern Recognition Receptor (PRR), has not been identified in numerous bird species. Additionally, chicken, for instance, lacks the presence of RIG-1, a cytoplasmic PRR. The absence of these genes has been suggested to be the reason for the heightened susceptibility of birds, particularly chickens, to viral diseases (9).

2 Chicken MHC is one of the great research interests in avian immunogenetics

The Major Histocompatibility Complex (MHC) is a topic of great research interest and important in immunogenetics. This is because the MHC gene region exhibits one of the highest levels of genetic variability observed in living organisms. MHC consists of a cluster of ancient genes essential for the immune system, distinguishing between one's molecules and foreign entities (10). MHC was originally discovered in mice; subsequently, Briles et al. identified two highly diverse blood group systems in chickens. One of these systems, named B, was later identified as the determinant for erythroid alloantigens and regarded as the chicken MHC (11, 12). It has been found that the MHC is responsible for the binding and presenting peptide fragments to T lymphocytes. Additionally, the MHC gene region is where certain genes encoding for molecules involved in innate immunity are located (13).

While the MHC structure of different bird species might vary, this section will focus on chicken MHC. Previous research on bird MHC has primarily centered around chickens (14-17).

In mammals, the MHC classes are made up of many genes and exhibit an incredibly diverse range of allelic polymorphisms (18). However, like other protein-encoding genes of the avian immune system, the chicken MHC contains fewer genes. Even though the chicken MHC may seem simple, it still has the important genes found in the mammalian MHC. In chickens, the MHC is made up of two distinct polymorphic regions known as MHC-B (B complex) and MHC-Y (Rfp-Y); these regions are found on microchromosome 16, but they have their independent assortment (19-21). The MHC-B region only contains 19 genes and has an approximate length of 92kb. MHC-B has two polymorphic regions called B-F (classical class I MHC molecule) and B-L (classical class II MHC molecule), which are closely linked together (19-21). The B-F antigen was initially observed on the outer membrane of erythrocytes and lymphocytes, whereas the B-L antigen was first detected on B lymphocytes (13). B complex also has another region called B-G (class IV MHC molecule), which is unique to birds and not found in other animals. The MHC-Y region contains a separate group of non-classical MHC class I and II genes. Based on the previous studies, this region seems associated with mild graft rejection and the natural killer recognition process via MHC 1 and C-type lectin molecules (22). The physical separation of MHC-B and MHC-Y gene loci enables novel combinations of MHC-Y/B haplotypes in offspring, expanding immune gene diversity beyond what either region could achieve alone (19-21).

3 Unique characteristics of chicken MHC

Despite being smaller and less complex than mammals, the study of the chicken MHC has provided valuable insights into understanding the association between different MHC alleles and resistance/susceptibility to the diseases. This is because there are multiple genes in the MHC class I and II gene regions in humans and other mammals, and they are all expressed co-dominantly. This means there are different

forms of MHC class I and II molecules on the surface of mammalian cells, each with a high affinity for certain peptides (23). This allows these MHC molecules to recognize and present a wide variety of peptides. When a virus enters the body, for example, one of the MHC molecules forms with a higher affinity against the entered viral peptide and will eventually bind and present it to T-lymphocytes.

On the other hand, in chickens, there is one dominantly expressed MHC molecule on the cells' surface; this form makes up most of the MHC molecules (especially in the case of MHC class I) (23). As a result, a chicken is either genetically resistant or susceptible to a certain type of pathogen. Thus, studying the association between susceptibility/resistance of different alleles in polymorphic regions of chicken MHC and pathogenic agents will be simpler compared to humans and other mammals (23, 24) (Figure 1).

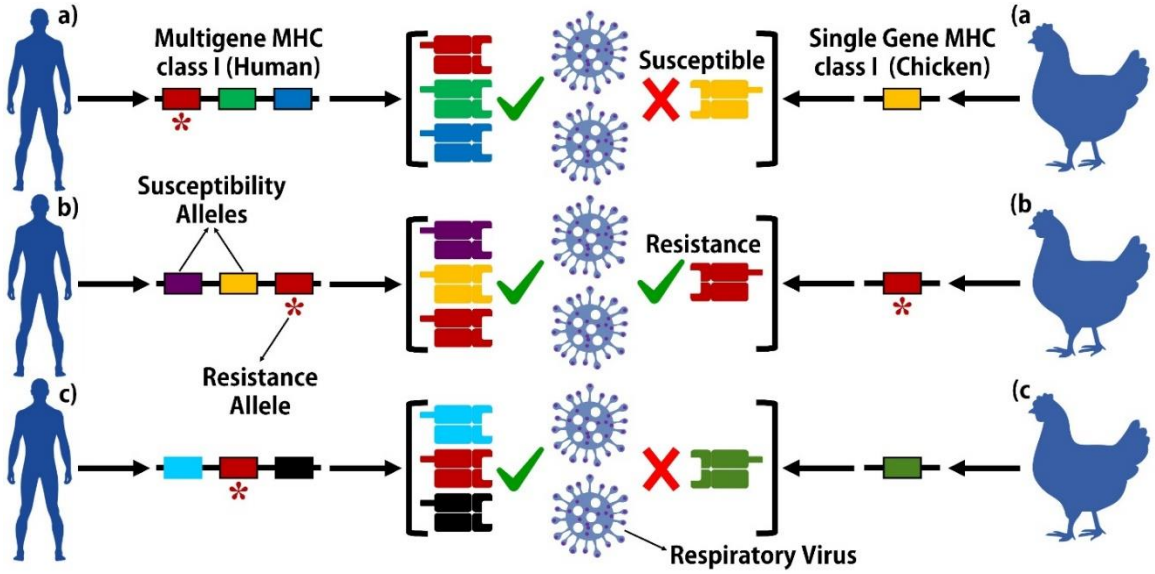

Figure 1. One of the main differences between the MHC class I gene locus in humans and chickens lies in the number of coding genes present. In humans, each individual haplotype contains three protein-coding genes, resulting in the production of six distinct MHC class I molecules from homologous chromosomes. Conversely, in chickens, each haplotype only contains a single protein-coding gene (BF2). The figure illustrates this difference by showcasing three individuals: humans a, b, and c, each possessing a resistant allele to a respiratory virus, thereby rendering them resistant to infection. In contrast, among chickens a, b, and c, only chicken b possesses a resistance allele to the respiratory virus, leaving chickens a and c susceptible to severe illness or death due to the absence of the resistant allele.

4 Association between MHC alleles and susceptibility/resistance to infectious agents

Owing to chicken MHC's unique characteristics, extensive research has been carried out in recent decades to explore the association between different chicken MHC alleles and susceptibility/resistance to infectious agents, production traits, reproductive strategies, and other related factors. The subsequent part will provide a brief overview of several studies published in this particular field.

In a study, six congenic lines of chickens were infected with virulent infectious bursal disease virus (IBDV), and the association between different MHC-B haplotypes and the survival of chickens after infection was investigated. The findings of this study revealed that the B12B12 haplotype displayed the greatest susceptibility to IBDV, with a mortality rate of 79% among chickens with this particular haplotype. On the other hand, lower mortality rates were observed in other haplotypes (25). Another study examined the association of different B complex haplotypes and the susceptibility or resistance of white Leghorn chickens to Marek's disease (MD). The study focused on a commercial pure line of these chickens. The findings revealed that chickens with B complex types B21/B21, B134/B21, and B234/B21 demonstrated a relatively high resistance level to MD, with mortality rates ranging from 24% to 32%. Conversely, birds with B19/B19 haplotypes were highly susceptible to the disease, experiencing a mortality rate of 68% (26).

Nevertheless, the apparent superior resistance of the B21/B21 haplotype to Marek's disease relative to other haplotypes requires much more extensive validation, as findings from other studies might contradict these results. In a study conducted by Banat *et al*., the susceptibility of five chicken lines, all homozygous for MHC-B and derived from white Leghorn and Ancona lineages, to infectious bronchitis virus (IBV) was examined. The findings of their investigation indicated that the Gray strain of IBV caused significant respiratory infection in chickens with homozygous haplotypes B12 and B19. On the other hand, chickens with haplotypes B2 and B5 displayed a higher level of resistance to this virus (27). In multiple similar studies, researchers have examined the association between different MHC haplotypes and alleles and chickens' susceptibility or resistance to diseases and pathologic agents such as Northern fowl mite infestations(28), *Ascaridia* sp. Infestations (29), bacterial skeletal diseases (30), *Salmonella* enteritidis (31), Rous sarcoma virus (32), Newcastle disease virus (33), high-pathogenicity avian influenza (34), avian leukosis virus (35), *Escherichia coli*-induced cellulitis (36), and infectious laryngotracheitis virus (37).

5 Association between MHC alleles and economic traits

The research conducted in this area has encompassed more than just infectious diseases. An illustrative instance is the study where they used PCR-based fragment analysis to genotype the LEI0258 microsatellite locus in the chicken MHC gene region. In this regard, genomic DNA was amplified using fluorescently labeled primers, and the PCR products were analyzed using an ABI 3130 genetic analyzer with GeneScan 500 LIZ® Size Standard. Fragment sizing was performed using Peak Scanner software to determine MHC haplotypes. Their findings revealed a significant association between different alleles of this region and numerous production traits in Khorasan chickens, including egg-laying intensity (eggs/hen/day), egg weight, body weight, and weight at sexual maturity (38). A similar study has been conducted on the association between different MHC alleles and production traits in indigenous Indian chickens (39). While various factors influence the production traits of chickens, the published articles in this field have provided clear evidence of the association between MHC alleles and these traits (40-48).

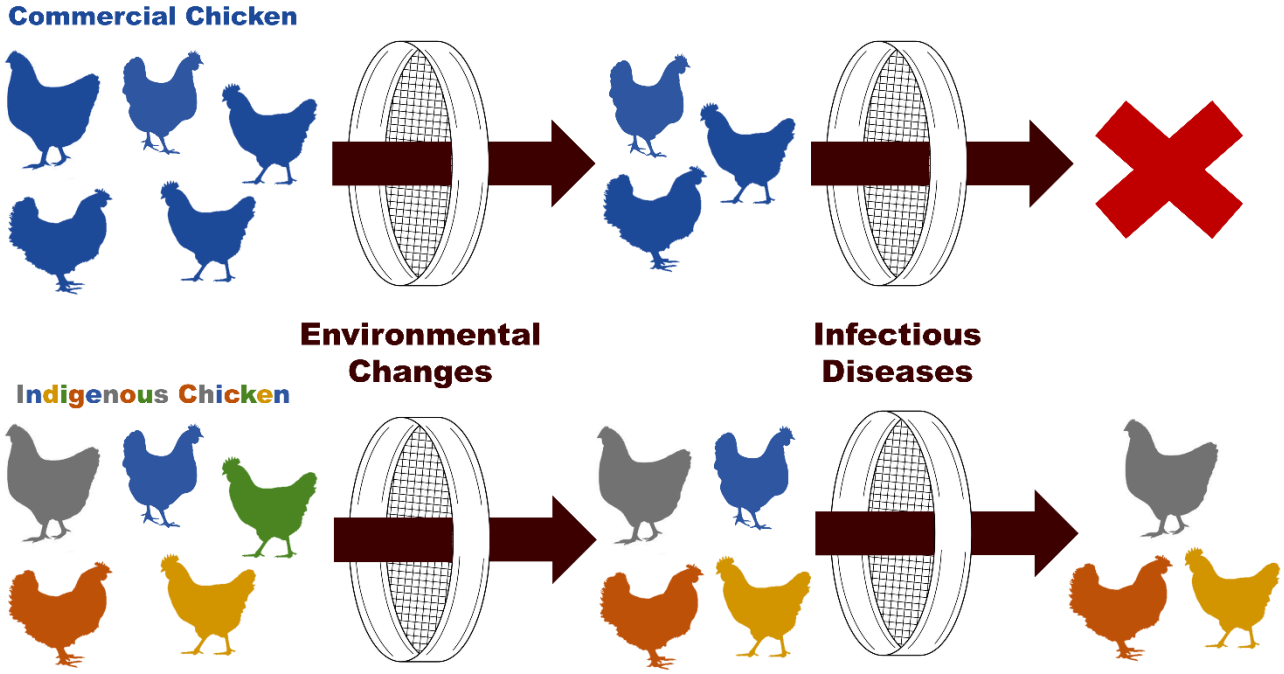

Figure 2. Comparison of indigenous and pure commercial chicken populations in the face of environmental changes and infectious diseases. While breeding programs have successfully developed high-production populations in economically important animals, the focus on purity and phenotypic traits often overlooks crucial molecular markers like disease-resistant MHC alleles, which play a vital role in maintaining a robust immune system. Consequently, after multiple generations, the resulting populations may lack the necessary genetic diversity and may exhibit insufficient immunocompetence. Typically, such populations are at risk of being eliminated from their environment.

6 Molecular marker-assisted breeding programs

The mentioned studies demonstrate the significance of genetic characteristics in economically valuable animals like chickens. In recent decades, livestock breeding programs have successfully developed high-production livestock. However, despite their potential importance, these programs usually do not consider genetic characteristics and molecular markers in their breeding strategies. These strategies have decreased genetic diversity and a deviation from the Hardy-Weinberg equilibrium within livestock populations (10). Considering the principles of evolution and the survival advantage of populations with greater genetic diversity in the face of environmental changes and pathogenic agents, there is a pressing need to prioritize molecular markers, such as MHC alleles that proved to be associated with immunocompetency, in animal breeding programs. If the current trajectory persists, there will be a potential decline in the number of immunocompetent animals over time. This situation poses a significant threat to the animal welfare and human well-being (10) (Figure 2).

7 Conclusions

The study of avian immunogenetics, particularly in chickens, has provided profound insights into the intricate relationship between genetic diversity and immune competence. The chicken MHC, despite its relatively compact and less complex structure than mammals, is pivotal in determining susceptibility or resistance to various pathogens. Furthermore, the linkage between MHC alleles and economically important traits, including body weight and egg production, highlights the dual role of the MHC in both immunity and productivity (Figure 3).

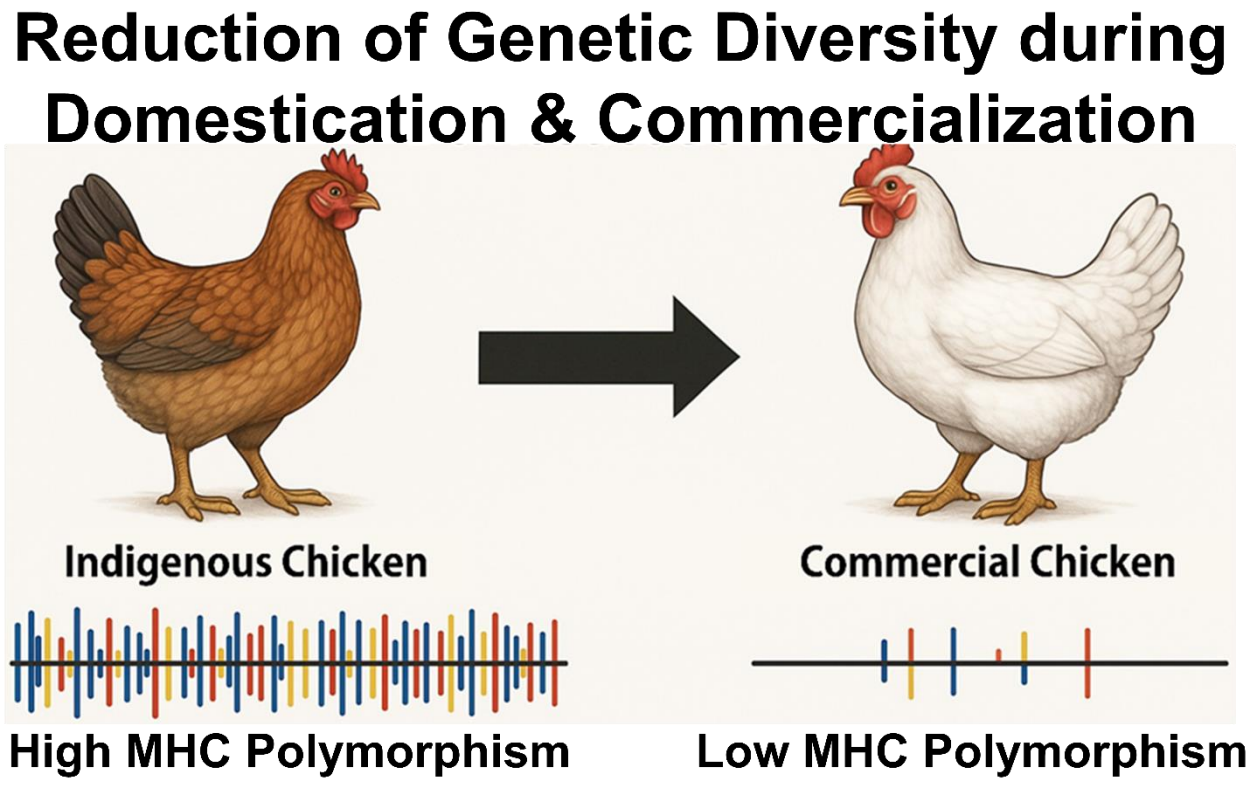

Figure 3. Domestication along with commercialization in poultry program and production weakens genetic diversity and MHC polymorphism, which results in susceptibility to many avian diseases.

The findings summarized in this review emphasize the critical need for integrating molecular marker-assisted breeding programs into poultry production systems. Current breeding strategies are often focused solely on production traits, risking eroding genetic diversity and compromising immunocompetence. By prioritizing MHC alleles and other genetic markers associated with disease resistance, future breeding programs can enhance the resilience and productivity of poultry populations. Such an approach aligns with evolutionary principles, ensuring that populations

retain the genetic variability necessary to adapt to emerging pathogens and environmental challenges.

In conclusion, advancing our understanding of avian immunogenetics enriches fundamental immunology and holds significant practical implications for sustainable poultry farming. Future research should include a broader range of avian species, such as quail, guinea fowl, goose, partridge, turkey, duck, and ostrich. Furthermore, cutting-edge genomic technologies uncover novel immune-related genes and their functional roles. We can foster healthier, more robust poultry populations by bridging the gap between genetic research and applied breeding practices, benefiting animal welfare and global food security.

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None.

Conflict of Interest

The authors declare no competing interests.

Author Contributions

JM designed the study, generated the research idea and schemes, organized and conducted the data collection and analysis, wrote and interpreted the text, and PH participated in preparing the study design and manuscript, writing, and reading and helped with all processes.

Data Availability Statement

The data produced and examined during this study are not openly accessible but can be obtained from the corresponding author upon a reasonable request.

Ethical Considerations

Not applicable.

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