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Article

Genome-Wide Association Studies and Candidate Genes for Egg Production Traits in Layers from an F₂ Crossbred Population Produced Using Two Divergently Selected Chicken Breeds, Russian White and Cornish White

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Abstract: Background/Objectives: Finding single nucleotide polymorphisms (SNPs) and candidate genes that influence the expression of key traits is essential for genomic selection and helps improve the efficiency of poultry production. Here, we aimed to conduct a genome-wide association study (GWAS) for egg production traits in an F₂ resource population of chickens (*Gallus gallus*). **Methods:** The examined F₂ population was produced by crossing two divergently selected breeds with contrasting phenotypes for egg performance traits, namely Russian White (of higher egg production) and Cornish White (of lower egg production). Sampled birds ($n = 142$) were genotyped using the Illumina Chicken 60K SNP iSelect BeadChip. **Results:** In the course of the GWAS analysis, we were able to clarify significant associations with phenotypic traits of interest and economic value by using 47,432 SNPs after the genotype dataset was filtered. At the threshold $p < 1.06 \times 10^{-6}$, we found 23 prioritized candidate genes (PCGs) associated with egg weight at the age of 42–52 weeks (*FGF14*, *GCK*), duration of egg laying (*CNTN4*), egg laying cycle (*SAMD12*) and egg laying interval (*PHF5A*, *AKR1B1*, *CALD1*, *ATP7B*, *PIK3R4*, *PTK2*, *PRKCE*, *FAT1*, *PCM1*, *CC2D2A*, *BMS1*, *SEMA6D*, *CDH13*, *SLIT3*, *ATP10B*, *ISCU*, *LRRC75A*, *LETM2*, *ANKRD24*). Moreover, two SNPs were co-localized within the *FGF14* gene. **Conclusions:** Based on our GWAS findings, the revealed SNPs and candidate genes can be used as genetic markers for egg weight and other performance characteristics in chickens to attain genetic enhancement in production and for further genomic selection.

Keywords: chicken (*Gallus gallus*); genome-wide association study (GWAS); single nucleotide polymorphisms (SNPs); candidate genes; egg performance



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1. Introduction

The search for, and identification of, gene variants that underlie the manifestation of selection-significant traits in livestock [1,2] is one of the prerequisites and main goals of genomic selection that aims to improve animal production efficiency [3–5]. In egg poultry

farming, much attention is paid to the phenotypic and genetic indicators characterizing the productive potential of laying hens [6,7]. Finding a set of characteristics that indicate increased egg yield through targeted selection is crucial [8,9], and some of the main criteria for selecting poultry breeds, lines and crosses for industrial egg production are such traits as egg number (EN) and egg weight (EW) [10–12]. The history of the creation and improvement of layer breeds is directly related to selection for the expression of these traits [13,14]. EN produced over a certain period of time per laying hen is an important indicator relevant to the egg industry in terms of profitability and economic efficiency [15]. EW is a primary trait in relation to commercial quality of eggs [16], which determines the sale value of this poultry produce. In addition, larger eggs tend to have higher consumer demand [17].

EN laid by a hen during a certain laying period is largely determined by such characteristics as age at first egg (AFE), duration of egg laying (DEL), and egg laying cycle (ELC) [18,19]. Since the initiation of sexual maturity in females coincides with the start of egg laying, AFE is regarded as an indicator that enables prediction of both the bird's reproductive capacity and egg performance [20–22]. Selection of poultry for this trait when developing industrial egg lines and crosses is of particular significance, since a homogeneity of an industrial population of laying hens in terms of the onset of egg laying makes it possible to synchronize the duration of productive use of the layers and enhance the overall egg productivity of the flock [23]. Length of laying cycles and egg laying interval (ELI) directly affect the number of eggs produced by hens during their productive period. Birds with higher egg production are usually characterized by longer laying cycles and shorter periods without laying [19].

The productive potential of layers and its implications for poultry production conditions depend on many factors such as genotype [24–28], feeding [29–33] and maintenance conditions [34–37], with the latter including lighting and indoor microclimate, among others [38,39]. Some poultry species have seasonal egg laying, e.g., turkeys [40] and geese [41,42].

The genetic basis of egg performance traits in poultry females has been described in many studies [43–47]. With the advent of high-density single nucleotide polymorphism (SNP) arrays [48], genome-wide association studies (GWAS) have begun to play an essential role in pinpointing previously undetected genetic associations of SNPs and candidate genes with phenotypic traits in chickens [43,49–53], geese [54], quails [55] and ducks [56,57]. Nowadays, GWAS is a molecular tool of choice to investigate genetic blueprints and determinants for various chicken traits of interest, e.g., feed efficiency and growth traits [58], feed conversion ratio [59], muscle fiber and fat traits [60,61], body size [62], semen volume [63], beak deformity [64], response to Newcastle disease [65], and quantitative trait loci (QTL) for ascites syndrome [66], among many others. In our earlier studies using the Russian White (RW) layer breed and the Cornish White (CW) meat breed (Figure 1), we explored putative genes and selective sweeps under strong selection pressure for egg production [67] and identified SNPs and candidate genes associated with AFE in F₂ hens from a resource population generated by crossing these two breeds [23].

The objective of the present investigation was to extend the above previous works by focusing on SNP discovery and candidate gene identification associated with egg production traits in hens. These traits included AFE, EN, DEL, ELC, ELI, and EW at 18–28 (EW1), 29–41 (EW2) and 42–52 (EW3) weeks of age. To achieve this aim, a GWAS for egg production traits in F₂ resource chickens from a cross between the RW (of higher egg production) and CW (of lower egg production) breeds (Figure 1) was conducted using whole-genome genotyping (WGG) data.

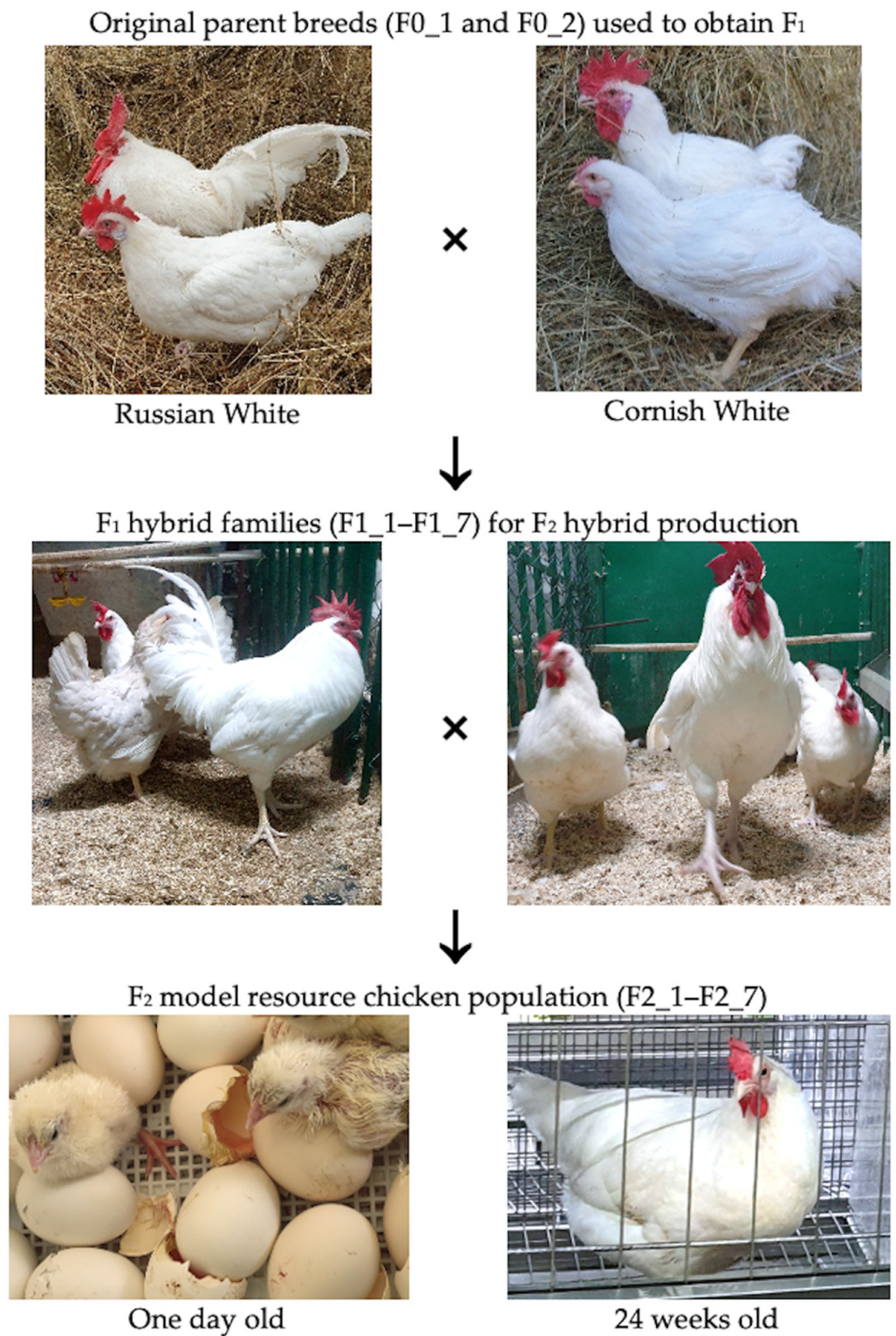


Figure 1. Initial parent breeds and F₁ hybrids used to obtain the F₂ model resource chicken population.

2. Materials and Methods

2.1. Experimental Birds

The original breed chickens were reared at the L. K. Ernst Federal Research Centre for Animal Husbandry (LKEFRCAH), hatched from eggs purchased from the Russian Research Institute of Farm Animal Genetics and Breeding (Pushkin, Russia). The F₂

resource population's chickens were obtained and raised at the LKEFRCAH (Figure 1), and their DNA was sampled.

To produce the F₂ chicken resource population, two breeds divergently selected and with contrasting egg production indicators were used, i.e., RW [48,50,68,69] and CW [67,70,71]. At the first stage, based on WGG data and in order to exclude close relationships, individuals of the original parental breeds were divided into two families (F0_1 and F0_2; Figure 1), each consisting of five CW females and one RW male. Each family produced F₁ hybrids ($n = 36$) through interbreed crosses, which were then selected for further study. These F₁ interbreed hybrids were utilized to produce F₂ individuals. For this purpose, seven families (F1_1–F1_7; Figure 1) were formed, each of which included one F₁ male and three F₁ females that were not close relatives. The resultant F₂ offspring ($n = 142$ females; groups F2_1–F2_7; Figure 1) served as a model resource population for additional molecular genetic research aimed at identifying SNPs linked to egg yield indicators of laying hens.

The temperature of the brooders was gradually lowered from 34 °C (in the first few hours after hatching) to 23 °C until the chicks were three weeks old, at which point they were moved to floor maintenance. F₂ progenies were housed according to their age, which included regular lighting, enough ventilation (to prevent moisture, drafts, and gas pollution), and permanent availability to fresh water and commercial complete compound feed as described elsewhere [72,73]. At the age of 15 weeks, the hens were moved to individual cages to record egg productivity indicators.

2.2. Performance Data

The 142 F₂ females of the resource population were phenotyped for egg production parameters: AFE, EN, DEL, ELC, ELI, plus average EW1, EW2 and EW3. The egg production parameters of each female were recorded individually in the period from the beginning of egg laying to the age of 52 weeks. EN was calculated in the age period from 18 to 52 weeks. ELC was estimated as the period (i.e., number of days) of continuous egg laying, and ELI as the period of absence of egg laying between two ELCs. Eggs were weighed on a laboratory scale. The average EW values were calculated in the first (EW1), second (EW2) and third (EW3) periods of egg laying. The same egg performance indicators (except ELC and ELI) were recorded for chickens of the original parental breeds, i.e., RW ($n = 20$) and CW ($n = 15$).

2.3. Sampling and DNA Isolation

Feather pulp was utilized for DNA extraction that was performed using the Syntol animal tissue DNA extraction kit (Syntol, Moscow, Russia). The concentration of DNA solutions was measured using a Qubit 3.0 Fluorimeter (Thermo Fisher Scientific, Wilmington, DE, USA). The NanoDrop-2000 device (Thermo Fisher Scientific) was used to estimate the OD260/280 ratio in order to verify the isolated DNA's purity.

2.4. Genotyping and Quality Control of SNPs

WGG of hens was conducted using the Illumina Chicken iSelect BeadChip DNA array containing ~60K SNPs. In the R-4.0 software environment [74], the PLINK 1.9 software package [75,76] was used to carry out quality control and filtering of WGG data for every sample and every SNP. The following program filters were applied: --mind 0.10, --geno 0.10, --maf 0.01, --hwe 10^{-6} . Following SNP pruning, 47,432 SNPs were used in the subsequent analysis.

2.5. Principal Component Analysis

Using PLINK, principal component analysis (PCA; [77]) was carried out based on the variance-standardized relationship matrix, and the R program ggplot2 was employed

to plot the findings [78,79]. In the R-4.0 software environment [74,80], the data files were created.

2.6. Genome-Wide Association Studies

To reveal SNP associations with egg production parameters in F₂ resource population hens, regression analysis in PLINK 1.9 was executed. The significance of SNP influence and chicken genome regions were identified and evaluated using the Bonferroni null hypothesis test with a p -value cutoff ($p < 1.06 \times 10^{-6}$). The qqman software (version 0.1.9) [81] in the R programming language [82] was used to visualize the data.

The Genome Data Viewer in the NCBI chicken databases [83] and the chicken (*G. gallus*; GGA) reference genome assembly GRCg6a [84] were used to search for putative genes located in the vicinity of the detected SNPs, including 0.2-Mb flanks on both sides. To obtain comprehensive information about SNPs found within or close to the identified candidate genes, the web-based Ensembl Genes release 106 database and the Ensembl BioMart data mining program [85] were used. The Ensembl BioMart data mining tool and Database for Annotation, Visualization, and Integrated Discovery (DAVID Knowledgebase; version DAVID 2021 (December 2021; v2023q4, quarterly updated)) [86,87] were utilized to conduct functional annotation and gene ontology (GO) term enrichment analysis for major candidate genes. The search for associations of identified SNPs and potential genes with selectively significant traits in chickens identified in other studies was carried out in the Animal QTLdb (<https://www.animalgenome.org/cgi-bin/QTLdb/index> (accessed on 21 April 2025)) and Chicken QTLdb (<https://www.animalgenome.org/cgi-bin/QTLdb/GG/index> (accessed on 21 April 2025)) databases. All required database data were extracted to build GRCg6a (https://www.animalgenome.org/QTLdb/doc/genome_versions#chicken (accessed on 21 April 2025)) in .bed format, .gff and .sam formats.

3. Results

3.1. Phenotypic Data and Population Stratification

Table 1 presents descriptive statistics characterizing the distribution of values established for the egg productivity traits studied in F₂ resource population hens. A higher variability of values was established for a number of traits, e.g., ELC and ELI had coefficients of variation up to 33.4 and 41.4%, respectively.

It should be noted that the obtained F₂ resource population hens had a tendency for higher variability in the phenotypic expression of the studied egg productivity traits compared to the original parent breeds (Table 1).

The distribution of the examined F₂ resource population was displayed by PCA across several clusters. In the projections of first component (PC1)–second component (PC2) and PC1–third component (PC3), differentiation of the studied population into four groups was noted, as follows: the first grouping included F2_1, F2_4, F2_5 and F2_6 progenies, the second grouping included F2_2 individuals, the third grouping included F2_3 chickens, and the fourth grouping included F2_7 offspring. These data are shown graphically in Figure 2a,b.

Consequently, we conducted a GWAS trial employing the first three PCs (i.e., PC1, PC2 and PC3) as covariates in light of the observed population stratification, or its disclosed structure.

Table 1. Descriptive statistics for egg production indicators ¹ in F₂ resource population hens as compared to the original parent breeds.

Trait	F ₂ Population (n = 142)		Russian White (n = 20)		Cornish White (n = 15)	
	Mean ± SD	CV, %	Mean ± SD	CV, %	Mean ± SD	CV, %
Age at first egg, days	131.6 ± 18.4	13.9	144.5 ± 6.3	4.4	180.6 ± 17.8	9.9
Duration of egg laying, days	232.4 ± 18.4	7.9	220.5 ± 6.3	2.9	184.4 ± 17.8	9.6
Egg number for 238 days	126.2 ± 31.6	25.1	150.3 ± 10.8	7.2	82.0 ± 11.1	13.5
Egg laying cycle, days	2.4 ± 0.8	33.4	N/A	N/A	N/A	N/A
Egg laying interval, days	2.4 ± 1.0	41.4	N/A	N/A	N/A	N/A
Egg weight at age of 18–28 weeks, g	43.0 ± 3.5	8.2	44.1 ± 3.2	7.2	N/A	N/A
Egg weight at age of 29–41 weeks, g	50.8 ± 4.7	9.3	50.6 ± 4.3	8.7	52.2 ± 4.2	8.0
Egg weight at age of 42–52 weeks, g	57.8 ± 3.9	6.7	55.1 ± 2.4	4.3	63.1 ± 4.6	7.4

¹ SD, standard deviation; CV, coefficient of variation; n, number of females; N/A, not available due to unavailability of individual trait recording.

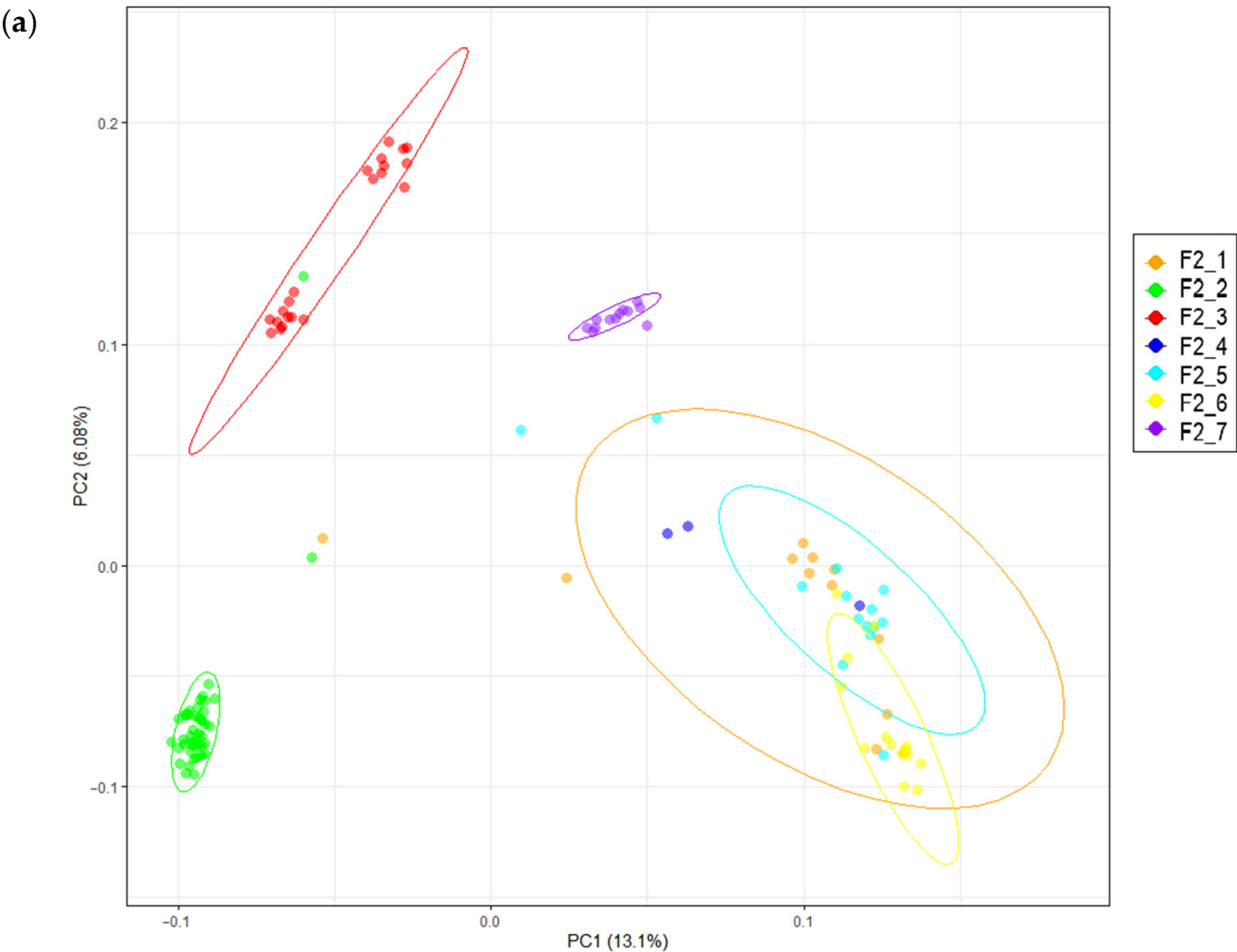


Figure 2. Cont.

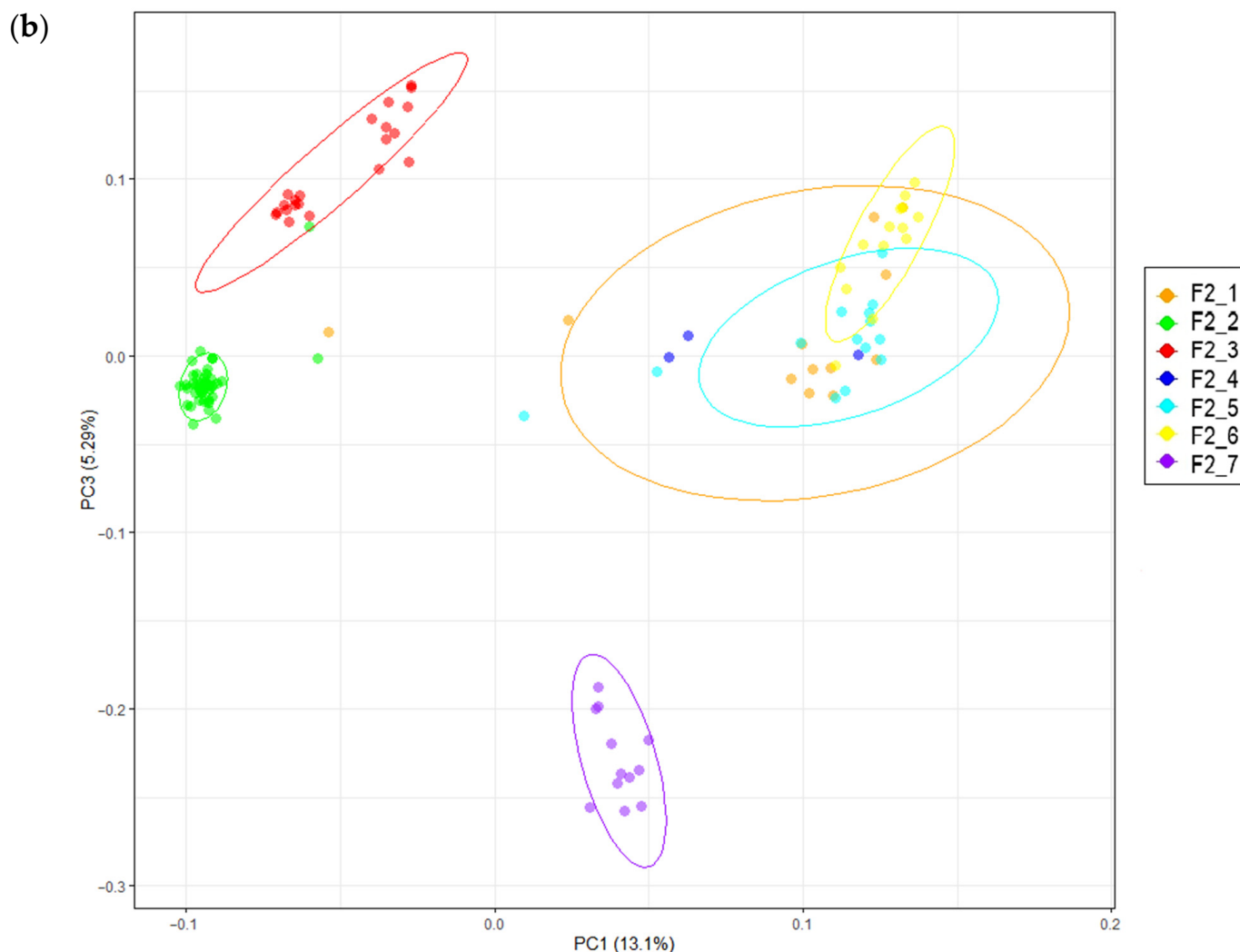


Figure 2. Principal component analysis (PCA) for the F₂ resource chicken population. (a) PCA performed in the projection of the first (PC1) and second (PC2) components. X-axis, PC1; Y-axis, PC2. (b) PCA performed in the projection of the PC1 and third (PC3) components. X-axis, PC1; Y-axis, PC3. Different colors are used to represent members of certain groups.

3.2. Genome-Wide Association Analysis Output

The obtained phenotypic data on egg production parameters in F₂ resource population hens (Table 1) were used for the subsequent GWAS. Figure 3 presents the respective GWAS results.

The completed analysis discovered six SNPs associated with EN in hens of the resource population and EW in different periods of their egg laying, and 45 SNPs associated with the studied DEL and ELI parameters at the level of established significance value $p < 1.06 \times 10^{-6}$ (Supplementary Table S1). These SNPs were identified on 19 of 28 chromosomes explored. The maximum number of significant SNPs was localized on GGA1 (14 SNPs), and the minimum (1 SNP) on GGA5, GGA6, GGA8, GGA9, GGA11, GGA12, GGA15, GGA19, GGA25, GGA27 and GGA28. No significant SNPs were identified on chromosomes GGA7, GGA16–GGA18, GGA20, GGA21, GGA23, GGA24 and GGA26 for any of the studied parameters.

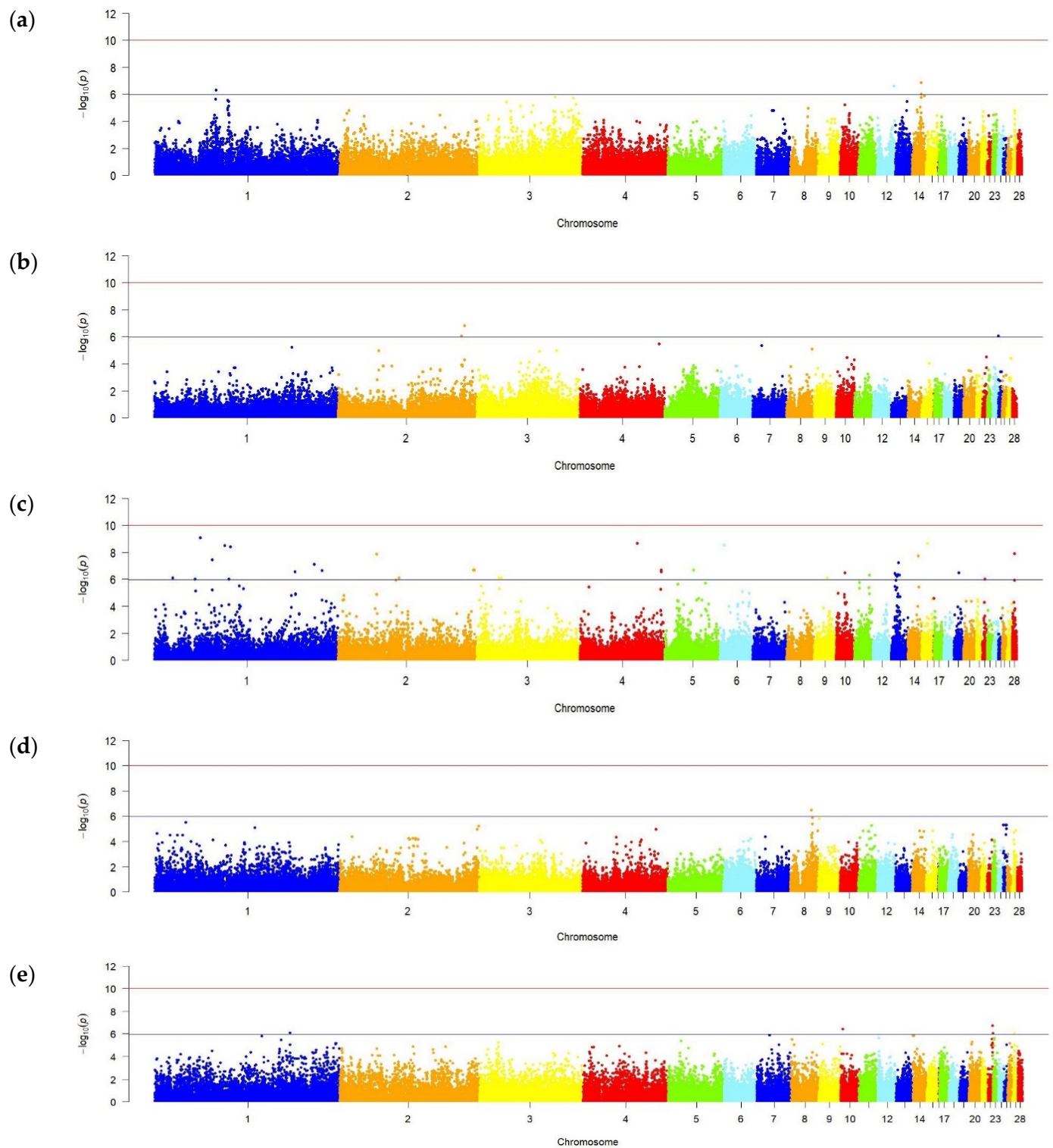


Figure 3. Manhattan plots resulting from GWAS for the studied egg production traits in the F₂ resource chicken population. (a) Duration of egg laying from age at first egg to 52 weeks of age; (b) egg laying cycle; (c) egg laying interval; (d) mean egg weight at 18–28 weeks of age; and (e) mean egg weight at 42–52 weeks of age. Manhattan plots: distribution of single nucleotide changes across 28 chicken chromosomes (autosomes) at the significance level ($-\log_{10}(p)$) based on the traits' predicted probability values. The only purpose of color-coding dots is to show chromosomal segregation.

Information about the distribution and quantity of significant SNPs found on chromosomes, taking into account each specifically studied egg productivity indicator in F₂ resource population hens, is shown in Table 2.

Table 2. Chromosomal distribution of significant SNPs ($p < 1.06 \times 10^{-6}$) associated with egg production indicators in F₂ resource population hens.

Trait	No. of SNPs	Chromosomes ¹
Duration of egg laying	4	GGA1, GGA12, GGA14
Egg laying cycle	3	GGA2, GGA25
Egg laying interval	38	GGA1–GGA6, GGA9–GGA11, GGA13–GGA15, GGA19, GGA22, GGA28
Egg weight at age of 18–28 weeks	1	GGA8
Egg weight at age of 42–52 weeks	5	GGA1, GGA10, GGA22, GGA27

¹ GGA, chicken (*G. gallus*) chromosome.

The number of significant SNPs associated with the studied egg laying parameters (DEL, ELI, ELC and ELI) varied from 3 to 38. A significant proportion of these SNPs were localized on chromosomes GGA1, GGA4 and GGA13 (5–12 SNPs).

GWAS of EW parameters in the studied F₂ population hens revealed one and five SNPs, respectively, associated with this trait in the first (18–28 weeks) and third (42–52 weeks) periods of egg laying. These SNPs were established on five chromosomes (GGA8, GGA1, GGA10, GGA22, and GGA27).

For three indicators (EN, AFE and EW2), no significant SNPs were identified in this study at the established significance threshold.

3.3. Candidate Genes

Candidate genes linked to the studied egg productivity parameters in F₂ resource population hens were annotated using the significant SNPs that were found. In the regions of identified SNPs (i.e., SNP position ± 0.2 Mb), a total of 219 genes described in the NCBI databases [83,84] were detected (Supplementary Table S1), including 23 prioritized candidate genes (PCGs) within which the identified SNPs were localized. The latter genes were found on 13 chromosomes (GGA1–GGA4, GGA6, GGA10–GGA13, GGA15, GGA19, GGA22 and GGA28). In the case of one PCG, for fibroblast growth factor 14 (*FGF14*), two SNPs associated with EW3 were identified. Significant SNPs ($p < 1.06 \times 10^{-6}$) associated with egg performance of F₂ resource population hens and the appropriate candidate genes are shown in Table 3.

The annotated genes were categorized into four functional clusters according to the GO term enrichment score. Three clusters, however, were deemed insignificant since their enrichment scores were less than one. The remaining one cluster (with enrichment scores > 1.15) included genes related to protein phosphorylation and ATP binding.

Supplementary Table S2 lists every gene that was annotated along with its function. Comparative analysis of the results obtained in this study with information available in the Animal QTLdb database (<https://www.animalgenome.org/cgi-bin/QTLdb/index> (accessed on 21 April 2025)) confirmed the significant association of four identified candidate genes with selectively important traits in chickens, including five genes with egg production indicators (Supplementary Table S3).

Table 3. Significant SNPs and prioritized candidate genes (in SNP positions) associated with egg production indicators in F₂ resource population hens.

Trait	GGA ¹	SNP	Location, bp	Gene	p-Value
Egg weight at 42–52 weeks of age	1	Gga_rs13950763	144,541,672	<i>FGF14</i>	7.893×10^{-7}
		Gga_rs13950783	144,581,256	<i>FGF14</i>	7.893×10^{-7}
	22	Gga_rs16733701	5,254,215	<i>GCK</i>	8.868×10^{-7}
Duration of egg laying	12	Gga_rs14048080	18,439,246	<i>CNTN4</i>	2.497×10^{-7}
Egg laying cycle	2	Gga_rs13772998	136,095,111	<i>SAMD12</i>	1.565×10^{-7}
Egg laying interval	1	GGaluGA016975	49,631,028	<i>PHF5A</i>	8.431×10^{-10}
		GGaluGA021889	62,111,416	<i>AKR1B1</i>	3.519×10^{-8}
		Gga_rs14835481	62,385,811	<i>CALD1</i>	4.072×10^{-15}
		Gga_rs13973123	171,655,178	<i>ATP7B</i>	7.489×10^{-8}
	2	Gga_rs13670867	41,560,503	<i>PIK3R4</i>	1.337×10^{-8}
		Gga_rs14258322	145,755,426	<i>PTK2</i>	2.003×10^{-7}
	3	Gga_rs14329753	26,472,162	<i>PRKCE</i>	7.511×10^{-7}
	4	Gga_rs15598417	61,793,533	<i>FAT1</i>	2.166×10^{-9}
		Gga_rs15600128	62,825,026	<i>PCM1</i>	4.072×10^{-15}
		GGaluGA266321	76,726,036	<i>CC2D2A</i>	5.887×10^{-15}
	6	Gga_rs14564900	5,790,608	<i>BMS1</i>	2.811×10^{-9}
	10	GGaluGA068824	10,301,717	<i>SEMA6D</i>	3.172×10^{-7}
	11	GGaluGA078973	16,137,404	<i>CDH13</i>	4.874×10^{-7}
	13	GGaluGA092132	5,413,088	<i>SLIT3</i>	3.573×10^{-7}
		Gga_rs14050895	8,419,842	<i>ATP10B</i>	4.550×10^{-7}
	15	Gga_rs15773720	6,817,919	<i>ISCU</i>	2.166×10^{-9}
	19	GGaluGA126763	5,248,070	<i>LRRC75A</i>	3.247×10^{-7}
	22	Gga_rs14684608	2,639,829	<i>LETM2</i>	9.628×10^{-7}
	28	Gga_rs16210664	2,694,485	<i>ANKRD24</i>	1.184×10^{-7}

¹ GGA, chicken (*G. gallus*) chromosome.

4. Discussion

Elucidating the genetic basis for efficient poultry breeding involves the search for, and identification of, valuable genotypes focusing on the use of genomic technologies [88,89]. This has become possible thanks to the initial generation of the complete chicken genome sequence [90,91] that contributed to advances in the genomics of other bird species [92–98]. For the successful implementation of genomic technologies in poultry farming practice, it is essential to explore the molecular genetic mechanisms underlying the phenotypic variability of economically important traits that are crucial for improving the efficiency of agriculture and increasing the production of competitive products [99,100]. Our work presented here yielded the associations of SNPs and candidate genes with the main egg productivity traits in F₂ chickens of the resource population produced through interbreeding of the divergently selected breeds, RW and CW, that contrast in egg performance.

4.1. Egg Number and Egg Weight

EN and EW are the main egg performance indicators for which egg breeds are selected [101]. Intensive selection of chickens for these traits contributed to the creation of highly productive egg crosses, from which more than 300 eggs are expected per year per layer [9]. At the same time, long-term selection of chickens for high egg production contributed to a decline in genetic variability for this trait [102]. To date, many studies

have been conducted aimed at finding candidate genes associated with EN [103–107] and EW [108–111].

In our study, two PCGs were identified that were associated with EW3, including the *FGF14* gene [112] and the glucokinase (*GCK*) gene [113]. To the best of our knowledge, previous investigations have not revealed any direct connection between these genes and EW in chickens. At the same time, in research by Li et al. [114], the influence of *FGF14* on the eggshell qualitative characteristics in hens in the late period of egg laying was demonstrated. These authors described the expression profiles of mRNAs and long non-coding RNAs (lncRNAs) in the eggshell glands of young and older laying chickens, comparing each in order to find potential genes linked to aging in the laying hen's uterus. The eggshell's thickness correlates with its strength [115] and also determines the weight indicators of both the shell and the whole egg. Taking this into account, the results of that study [115] can be considered as an indirect confirmation of the *FGF14* gene association with EW established in our investigation.

The *GCK* gene enables glucokinase activity by its involvement in the glucose 6-phosphate metabolic process and in the glycolytic process. A number of studies have shown the involvement of *GCK* in the glycolytic process in poultry, in particular, in chickens [116,117] and ducks [118]. Its relationships with feed consumption [116,117], embryo development, muscle development and egg production in chickens [119] have been established. Christensen et al. [120] established a positive correlation between high glucose concentration, on the one hand, and survival, weight and rapid growth of embryos and hatched turkey chicks, on the other. The weight of the hatching egg is positively correlated with the development and weight of embryos [121] and hatched chicks [122,123]. Based on this, it can be assumed that *GCK* may indirectly affect EW.

4.2. Age at First Egg and Duration of Egg Laying

AFE, or the start of egg laying in poultry, relates to the sexual maturation process of growing birds and the commencement of sexual maturity, which are both controlled by the hypothalamic–pituitary–gonadal system [20,124]. Many studies have shown the influence of the hypothalamic–pituitary–gonadal axis on hormones and genes related to egg production indicators, including AFE, in various poultry species [20–22].

Previously, we demonstrated the association of the genes for axin interactor, dorsalization associated (*AIDA*), Na^+/K^+ transporting ATPase interacting 2 (*NKAIN2*), lin-9 DREAM MuvB core complex component (*LIN9*) and mitogen-activated protein kinase kinase kinase 3 (*MAP4K3*) with AFE [23]. In the present work, we did not identify genes associated with AFE at the level of the significance threshold established in this study. One respective PCG, contactin 4 (*CNTN4*), was identified on GGA12 that was associated with DEL. This productive trait is directly related to AFE [20,124]. Liu et al. [125] established a significant association between *CNTN4* and feed conversion ratio in an F₂ resource population of laying ducks during the egg laying period. In the same experiment, correlations were found between the feed conversion ratio and egg production traits. This may partly confirm our results on the association of *CNTN4* with DEL, since egg production determines the duration of the productive use of laying hens.

4.3. Egg Laying Cycle and Egg Laying Interval

The duration of ELCs and ELIs are important selection indicators that determine the egg productivity and the productive use duration of poultry, including chickens [126–128]. The implementation of the productive potential of laying hens in terms of these indicators depends on a number of factors, including the development and functional character-

istics of the reproductive organs associated with egg laying [102,129], as well as feed intake [126,130–134] and housing conditions [39,135].

Relative to our experimental data, a comparative analysis of open information sources, e.g., the Chicken QTLdb database (<https://www.animalgenome.org/cgi-bin/QTLdb/GG/index> (accessed on 21 April 2025)), demonstrated that, for eight PCGs identified in our research, other studies have also shown close relationships with selection-significant traits in chickens. These PCGs included ATPase copper transporting beta (*ATP7B*), aldo-keto reductase family 1, member B10 (aldose reductase) (*AKR1B1*), caldesmon 1 (*CALD1*), slit guidance ligand 3 (*SLIT3*), coiled-coil and C2 domain containing 2A (*CC2D2A*), BMS1, ribosome biogenesis factor (*BMS1*), semaphorin 6D (*SEMA6D*), and ATPase phospholipid transporting 10B (putative) (*ATP10B*) that were related to egg laying performance in F₂ resource population hens. In particular, two genes are known to be associated with the development of reproductive organs and egg laying in chickens, i.e., *CALD1* with the morphogenesis of the Müllerian ducts, which develop into the reproductive tract of female vertebrates [136], and *SLIT3* with ovarian follicle growth [137]. Also, other studies reported associations of these genes with eggshell quality characteristics such as eggshell strength [138–140], and eggshell effective layer thickness (https://www.animalgenome.org/cgi-bin/QTLdb/GG/qdetails?QTL_ID=159369 (accessed on 21 April 2025); [141]).

Curiously, the work presented here has parallels beyond birds into mammalian egg production. In sheep oocytes, a significant upregulation of the *AKR1B1* gene was observed in the warm season [142], which may be suggestive of its role in the reproductive cycle of homeothermic species. In the works of Jehl et al. [143] and Yuan et al. [144], a search was performed for candidate genes associated with the efficiency of daily feed intake in laying hens. A definite association was established for *AKR1B1* [143] and *ATP7B* [144] with this indicator. Also, for the genes associated in our study with ELI, other works reported their relationship with poultry growth and meat productivity. In particular, *AKR1B1* was shown to be associated with growth and abdominal fat deposition [145], and with chest width in 7-week-old chickens (https://www.animalgenome.org/cgi-bin/QTLdb/GG/qdetails?QTL_ID=257052 (accessed on 21 April 2025); [146]). Furthermore, associations were suggested for *BMS1* [147], *ATP10B* [51] and *ATP7B* (https://www.animalgenome.org/cgi-bin/QTLdb/GG/qdetails?QTL_ID=261257 (accessed on 21 April 2025); [148]) with chicken growth rates; *SEMA6D* with growth and body weight in laying ducks aged 18 weeks [149]; and *CC2D2A* with shank weight, tibia weight and femur weight in ducks during the laying period [150].

With all the above in mind, the available results of other studies largely agree with our data on the direct effect of the *CALD1*, *SLIT3* and *FGF14* genes on the egg productivity indices of hens. For other genes identified in our work, a number of studies have also shown their relationship with growth and meat productivity indices (*ATP7B*, *CC2D2A*, *AKR1B1*, *SLIT3*, *BMS1* and *ATP10B*), feed consumption of laying hens during the egg laying period (*CNTN4*, *ATP7B* and *AKR1B1*) in chickens, growth indices (*SEMA6D*), and the state of the musculoskeletal system (*CC2D2A*) in laying ducks. Based on the hypothesis that genes interrelating in similar biological networks may collectively affect the egg production phenotype [151], we also examined all genes that overlapped the significant SNP regions that we identified in our GWAS for functional enrichment (Supplementary Table S2). According to GO analysis, the best candidates were enriched for protein phosphorylation and ATP binding, and calcium ion binding, which have broad biological/metabolic functions and roles [85–87]. Further studies using GWAS, whole-genome sequencing and other approaches (e.g., [104,152–155]) are required to confirm the association of these potential genes with egg production in layers and elucidate endocrine and genetic factors affecting egg laying performance [106].

5. Conclusions

In this investigation, we performed a GWAS for traits associated with egg production in an F₂ resource population using the Illumina Chicken 60K SNP iSelect BeadChip. The conducted studies revealed 51 SNPs and 23 PCGs showing a significant association with EW1 (one SNP) and EW3 (five SNPs; *FGF14* and *GCK* genes), as well as with DEL (four SNPs; *CNTN4* gene), ELC (three SNPs; *SAMD12* gene), and ELI (38 SNPs; *PHF5A*, *AKR1B1*, *CALD1*, *ATP7B*, *PIK3R4*, *PTK2*, *PRKCE*, *FAT1*, *PCM1*, *CC2D2A*, *BMS1*, *SEMA6D*, *CDH13*, *SLIT3*, *ATP10B*, *ISCU*, *LRRC75A*, *LETM2*, and *ANKRD24* genes) in the studied birds. The maximum number of identified SNPs and candidate genes was detected on chromosome GGA1 (14 SNPs), while the minimum number was observed on chromosomes GGA5, GGA6, GGA8, GGA9, GGA11, GGA12, GGA15, GGA19, GGA25, GGA27 and GGA28 (one SNP each). In one of the 23 identified PCGs, *FGF14*, two SNPs were localized associated with EW3. These findings are crucial for comprehending the molecular genetic underpinnings of development and implementation of productive potential in hens. Although they need more research, the discovered SNPs and PCGs can be utilized as genetic markers in breeding initiatives meant to boost and enhance egg yield.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/genes16050583/s1>, Table S1: SNPs and candidate genes associated with egg production parameters in F₂ resource population hens; Table S2: Gene ontology (GO) term enrichment analysis at the positions of the determined SNPs in F₂ resource population chickens; Table S3: Comparative analysis of the obtained experimental data relative to the Animal QTLdb database (<https://www.animalgenome.org/cgi-bin/QTLdb/index>).

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Institutional Review Board Statement: The study was conducted according to the guidelines of the Declaration of Helsinki and the LKEFRCAH ethical guidelines. Protocol No. 3/1 was approved by the LKEFRCAH Commission on the Ethics of Animal Experiments on 4 December 2019.

Informed Consent Statement: Not applicable.

Data Availability Statement: The genotyping data presented in this study can be shared with the third parties upon approval with the GWMAS Consortium. Other original contributions presented in the study are included in the article and Supplementary Materials; further inquiries can be directed to the corresponding authors with the permission provided by the chickens' owners.

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References

1. Meuwissen, T.; Hayes, B.; MacLeod, I.; Goddard, M. Identification of genomic variants causing variation in quantitative traits: A review. *Agriculture* **2022**, *12*, 1713. [CrossRef]

2. Plemyashov, K.V.; Smaragdov, M.G.; Romanov, M.N. Molekulyarno-geneticheskiy polimorfizm v populyatsiyakh zhivotnykh i yego primeneniye v intensivnoy selektsii molochnogo skota: Obzor [Molecular Genetic Polymorphism in Animal Populations and Its Application in Intensive Breeding of Dairy Cattle—A Review]. In *Molecular Genetic Technologies for Analysis of Gene Expression Related to Animal Productivity and Disease Resistance, Proceedings of the Materials of the 3rd International Scientific and Practical Conference, Moscow, Russia, 30 September 2021*; Sel'skokhozyaistvennye Tekhnologii: Moscow, Russia, 2021; pp. 368–378, (In Russian with English summary).
3. Meuwissen, T.; Hayes, B.; Goddard, M. Accelerating improvement of livestock with genomic selection. *Annu. Rev. Anim. Biosci.* **2013**, *1*, 221–237. [CrossRef]
4. Georges, M.; Charlier, C.; Hayes, B. Harnessing genomic information for livestock improvement. *Nat. Rev. Genet.* **2019**, *20*, 135–156. [CrossRef]
5. Plemyashov, K.V.; Smaragdov, M.G.; Romanov, M.N. Genomnaya otsenka plemennykh bykov [Genomic Assessment of Breeding Bulls]. In *Molecular Genetic Technologies for Analysis of Gene Expression Related to Animal Productivity and Disease Resistance, Proceedings of the Materials of the 3rd International Scientific and Practical Conference, Moscow, Russia, 30 September 2021*; Pozyabin, S.V., Kochish, I.I., Romanov, M.N., Eds.; Sel'skokhozyaistvennye Tekhnologii: Moscow, Russia, 2021; pp. 363–367. Available online: <https://elib.spbstu.ru/dl/2/z21-43.pdf/info> (accessed on 21 April 2025).
6. Romanov, M.N.; Kochish, I.I.; Sharafetdinov, G.R.; Myasnikova, O.V.; Nikonov, I.N.; Selina, M.V.; Surai, P.F. Napravleniya sovremennykh biotekhnologicheskikh razrabotok dlya realizatsii geneticheskogo potentsiala yaichnoy ptitsy [Towards Advanced Biotechnological Developments to Realize the Genetic Potential of Egg-type Poultry]. In *Molecular Genetic Technologies for Analysis of Gene Expression Related to Animal Productivity and Disease Resistance, Proceedings of the Materials of the 3rd International Scientific and Practical Conference, Moscow, Russia, 30 September 2021*; Pozyabin, S.V., Kochish, I.I., Romanov, M.N., Eds.; Sel'skokhozyaistvennye Tekhnologii: Moscow, Russia, 2021; pp. 40–51, (In Russian with English summary).
7. Kutnyuk, P.I.; Bondarenko, Y.V.; Ivanova, T.V. Kariometrychnyy metod vyznachennya henetychnoho potentsialu nesuchosti kurey [Karyometric method of determining the genetic potential of laying hens]. *Ptakhivnytstvo [Poult. Farming]* **2001**, *50*, 75–81. (In Ukrainian)
8. Chomchuen, K.; Tuntiyasawadikul, V.; Chankitisakul, V.; Boonkum, W. Genetic Evaluation of body weights and egg production traits using a multi-trait animal model and selection index in Thai native synthetic chickens (Kaimook e-san2). *Animals* **2022**, *12*, 335. [CrossRef]
9. Shtele, A.L. Problem of egg productivity in hens and its early prediction. *Sel'skokhozyaistvennaya Biol. [Agric. Biol.]* **2014**, *6*, 26–35. [CrossRef]
10. Groen, A.F. Breeding objectives and selection strategies for layer production. In *Poultry Genetic, Breeding and Biotechnology*; Muir, W.M., Aggrey, S.E., Eds.; CABI Publishing: Wallingford, UK, 2003; pp. 101–112. Available online: <https://books.google.com/books?id=IPSSDwAAQBAJ&pg=PA101> (accessed on 21 April 2025).
11. Narushin, V.G.; Volkova, N.A.; Vetokh, A.N.; Dzhagaev, A.Y.; Volkova, L.A.; Griffin, D.K.; Romanov, M.N.; Zinovieva, N.A. Metabolic rate and egg production in Japanese quails can be predicted by assessing growth parameters of laying hens. *Animals* **2024**, *14*, 258. [CrossRef]
12. Lukianova, V.D.; Kovalenko, V.P.; Kosenko, N.F.; Bondarenko, Y.V. Immunogenetic Method in Poultry Line Selection for Heterosis Effect on Egg Production. In *Proceedings of the XVI World's Poultry Congress, Proceedings & Abstracts, Rio de Janeiro, Brazil, 17–21 September 1978*; World's Poultry Science Association Brazil Branch: Sao Paulo, Brazil, 1978; Volume 12, pp. 2116–2122. Available online: https://scholar.google.com/citations?view_op=view_citation&citation_for_view=c1PnDYEAAAAJ:K3LRdlH-MEOC (accessed on 21 April 2025).
13. Podstreshny, A.P.; Bondarenko, Y.V.; Rozhkovskiy, A.V.; Gintovt, V.E. Ispolzovanie markernykh priznakov pri sozdanii perspektivnykh kombinatsiy yaichnykh kur [The use of marker traits in the creation of promising combinations of egg-laying hens]. *Ptitsevodstvo [Poult. Farming]* **1984**, *37*, 9–14. (In Russian)
14. Khvostik, V.P.; Bondarenko, Y.V.; Paskevych, G.A. Prohnozuvannya nesuchosti kurey riznoho henetychnoho pokhodzhennya [Prediction of laying hens of different genetic origins]. *Nauk. Visn. L'viv's'koho Nats. un-tu vet. Medytsyny ta Biotekhnolohiy im. S. Z. Gzhyts'koho Ser. Sil's'kohospodars'ki Nauky [Sci. Messin. LNU Vet. Med. Biotech. Ser. Agric. Sci.]* **2023**, *25*, 60–65, (In Ukrainian with English summary). [CrossRef]
15. Altaht, E.; Al-Sharafat, A.; Altarawneh, M. Factors affecting profitability of layer hens enterprises. *Am. J. Agric. Biol. Sci.* **2012**, *7*, 106–113. [CrossRef]
16. Romanov, M.N. Qualitative and Quantitative Egg Characteristics in Laying Hens of Different Genotype. In *Egg and Egg Products Quality, Proceedings of the 6th European Symposium on Quality of Eggs and Eggs Products, Zaragoza, Spain, 25–29 September 1995*; World's Poultry Science Association Spanish Branch: Madrid, Spain; pp. 203–206. Available online: https://scholar.google.com/citations?view_op=view_citation&citation_for_view=1fz40BYAAAAJ:KYgttONoxcsC (accessed on 21 April 2025).
17. Mesías, F.J.; Martínez-Carrasco, F.; Martínez, J.M.; Gaspar, P. Functional and organic eggs as an alternative to conventional production: A conjoint analysis of consumers' preferences. *J. Sci. Food Agric.* **2011**, *91*, 532–538. [CrossRef] [PubMed]

18. Liu, W.; Li, D.; Liu, J.; Chen, S.; Qu, L.; Zheng, J.; Xu, G.; Yang, N. A genome-wide SNP scan reveals novel loci for egg production and quality traits in White Leghorn and brown-egg dwarf layers. *PLoS ONE* **2011**, *6*, e28600. [CrossRef] [PubMed]
19. Shcherbatov, V.I.; Shkuro, A.G. Cycles and intervals in hen egg laying. *E3S Web Conf.* **2021**, *285*, 04009. [CrossRef]
20. Tan, Y.G.; Xu, X.L.; Cao, H.Y.; Zhou, W.; Yin, Z.Z. Effect of age at first egg on reproduction performance and characterization of the hypothalamo-pituitary-gonadal axis in chickens. *Poult. Sci.* **2021**, *100*, 101325. [CrossRef]
21. Xu, H.; Zeng, H.; Luo, C.; Zhang, D.; Wang, Q.; Sun, L.; Yang, L.; Zhou, M.; Nie, Q.; Zhang, X. Genetic effects of polymorphisms in candidate genes and the QTL region on chicken age at first egg. *BMC Genet.* **2011**, *12*, 33. [CrossRef]
22. He, Z.; Ouyang, Q.; Chen, Q.; Song, Y.; Hu, J.; Hu, S.; He, H.; Li, L.; Liu, H.; Wang, J. Molecular mechanisms of hypothalamic-pituitary-ovarian/thyroid axis regulating age at first egg in geese. *Poult. Sci.* **2024**, *103*, 103478. [CrossRef]
23. Dzhagaev, A.Y.; Volkova, N.A.; Zinovieva, N.A. Search for genes associated with the age at first egg in laying hens (*Gallus gallus* L.). *Sel'skokhozyaistvennaya Biol. [Agric. Biol.]* **2024**, *59*, 658–665. [CrossRef]
24. Wang, J.; Liu, Z.; Cao, D.; Liu, J.; Li, F.; Han, H.; Han, H.; Lei, Q.; Liu, W.; Li, D.; et al. Elucidation of the genetic determination of clutch traits in Chinese local chickens of the Laiwu Black breed. *BMC Genom.* **2023**, *24*, 686. [CrossRef]
25. Vargas, D.; Galíndez, R.; De Basilio, V.; Martínez, G. Age at the first egg in Japanese quail (*Coturnix coturnix japonica*) under experimental conditions. *Rev. Cient. Fac. Cienc. Vet. Univ. Zulia* **2009**, *19*, 181–186.
26. Balcha, K.A.; Mengesha, Y.T.; Senbeta, E.K.; Zeleke, N.A. Evaluation of different traits from day-old to age at first eggs of Fayoumi and White leghorn chickens and their reciprocal crossbreeds. *J. Adv. Vet. Anim. Res.* **2021**, *8*, 1–6. [CrossRef]
27. Mesele, T.L. Reproduction and production performance of improved chickens, their production constraints, and opportunities under Ethiopian conditions. *Trop. Anim. Health Prod.* **2023**, *55*, 245. [CrossRef] [PubMed]
28. Romanov, M.N. Impact of genotype, nutrition and management systems on goose production efficiency. In Proceedings of the 11th European Symposium on Waterfowl, Nantes, France, 8–10 September 1997; Association Groupe Français de la WPSA (French Branch): Paris, France; World Society for the Protection of Animals French Branch: Nantes, France, 1997; pp. 33–41. Available online: <https://kar.kent.ac.uk/46409/> (accessed on 21 April 2025).
29. De Juan, A.F.; Scappaticcio, R.; Aguirre, L.; Mateos, G.G.; Camara, L. Effects of the composition of the pre-peak diet fed from 18 to 29 wk of age on egg production, egg quality, and the development of the gastrointestinal tract of brown-egg laying hens from 18 to 61 wk. *J. Appl. Poult. Res.* **2024**, *33*, 100415. [CrossRef]
30. Bi, R.; Yang, M.; Liu, X.; Guo, F.; Hu, F.; Huang, J.; Abbas, W.; Xu, T.; Liu, W.; Wang, Z. Effects of chlorogenic acid on productive and reproductive performances, egg quality, antioxidant functions, and intestinal microenvironment in aged breeder laying hens. *Poult. Sci.* **2024**, *103*, 104060. [CrossRef]
31. Kochish, I.I.; Surai, P.F.; Romanov, M.N.; Smolensky, V.I.; Nikonov, I.N.; Selina, M.V.; Myasnikova, O.V.; Kolesnikova, R.R. *Metodicheskiye Rekomendatsii po Primeneniyu Osnov Tekhnologii Kormleniya Yaichnykh kur, Obespechivayushchey Vysokiy Protsent Realizatsii ikh Geneticheskogo Potentsiala Produktivnosti [Methodical Recommendations on the Application of the Foundations of the Technology of Feeding Egg-Type Chickens, Providing a High Percentage of Realization of Their Genetic Potential for Productivity]*; Sel'skokhozyaistvennyye Tekhnologii: Moscow, Russia, 2019; ISBN 978-5-6043642-6-0. Available online: https://www.researchgate.net/publication/371531267_Methodical_recommendations_on_the_application_of_the_foundations_of_the_technology_of_feeding_egg-type_chickens_providing_a_high_percentage_of_realization_of_their_genetic_potential_for_productivity_M (accessed on 21 April 2025). (In Russian)
32. Romanov, M.N.; Grozina, A.A.; Ilina, L.A.; Laptev, G.Y.; Yildirim, E.A.; Filippova, V.A.; Tyurina, D.G.; Fisinin, V.I.; Kochish, I.I.; Griffin, D.K.; et al. From feed regulation to regulated feeding: Intestinal microbiome and performance optimization in broiler chickens in response to antibiotic and probiotic treatment. In Proceedings of the Life of Genomes 2022, Abstracts of the International Conference, Kazan, Russia, 23–24 November 2022; Research Center “Regulatory Genomics”, Institute of Fundamental Medicine and Biology, Kazan (Volga Region) Federal University: Kazan, Russia, 2022; pp. 44–45. Available online: <http://lifeofgenomes.r-genomics.com/wp-content/uploads/2022/12/Absctracts.pdf> (accessed on 21 April 2025).
33. Bratyshko, N.I.; Prytulenko, O.V.; Lemesheva, M.M.; Tereshchenko, O.V. *Rekomendatsiyi z Normuvannya Hodioli Sil's'kohospodars'koyi Ptytsi [Recommendations on Rationing of Feeding of Agricultural Poultry]*, 3rd ed.; Tereshchenko, O.V., Ed.; Poultry Research Institute, NAAS, NTMT: Birky, Ukraine, 2010; Available online: https://scholar.google.com/citations?view_op=view_citation&citation_for_view=deB5xCwAAAAJ:RHpTSmoSYBkC (accessed on 21 April 2025). (In Ukrainian)
34. Katerynych, O.O.; Pankova, S.M.; Tereshchenko, O.V.; Ruda, S.V.; Havilei, O.V.; Riabinina, O.V.; Muzyka, N.M.; Ionov, I.A. *Vyroshchuvannya, Utrymannia ta Hodiolia Yaiechnykh ta Miaso-Yaiechnykh Kurei [Rearing, Maintenance and Feeding of Egg and Meat-Egg Hens: Scientific and Practical Guide]*; Poultry Research Institute, DDSP NAAS: Birky, Ukraine, 2017; Available online: <https://scholar.google.com/scholar?cluster=10199343115289849189> (accessed on 21 April 2025). (In Ukrainian)
35. Shkurko, M.I.; Bondarenko, U.V.; Ostapenko, V.I. Produktivnist' molodnyaka kachok riznykh henotypiv v umovakh prysadybnoho hospodarstva [Productivity of young ducks of different genotypes under conditions of farming household]. *Visn. Sums'kogo Nac. Agrar. Un-tu Ser. Tvarynyystvo [Bull. Sumy Natl. Agrar. Univ. Ser. Livest.]* **2015**, *6*, 75–78, (In Ukrainian with English summary).

36. Shkurko, M.I.; Bondarenko, Y.V. Porivnyal'na kharakterystyka molodnyaka kachok riznykh henotypiv v umovakh prysadybnoho hospodarstva [Comparative Characteristics of Young Ducks of Different Genotypes in Homestead Farming Conditions]. In Proceedings of the Materials of the Scientific Practical Conference of Teachers, Postgraduates and Students of the Sumy National Agrarian University, Sumy, Ukraine, 20–24 April 2015; Sumy National Agrarian University: Sumy, Ukraine, 2015; Volume 2, p. 103. Available online: https://scholar.google.com/citations?view_op=view_citation&citation_for_view=c1PnDYEAAAAJ:nrtMV_XWKgEC (accessed on 21 April 2025). (In Ukrainian).
37. Podstreshnyi, O.; Tereshchenko, O. Utrymannya doroslykh perepeliv [Maintenance of adult quails]. *Ahrar. Krayina [Agrar. Country]* **2012**, *6*, 8–9. (In Ukrainian)
38. Wang, S.D.; Jan, D.F.; Yeh, L.T.; Wu, G.C.; Chen, L.R. Effect of exposure to long photoperiod during the rearing period on the age at first egg and the subsequent reproductive performance in geese. *Anim. Reprod. Sci.* **2002**, *73*, 227–234. [\[CrossRef\]](#)
39. Kavtarashvili, A.S.; Fisinin, V.I.; Buyarov, V.S.; Kolokolnikova, T.N. The effects of lighting regimes on the oviposition time and egg quality in laying hens (review). *Sel'skokhozyaistvennaya Biol. [Agric. Biol.]* **2019**, *54*, 1095–1109. [\[CrossRef\]](#)
40. Siopes, T.D. Initiation of egg production by turkey breeder hens: Sexual maturation and age at lighting. *Poult. Sci.* **2010**, *89*, 1490–1496. [\[CrossRef\]](#)
41. Zhao, X.; Yue, S.; Zhang, Y.; Sun, J.; Peng, F.; Guo, Z. The *TRHDE* and *TSHR* genes regulate laying traits in domesticated Zi geese. *Curr. Issues Mol. Biol.* **2025**, *47*, 331. [\[CrossRef\]](#)
42. Zhao, X.; Yue, S.; Sun, J.; Zhang, Y.; Peng, F.; Ma, Z.; He, H.; Li, M.; Guo, Z. RNA-seq reveals the effects of light on reproductive traits in domesticated geese. *Braz. J. Poult. Sci.* **2025**, *27*, eRBCA-2024-2016. [\[CrossRef\]](#)
43. Liu, Z.; Yang, N.; Yan, Y.; Li, G.; Liu, A.; Wu, G.; Sun, C. Genome-wide association analysis of egg production performance in chickens across the whole laying period. *BMC Genet.* **2019**, *20*, 67. [\[CrossRef\]](#)
44. Chen, A.; Zhao, X.; Wen, J.; Zhao, X.; Wang, G.; Zhang, X.; Ren, X.; Zhang, Y.; Cheng, X.; Yu, X.; et al. Genetic parameter estimation and molecular foundation of chicken egg-laying trait. *Poult. Sci.* **2024**, *103*, 103627. [\[CrossRef\]](#)
45. Ou, J.T.; Tang, S.Q.; Sun, D.X.; Zhang, Y. Polymorphisms of three neuroendocrine-correlated genes associated with growth and reproductive traits in the chicken. *Poult. Sci.* **2009**, *88*, 722–727. [\[CrossRef\]](#)
46. Gorodnaja, A.V.; Moiseeva, I.G.; Glazko, V.I.; Sevastjanova, A.A. Polimorfizm nekotorykh genetiko-biokhimicheskikh sistem u kur [Polymorphism of some genetic-biochemical systems in chicken]. *Dokl. Ross. Akad. s-kh. Nauk [Proc. Russ. Acad. Agric. Sci.]* **1997**, *2*, 31–33, (In Russian with English summary).
47. Wolc, A.; Arango, J.; Jankowski, T.; Dunn, I.; Settari, P.; Fulton, J.E.; O'Sullivan, N.P.; Preisinger, R.; Fernando, R.L.; Garrick, D.J.; et al. Genome-wide association study for egg production and quality in layer chickens. *J. Anim. Breed. Genet.* **2014**, *131*, 173–182. [\[CrossRef\]](#)
48. Dementeva, N.V.; Romanov, M.N.; Kudinov, A.A.; Mitrofanova, O.V.; Stanishevskaya, O.I.; Terletsky, V.P.; Fedorova, E.S.; Nikitkina, E.V.; Plemyashov, K.V. Studying the structure of a gene pool population of the Russian White chicken breed by genome-wide SNP scan. *Sel'skokhozyaistvennaya Biol. [Agric. Biol.]* **2017**, *52*, 1166–1174. [\[CrossRef\]](#)
49. Zhang, L.; Zheng, M.Q.; Liu, R.R.; Wen, J.; Wu, D.; Hu, Y.D.; Sun, Y.F.; Li, P.; Liu, L.; Zhao, G.P. Genome-wide association of thymus and spleen mass in chicken. *Sci. Agric. Sin.* **2012**, *45*, 3165–3175. [\[CrossRef\]](#)
50. Dementeva, N.V.; Kudinov, A.A.; Mitrofanova, O.V.; Stanishevskaya, O.I.; Fedorova, E.S.; Romanov, M.N. Genome-wide association study of reproductive traits in a gene pool breed of the Russian White chickens. *Reprod. Domest. Anim.* **2018**, *53* (Suppl. S2), 123–124.
51. Volkova, N.A.; Romanov, M.N.; Vetokh, A.N.; Larionova, P.V.; Volkova, L.A.; Abdelmanova, A.S.; Sermyagin, A.A.; Griffin, D.K.; Zinovieva, N.A. Genome-wide association study reveals the genetic architecture of growth and meat production traits in a chicken F₂ resource population. *Genes* **2024**, *15*, 1246. [\[CrossRef\]](#)
52. Tan, L.; Xu, N.; Liu, Z.; Cai, X.; Kong, Y.; Wen, Z.; Wang, Y.; Zhao, Y. Genome-wide association studies on longitudinal phenotypes reveal genetic mechanisms of egg production in chickens. *Poult. Sci.* **2025**, 105280, *in press*. [\[CrossRef\]](#)
53. Tu, T.-C.; Lin, C.-J.; Liu, M.-C.; Hsu, Z.-T.; Chen, C.-F. Genomic prediction and genome-wide association study for growth-related traits in Taiwan country chicken. *Animals* **2025**, *15*, 376. [\[CrossRef\]](#)
54. Gao, G.; Gao, D.; Zhao, X.; Xu, S.; Zhang, K.; Wu, R.; Yin, C.; Li, J.; Xie, Y.; Hu, S.; et al. Genome-wide association study-based identification of SNPs and haplotypes associated with goose reproductive performance and egg quality. *Front. Genet.* **2021**, *12*, 602583. [\[CrossRef\]](#)
55. Volkova, N.A.; Romanov, M.N.; Abdelmanova, A.S.; Larionova, P.V.; German, N.Y.; Vetokh, A.N.; Shakhin, A.V.; Volkova, L.A.; Sermyagin, A.A.; Anshakov, D.V.; et al. Genome-wide association study revealed putative SNPs and candidate genes associated with growth and meat traits in Japanese quail. *Genes* **2024**, *15*, 294. [\[CrossRef\]](#)
56. Sun, Y.; Zhang, Y.; Wu, Q.; Lin, R.; Chen, H.; Zhang, M.; Lin, J.; Xu, E.; Li, M.; Cai, Y.; et al. Whole-genome sequencing identifies potential candidate genes for egg production traits in laying ducks (*Anas platyrhynchos*). *Sci. Rep.* **2023**, *13*, 1821. [\[CrossRef\]](#)
57. Lu, Y.; Wei, B.; Yang, Q.; Han, X.; He, X.; Tao, Q.; Jiang, S.; Xu, M.; Bai, Y.; Zhang, T.; et al. Identification of candidate genes affecting the tibia quality in Nonghua duck. *Poult. Sci.* **2024**, *103*, 103515. [\[CrossRef\]](#)

58. Cai, K.; Liu, R.; Wei, L.; Wang, X.; Cui, H.; Luo, N.; Wen, J.; Chang, Y.; Zhao, G. Genome-wide association analysis identify candidate genes for feed efficiency and growth traits in Wenchang chickens. *BMC Genom.* **2024**, *25*, 645. [\[CrossRef\]](#)
59. Shah, T.M.; Patel, N.V.; Patel, A.B.; Upadhyay, M.R.; Mohapatra, A.; Singh, K.M.; Deshpande, S.D.; Joshi, C.G. A genome-wide approach to screen for genetic variants in broilers (*Gallus gallus*) with divergent feed conversion ratio. *Mol. Genet. Genom.* **2016**, *291*, 1715–1725. [\[CrossRef\]](#)
60. Li, H.; Li, S.; Zhang, H.; Gu, J.; Dai, Y.; Wu, R.; Wang, Y.; Han, R.; Sun, G.; Zhang, Y.; et al. Integrated GWAS and transcriptome analysis reveals key genes associated with muscle fibre and fat traits in Gushi chicken. *Br. Poult. Sci.* **2025**, *66*, 31–41. [\[CrossRef\]](#)
61. Fan, S.; Yuan, P.; Li, S.; Li, H.; Zhai, B.; Li, Y.; Zhang, H.; Gu, J.; Li, H.; Tian, Y.; et al. Genetic architecture and key regulatory genes of fatty acid composition in Gushi chicken breast muscle determined by GWAS and WGCNA. *BMC Genom.* **2023**, *24*, 434. [\[CrossRef\]](#)
62. Luo, N.; An, B.; Wei, L.; Wen, J.; Zhao, G. Identification of molecular markers associated with body size traits through genome-wide association analysis in Wenchang chickens. *Sci. Agric. Sin.* **2024**, *57*, 2046–2060. [\[CrossRef\]](#)
63. Zhang, G.M.; Liu, P.H.; Chen, L.; Zheng, J.M.; Zhao, G.P.; Xing, W.H.; Wen, J.; Li, Q.H. Genome-wide association study identifies variants associated with semen volume in white-feathered broilers. *Anim. Genet.* **2023**, *54*, 803–807. [\[CrossRef\]](#) [\[PubMed\]](#)
64. Bai, H.; Sun, Y.; Liu, N.; Xue, F.; Li, Y.; Xu, S.; Ye, J.; Zhang, L.; Chen, Y.; Chen, J. Single SNP- and pathway-based genome-wide association studies for beak deformity in chickens using high-density 600K SNP arrays. *BMC Genom.* **2018**, *19*, 501. [\[CrossRef\]](#) [\[PubMed\]](#)
65. Walugembe, M.; Amuzu-Aweh, E.N.; Botchway, P.K.; Naazie, A.; Aning, G.; Wang, Y.; Saelao, P.; Kelly, T.; Gallardo, R.A.; Zhou, H.; et al. Genetic basis of response of Ghanaian local chickens to infection with a lentogenic Newcastle disease virus. *Front. Genet.* **2020**, *11*, 739. [\[CrossRef\]](#) [\[PubMed\]](#)
66. Parveen, A.; Jackson, C.D.; Dey, S.; Tarrant, K.; Anthony, N.; Rhoads, D.D. Identification and validation of quantitative trait loci for ascites syndrome in broiler chickens using whole genome resequencing. *BMC Genet.* **2020**, *21*, 54. [\[CrossRef\]](#)
67. Abdelmanova, A.S.; Dotsev, A.V.; Romanov, M.N.; Stanishevskaya, O.I.; Gladys, E.A.; Rodionov, A.N.; Vetokh, A.N.; Volkova, N.A.; Fedorova, E.S.; Gusev, I.V.; et al. Unveiling comparative genomic trajectories of selection and key candidate genes in egg-type Russian White and meat-type White Cornish chickens. *Biology* **2021**, *10*, 876. [\[CrossRef\]](#)
68. Moiseeva, I.G. Izmenchivost' i nasleduyemost' nekotorykh pokazateley kachestva yaits u kur russkoy beloy porody [Variability and heritability of some features of egg quality in Russkaya Belaya chickens]. *Tr. In-ta Genet. AN SSSR [Trudy Inst. Genet.]* **1964**, *31*, 302–308. (In Russian)
69. Moiseeva, I.G. Soderzhaniye lipidov i kholesterina v yaytsakh kur russkoy beloy porody [Content of lipids and cholesterol in eggs of Russian White chickens]. *Collect. Works Young Sci. All-Union Res. Tech. Poult. Inst.* **1966**, *8*, 225–235. (In Russian)
70. Romanov, M.N.; Shakhin, A.V.; Abdelmanova, A.S.; Volkova, N.A.; Efimov, D.N.; Fisinin, V.I.; Korshunova, L.G.; Anshakov, D.V.; Dotsev, A.V.; Griffin, D.K.; et al. Dissecting selective signatures and candidate genes in grandparent lines subject to high selection pressure for broiler production and in a local Russian chicken breed of Ushanka. *Genes* **2024**, *15*, 524. [\[CrossRef\]](#)
71. Bondarenko, Y.V.; Serghyeva, V.D.; Kuranova, E.N.; Krasnozhan, S.A.; Romanov, M.N. Autoseksnaya materinskaya forma myasnykh kur [Autosexing maternal form of meat-type chickens]. *Ptitsevodstvo [Poult. Farming]* **1987**, *40*, 6–11. (In Russian)
72. Melnyk, V.O.; Ivko, I.I.; Tereshchenko, O.V. Resursozberihayuchi Tekhnolohiyi Vyroshchuvannya, Utrymannya ta Hodioli Yayechnykh i M'iaso-Yayechnykh Kurey: Metodichni Rekomendatsiyi [Resource-Saving Technologies for Raising, Keeping and Feeding Egg and Meat-Egg Chickens: Methodological Recommendations]; Poultry Research Institute, NAAS: Birky, Ukraine, 2011; Available online: https://scholar.google.com/citations?view_op=view_citation&citation_for_view=deB5xCwAAAAJ:FAceZFleit8C (accessed on 21 April 2025). (In Ukrainian)
73. Tereshchenko, A.V.; Artemenko, A.B.; Pudov, V.Y. Skrytyj istocnik uvelichenia proizvodstva cyplat-brojlerov [A hidden source of increasing the production of broiler chickens]. *Eksklyuziv Agro [Exclus. Agro]* **2007**, *4*, 64–65. (In Russian)
74. R Core Team. *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing: Vienna, Austria, 2018. Available online: <https://www.r-project.org/> (accessed on 21 April 2025).
75. Purcell, S.; Neale, B.; Todd-Brown, K.; Thomas, L.; Ferreira, M.A.; Bender, D.; Maller, J.; Sklar, P.; De Bakker, P.I.; Daly, M.J.; et al. PLINK: A tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* **2007**, *81*, 559–575. [\[CrossRef\]](#) [\[PubMed\]](#)
76. Purcell, S. *PLINK 1.9*; Center for Human Genetic Research: Boston, MA, USA; Massachusetts General Hospital: Boston, MA, USA; Broad Institute of Harvard & MIT: Cambridge, MA, USA, 2017; Available online: <https://zzz.bwh.harvard.edu/plink/index.shtml> (accessed on 21 April 2025).
77. DataCamp. Principal Component Analysis in R Tutorial. In *Tutorials, R Programming*; DataCamp, Inc.: New York, NY, USA, 2023; Available online: <https://www.datacamp.com/tutorial/pca-analysis-r> (accessed on 21 April 2025).
78. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*; Springer: New York, NY, USA, 2009; ISBN 978-0-387-98141-3. [\[CrossRef\]](#)
79. GitHub. *ggplot2*. Tidyverse, GitHub, Inc.: San Francisco, CA, USA, 2023. Available online: <https://github.com/tidyverse/ggplot2> (accessed on 21 April 2025).

80. R Core Team. *R-4*, R Foundation for Statistical Computing: Vienna, Austria, 2020. Available online: <https://cran.r-project.org/src/base/R-4/> (accessed on 21 April 2025).
81. GitHub. *qqman*, GitHub, Inc.: San Francisco, CA, USA, 2024. Available online: <https://github.com/qqman> (accessed on 21 April 2025).
82. Turner, S.D. qqman: An R package for visualizing GWAS results using Q-Q and Manhattan plots. *J. Open Source Softw.* **2018**, *3*, 731. [CrossRef]
83. NCBI. *Gallus gallus Genome Assembly GRCg6a. Genome*; National Library of Medicine: Bethesda, MD, USA, 2018. Available online: https://ncbi.nlm.nih.gov/datasets/genome/GCF_000002315.6/ (accessed on 21 April 2025).
84. NCBI. *Gallus gallus (Chicken). Genome*; National Library of Medicine: Bethesda, MD, USA, 2024. Available online: <https://www.ncbi.nlm.nih.gov/datasets/genome/?taxon=9031> (accessed on 21 April 2025).
85. Kinsella, R.J.; Kähäri, A.; Haider, S.; Zamora, J.; Proctor, G.; Spudich, G.; Almeida-King, J.; Staines, D.; Derwent, P.; Kerhornou, A.; et al. Ensembl BioMart: A hub for data retrieval across taxonomic space. *Database* **2011**, *2011*, bar030. [CrossRef]
86. Huang, D.W.; Sherman, B.T.; Lempicki, R.A. Systematic and integrative analysis of large gene lists using DAVID Bioinformatics Resources. *Nature Protoc.* **2009**, *4*, 44–57. [CrossRef]
87. Huang, D.W.; Sherman, B.T.; Lempicki, R.A. Bioinformatics enrichment tools: Paths toward the comprehensive functional analysis of large gene lists. *Nucleic Acids Res.* **2009**, *37*, 1–13. [CrossRef]
88. Ren, J.; Gao, Z.; Lu, Y.; Li, M.; Hong, J.; Wu, J.; Wu, D.; Deng, W.; Xi, D.; Chong, Y. Application of GWAS and mGWAS in livestock and poultry breeding. *Animals* **2024**, *14*, 2382. [CrossRef]
89. Sharma, A.; Lee, J.S.; Dang, C.G.; Sudrajat, P.; Kim, H.C.; Yeon, S.H.; Kang, H.S.; Lee, S.-H. Stories and challenges of genome wide association studies in livestock—A review. *Asian-Australas. J. Anim. Sci.* **2015**, *28*, 1371–1379. [CrossRef]
90. International Chicken Genome Sequencing Consortium. Sequence and comparative analysis of the chicken genome provide unique perspectives on vertebrate evolution. *Nature* **2004**, *432*, 695–716. [CrossRef]
91. Dodgson, J.B.; Romanov, M.N. The Chicken Genome: From Maps to Sequence. In Proceedings of the 8th International Symposium on Avian Endocrinology: Symposium Talk and Plenary Lecture Abstracts, Scottsdale, AZ, USA, 6–11 June 2004; Arizona State University: Scottsdale, AZ, USA, 2004; Abstract T26. Available online: <https://kar.kent.ac.uk/46516/> (accessed on 21 April 2025).
92. Haqani, M.I.; Nakano, M.; Nagano, A.J.; Nakamura, Y.; Tsudzuki, M. Association analysis of production traits of Japanese quail (*Coturnix japonica*) using restriction-site associated DNA sequencing. *Sci. Rep.* **2023**, *13*, 21307. [CrossRef]
93. Haqani, M.I.; Nomura, S.; Nakano, M.; Goto, T.; Nagano, A.J.; Takenouchi, A.; Nakamura, Y.; Ishikawa, A.; Tsudzuki, M. Mapping of quantitative trait loci controlling egg-quality and -production traits in Japanese quail (*Coturnix japonica*) using restriction-site associated DNA sequencing. *Genes* **2021**, *12*, 735. [CrossRef]
94. Lithgow, P.E.; O'Connor, R.; Smith, D.; Fonseka, G.; Rathje, C.; Frodsham, R.; O'Brien, P.C.; Ferguson-Smith, M.A.; Skinner, B.M.; Griffin, D.K.; et al. Novel Tools for Characterising Inter- and Intra-chromosomal Rearrangements in Avian Microchromosomes. In Proceedings of the 2014 Meeting on Avian Model Systems, Cold Spring Harbor, New York, NY, USA, 5–8 March 2014; Cold Spring Harbor Laboratory: Cold Spring Harbor, NY, USA, 2014; p. 56. Available online: <https://kar.kent.ac.uk/46692/> (accessed on 21 April 2025).
95. Sazanov, A.A.; Sazanov, A.L.; Nefedov, M.D.; Griffin, D.K.; Romanov, M.N. A pair of gametologous genes provides further insights into avian comparative cytogenomics. *Biologia* **2023**, *78*, 2737–2746. [CrossRef]
96. Tuttle, E.; Korody, M.; Lear, T.; Gonser, R.; Houck, M.; Ryder, O.; Romanov, M.; Balakrishnan, C.; Bergland, A.; Warren, W. Whole Genome Sequence of the Behaviorally Polymorphic White-throated Sparrow. 1: Mapping Genes for Sociogenomics. In Proceedings of the Evolution 2014 Conference, Raleigh, NC, USA, 20–24 June 2014; Society for the Study of Evolution (SSE): St. Louis, MO, USA; Society of Systematic Biologists (SSB): Windsor, WI, USA; American Society of Naturalists (ASN): Pacific Grove, CA, USA, 2014; p. 183. Available online: <https://kar.kent.ac.uk/46698/> (accessed on 21 April 2025).
97. Griffin, D.K.; Kretschmer, R.; Srikulnath, K.; Singchat, W.; O'Connor, R.E.; Romanov, M.N. Insights into avian molecular cytogenetics—With reptilian comparisons. *Mol. Cytogenet.* **2024**, *17*, 24. [CrossRef] [PubMed]
98. Sazanov, A.A.; Sazanov, A.L.; Romanov, M.N.; Stekol'nikova, V.A.; Malewski, T.; Korczak, M.; Jaszcak, K.; Smirnov, A.F. Molecular Organization of Chicken Genome. In Proceedings of the Conference “Genomic and Microarray Analysis in Biology and Medicine”, Sucha Beskidzka, Poland, 25–28 June 2005; p. 26. Available online: <https://kar.kent.ac.uk/46616/> (accessed on 21 April 2025).
99. Jahuey-Martínez, F.J.; Martínez-Quintana, J.A.; Rodríguez-Almeida, F.A.; Parra-Bracamonte, G.M. Exploration and enrichment analysis of the QTLome for important traits in livestock species. *Genes* **2024**, *15*, 1513. [CrossRef]
100. Salvi, S.; Tuberossa, R. The crop QTLome comes of age. *Curr. Opin. Biotechnol.* **2015**, *32*, 179–185. [CrossRef]
101. Ji, H.; Xu, Y.; Teng, G. Predicting egg production rate and egg weight of broiler breeders based on machine learning and Shapley additive explanations. *Poult. Sci.* **2025**, *104*, 104458. [CrossRef]
102. Wolc, A.; Jankowski, T.; Arango, J.; Settar, P.; Fulton, J.E.; O'Sullivan, N.P.; Dekkers, J.C.M. Investigating the genetic determination of clutch traits in laying hens. *Poult. Sci.* **2019**, *98*, 39–45. [CrossRef]

103. Miao, X.; Huang, Z.; Liu, J.; Zhang, L.; Feng, Y.; Zhang, Y.; Li, D.; Ning, Z. Genomically selected genes associated with a high rate of egg production in Puan Panjiang black-bone chickens. *Animals* **2025**, *15*, 363. [\[CrossRef\]](#)
104. Lei, Q.; Zhang, S.; Wang, J.; Qi, C.; Liu, J.; Cao, D.; Li, F.; Han, H.; Liu, W.; Li, D.; et al. Genome-wide association studies of egg production traits by whole genome sequencing of Laiwu Black chicken. *Poult. Sci.* **2024**, *103*, 103705. [\[CrossRef\]](#)
105. Wang, D.; Tan, L.; Zhi, Y.; Bu, L.; Wang, Y.; Wang, Z.; Guo, Y.; Tian, W.; Xu, C.; Li, D.; et al. Genome-wide variation study and inter-tissue communication analysis unveil regulatory mechanisms of egg-laying performance in chickens. *Nat. Commun.* **2024**, *15*, 7069. [\[CrossRef\]](#)
106. Du, Y.; Liu, L.; He, Y.; Dou, T.; Jia, J.; Ge, C. Endocrine and genetic factors affecting egg laying performance in chickens: A review. *Br. Poult. Sci.* **2020**, *61*, 538–549. [\[CrossRef\]](#)
107. Zhao, X.; Nie, C.; Zhang, J.; Li, X.; Zhu, T.; Guan, Z.; Chen, Y.; Wang, L.; Lv, X.Z.; Yang, W.; et al. Identification of candidate genomic regions for chicken egg number traits based on genome-wide association study. *BMC Genom.* **2021**, *22*, 610. [\[CrossRef\]](#) [\[PubMed\]](#)
108. Fu, M.; Wu, Y.; Shen, J.; Pan, A.; Zhang, H.; Sun, J.; Liang, Z.; Huang, T.; Du, J.; Pi, J. Genome-wide association study of egg production traits in Shuanglian chickens using whole genome sequencing. *Genes* **2023**, *14*, 2129. [\[CrossRef\]](#) [\[PubMed\]](#)
109. Yi, G.; Shen, M.; Yuan, J.; Sun, C.; Duan, Z.; Qu, L.; Dou, T.; Ma, M.; Lu, J.; Guo, J.; et al. Genome-wide association study dissects genetic architecture underlying longitudinal egg weights in chickens. *BMC Genom.* **2015**, *16*, 746. [\[CrossRef\]](#)
110. Ma, X.; Ying, F.; Li, Z.; Bai, L.; Wang, M.; Zhu, D.; Liu, D.; Wen, J.; Zhao, G.; Liu, R. New insights into the genetic loci related to egg weight and age at first egg traits in broiler breeder. *Poult. Sci.* **2024**, *103*, 103613. [\[CrossRef\]](#)
111. Yang, S.; Ning, C.; Yang, C.; Li, W.; Zhang, Q.; Wang, D.; Tang, H. Identify candidate genes associated with the weight and egg quality traits in Wenshui green shell-laying chickens by the copy number variation-based genome-wide association study. *Vet. Sci.* **2024**, *11*, 76. [\[CrossRef\]](#)
112. Munoz-Sanjuan, I.; Smallwood, P.M.; Nathans, J. Isoform diversity among fibroblast growth factor homologous factors is generated by alternative promoter usage and differential splicing. *J. Biol. Chem.* **2000**, *275*, 2589–2597. [\[CrossRef\]](#) [\[PubMed\]](#)
113. Berradi, H.; Taouis, M.; Cassy, S.; Rideau, N. Glucokinase in chicken (*Gallus gallus*). Partial cDNA cloning, immunodetection and activity determination. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **2005**, *141*, 129–139. [\[CrossRef\]](#)
114. Li, G.; Yang, X.; Li, J.; Zhang, B. Genome-wide analysis of lncRNA and mRNA expression in the uterus of laying hens during aging. *Genes* **2023**, *14*, 639. [\[CrossRef\]](#)
115. Chen, X.; Li, X.; Zhong, C.; Jiang, X.; Wu, G.; Li, G.; Yan, Y.; Yang, N.; Sun, C. Genetic patterns and genome-wide association analysis of eggshell quality traits of egg-type chicken across an extended laying period. *Poult. Sci.* **2024**, *103*, 103458. [\[CrossRef\]](#)
116. Rideau, N.; Berradi, H.; Skiba-Cassy, S.; Panserat, S.; Cailleau-Audouin, E.; Dupont, J. Induction of glucokinase in chicken liver by dietary carbohydrates. *Gen. Comp. Endocrinol.* **2008**, *158*, 173–177. [\[CrossRef\]](#)
117. Rideau, N.; Derouet, M.; Grimsby, J.; Simon, J. Glucokinase activation induces potent hypoglycemia without recruiting insulin and inhibits food intake in chicken. *Gen. Comp. Endocrinol.* **2010**, *169*, 276–283. [\[CrossRef\]](#) [\[PubMed\]](#)
118. Berradi, H.; Bernadet, M.D.; Guy, G.; Rideau, N. Expression of the glucokinase gene in mule duck liver and glucokinase activities in chicken and mule duck livers. *Poult. Sci.* **2007**, *86*, 2216–2220. [\[CrossRef\]](#) [\[PubMed\]](#)
119. Kanakachari, M.; Ashwini, R.; Chatterjee, R.N.; Bhattacharya, T.K. Embryonic transcriptome unravels mechanisms and pathways underlying embryonic development with respect to muscle growth, egg production, and plumage formation in native and broiler chickens. *Front. Genet.* **2022**, *13*, 990849. [\[CrossRef\]](#)
120. Christensen, V.L.; Grimes, J.L.; Donaldson, W.E.; Lerner, S. Correlation of body weight with hatchling blood glucose concentration and its relationship to embryonic survival. *Poult. Sci.* **2000**, *79*, 1817–1822. [\[CrossRef\]](#)
121. Shanawany, M.M. Inter-relationship between egg weight, parental age and embryonic development. *Br. Poult. Sci.* **1984**, *25*, 449–455. [\[CrossRef\]](#)
122. Fathi, M.; Abou-Emera, O.; Al-Homidan, I.; Galal, A.; Rayan, G. Effect of genotype and egg weight on hatchability properties and embryonic mortality pattern of native chicken populations. *Poult. Sci.* **2022**, *101*, 102129. [\[CrossRef\]](#)
123. Duman, M.; Şekeroğlu, A. Effect of egg weights on hatching results, broiler performance and some stress parameters. *Rev. Bras. Cienc. Avic.* **2017**, *19*, 255–262. [\[CrossRef\]](#)
124. Siopes, T.D.; Millam, J.R.; Steinman, M.Q. Initiating egg production in turkey breeder hens: Thyroid hormone involvement. *Poult. Sci.* **2010**, *89*, 2265–2272. [\[CrossRef\]](#)
125. Liu, H.; Wang, L.; Guo, Z.; Xu, Q.; Fan, W.; Xu, Y.; Hu, J.; Zhang, Y.; Tang, J.; Xie, M.; et al. Genome-wide association and selective sweep analyses reveal genetic loci for FCR of egg production traits in ducks. *Genet. Sel. Evol.* **2021**, *53*, 98. [\[CrossRef\]](#)
126. Harms, R.H.; Waldroup, P.W. Length of laying cycle as influenced by dietary protein level. *Poult. Sci.* **1963**, *42*, 1195–1197. [\[CrossRef\]](#)
127. Arulnathan, V.; Turner, I.; Bamber, N.; Ferdous, J.; Grassauer, F.; Doyon, M.; Pelletier, N. A systematic review of potential productivity, egg quality, and animal welfare implications of extended lay cycles in commercial laying hens in Canada. *Poult. Sci.* **2024**, *103*, 103475. [\[CrossRef\]](#) [\[PubMed\]](#)

128. Bain, M.M.; Nys, Y.; Dunn, I.C. Increasing persistency in lay and stabilising egg quality in longer laying cycles. What are the challenges? *Br. Poult. Sci.* **2016**, *57*, 330–338. [\[CrossRef\]](#) [\[PubMed\]](#)
129. Yang, L.; Fan, X.; Tian, K.; Yan, S.; Xu, C.; Tian, Y.; Xiao, C.; Jia, X.; Shi, J.; Bai, Y.; et al. Dynamic expression profile of follicles at different stages in high- and low-production laying hens. *Genes* **2023**, *15*, 40. [\[CrossRef\]](#)
130. Bouvarel, I.; Nys, Y.; Lescoat, P. 12-Hen nutrition for sustained egg quality. In *Egg Chemistry, Production and Consumption*, Woodhead Publishing Series in Food Science, Technology and Nutrition, *Improving the Safety and Quality of Eggs and Egg Products*; Nys, Y., Bain, M., Van Immerseel, F., Eds.; Woodhead Publishing Ltd.: Sawston, UK, 2011; pp. 261–299. ISBN 9781845697549. [\[CrossRef\]](#)
131. Kazemi, V.; Zarghi, H.; Golian, A. The effect of dietary energy and nutrients density on performance, egg components, egg quality, and profits of Hy-Line W-36 during the peak stage of first laying cycle. *Ital. J. Anim. Sci.* **2022**, *21*, 1034–1046. [\[CrossRef\]](#)
132. Jahan, A.A.; Dao, T.H.; Morgan, N.K.; Crowley, T.M.; Moss, A.F. Effects of AM/PM diets on laying performance, egg quality, and nutrient utilisation in free-range laying hens. *Appl. Sci.* **2024**, *14*, 2163. [\[CrossRef\]](#)
133. Volyanskaya, A.R.; Akberdin, I.R.; Kulyashov, M.A.; Yevshin, I.S.; Romanov, M.N.; Shagimardanova, E.I.; Gusev, O.A.; Kolpakov, F.A. A bird's-eye overview of molecular mechanisms regulating feed intake in chickens—With mammalian comparisons. *Anim. Nutr.* **2024**, *17*, 61–74. [\[CrossRef\]](#)
134. Proszkowiec-Weglarz, M.; Dupont, J.; Rideau, N.; Gespach, C.; Simon, J.; Porter, T.E. Insulin immuno-neutralization decreases food intake in chickens without altering hypothalamic transcripts involved in food intake and metabolism. *Poult. Sci.* **2017**, *96*, 4409–4418. [\[CrossRef\]](#)
135. Bédécarrats, G.Y.; Hanlon, C. Chapter 7-Effect of lighting and photoperiod on chicken egg production and quality. In *Egg Innovations and Strategies for Improvements*; Hester, P.Y., Ed.; Academic Press: Cambridge, MA, USA; Elsevier: London, UK, 2017; pp. 65–75. ISBN 9780128008799. [\[CrossRef\]](#)
136. Roly, Z.Y.; Godini, R.; Estermann, M.A.; Major, A.T.; Pocock, R.; Smith, C.A. Transcriptional landscape of the embryonic chicken Müllerian duct. *BMC Genom.* **2020**, *21*, 688. [\[CrossRef\]](#)
137. Qin, N.; Fan, X.C.; Zhang, Y.Y.; Xu, X.X.; Tyasi, T.L.; Jing, Y.; Mu, F.; Wei, M.L.; Xu, R.F. New insights into implication of the SLIT/ROBO pathway in the prehierarchical follicle development of hen ovary. *Poult. Sci.* **2015**, *94*, 2235–2246. [\[CrossRef\]](#)
138. Gao, J.; Xu, W.; Zeng, T.; Tian, Y.; Wu, C.; Liu, S.; Zhao, Y.; Zhou, S.; Lin, X.; Cao, H.; et al. Genome-wide association study of egg-laying traits and egg quality in LingKun chickens. *Front. Vet. Sci.* **2022**, *9*, 877739. [\[CrossRef\]](#)
139. Liu, Z.; Zheng, Q.; Zhang, X.; Lu, L. Microarray analysis of genes involved with shell strength in layer shell gland at the early stage of active calcification. *Asian-Australas. J. Anim. Sci.* **2013**, *26*, 609–624. [\[CrossRef\]](#) [\[PubMed\]](#)
140. Yang, K.-T.; Lin, C.-Y.; Liou, J.-S.; Fan, Y.-H.; Chiou, S.-H.; Huang, C.-W.; Wu, C.-P.; Lin, E.-C.; Chen, C.-F.; Lee, Y.-P.; et al. Differentially expressed transcripts in shell glands from low and high egg production strains of chickens using cDNA microarrays. *Anim. Reprod. Sci.* **2007**, *101*, 113–124. [\[CrossRef\]](#) [\[PubMed\]](#)
141. Duan, Z.; Sun, C.; Shen, M.; Wang, K.; Yang, N.; Zheng, J.; Xu, G. Genetic architecture dissection by genome-wide association analysis reveals avian eggshell ultrastructure traits. *Sci. Rep.* **2016**, *6*, 28836. [\[CrossRef\]](#)
142. Sanchez-Ajofrin, I.; Iniesta-Cuerda, M.; Martin-Maestro, A.; Peris-Frau, P.; Garde, J.J.; Soler, A.J. The effect of maternal hyperthermia on oocyte quality in sheep. *Reprod. Domest. Anim.* **2018**, *53* (Suppl. S2), 192–193.
143. Jehl, F.; Désert, C.; Klopp, C.; Brenet, M.; Rau, A.; Leroux, S.; Boutin, M.; Lagoutte, L.; Muret, K.; Blum, Y.; et al. Chicken adaptive response to low energy diet: Main role of the hypothalamic lipid metabolism revealed by a phenotypic and multi-tissue transcriptomic approach. *BMC Genom.* **2019**, *20*, 1033. [\[CrossRef\]](#)
144. Yuan, J.; Wang, K.; Yi, G.; Ma, M.; Dou, T.; Sun, C.; Qu, L.-J.; Shen, M.; Qu, L.; Yang, N. Genome-wide association studies for feed intake and efficiency in two laying periods of chickens. *Genet. Sel. Evol.* **2015**, *47*, 82. [\[CrossRef\]](#)
145. Chen, A.; Zhao, X.; Zhao, X.; Wang, G.; Zhang, X.; Ren, X.; Zhang, Y.; Cheng, X.; Yu, X.; Wang, H.; et al. Genetic foundation of male spur length and its correlation with female egg production in chickens. *Animals* **2024**, *14*, 1780. [\[CrossRef\]](#)
146. Dou, D.; Shen, L.; Zhou, J.; Cao, Z.; Luan, P.; Li, Y.; Xiao, F.; Guo, H.; Li, H.; Zhang, H. Genome-wide association studies for growth traits in broilers. *BMC Genom. Data* **2022**, *23*, 1. [\[CrossRef\]](#)
147. Moroudi, R.S.; Mahyari, S.A.; Torshizi, R.V.; Lanjanian, H.; Masoudi-Nejad, A. Identification of new genes and quantitative trait loci associated with growth curve parameters in F2 chicken population using genome-wide association study. *Anim. Genet.* **2021**, *52*, 171–184. [\[CrossRef\]](#)
148. Wang, S.; Wang, Y.; Li, Y.; Xiao, F.; Guo, H.; Gao, H.; Wang, N.; Zhang, H.; Li, H. Genome-wide association study and selective sweep analysis reveal the genetic architecture of body weights in a chicken F₂ resource population. *Front. Vet. Sci.* **2022**, *9*, 875454. [\[CrossRef\]](#)
149. Abdalla, E.A.E.; Makanjuola, B.O.; Wood, B.J.; Baes, C.F. Genome-wide association study reveals candidate genes relevant to body weight in female turkeys (*Meleagris gallopavo*). *PLoS ONE* **2022**, *17*, e0264838. [\[CrossRef\]](#) [\[PubMed\]](#)
150. Yang, Q.; Liu, H.; Xi, Y.; Lu, Y.; Han, X.; He, X.; Qi, J.; Zhu, Y.; He, H.; Wang, J.; et al. Genome-wide association study for bone quality of ducks during the laying period. *Poult. Sci.* **2024**, *103*, 103575. [\[CrossRef\]](#)

151. Burge, S.; Kelly, E.; Lonsdale, D.; Mutowo-Muellenet, P.; McAnulla, C.; Mitchell, A.; Sangrador-Vegas, A.; Yong, S.Y.; Mulder, N.; Hunter, S. Manual GO annotation of predictive protein signatures: The InterPro approach to GO curation. *Database* **2012**, *2012*, bar068. [[CrossRef](#)]
152. Ye, H.; Ji, C.; Liu, X.; Bello, S.F.; Guo, L.; Fang, X.; Lin, D.; Mo, Y.; Lei, Z.; Cai, B.; et al. Improvement of the accuracy of breeding value prediction for egg production traits in Muscovy duck using low-coverage whole-genome sequence data. *Poult. Sci.* **2025**, *104*, 104812. [[CrossRef](#)]
153. Guo, Y.; Chen, Y.; Guo, H.; Wang, B.; Xiong, Y.; Ding, J.; Li, J. Genome-wide association study revealed candidate genes associated with egg-laying time traits in layer chicken. *Poult. Sci.* **2025**, *104*, 105255. [[CrossRef](#)]
154. Romanov, M.N.; Sazanov, A.A.; Moiseyeva, I.G.; Smirnov, A.F. Poultry. In *Genome Mapping and Genomics in Animals, Vol. 3: Genome Mapping and Genomics in Domestic Animals*; Cockett, N.E., Kole, C., Eds.; Springer: Berlin/Heidelberg, Germany; New York, NY, USA, 2009; pp. 75–141. ISBN 978-3-540-73834-3/978-3-540-73835-0. [[CrossRef](#)]
155. Yang, W.; Yu, S.; Song, D.; Lin, W.; Xu, H.; Lang, X.; Zhang, C.; Guo, L.; Chen, X. A genome-wide association study identified candidate genes associated with egg quality traits in Muscovy duck. *BMC Genom.* **2025**, *26*, 422. [[CrossRef](#)]

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