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Review Article

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Quantitative trait loci (QTL) and genetic parameters for economically important traits in chicken – A review

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ABSTRACT

The study was aimed at reviewing and summarization of previous findings on associated genomic loci and estimated genetic parameters for reproductive traits in chicken. It was approached by reviewing various journals, books, genome database and used various genome browsing tools to collect the required information. Most of the reviewed information sources indicated that reproductive traits in chicken are genetically correlated, have low heritability and are affected by several quantitative trait loci (QTLs) that are located either on the same or different chromosomes. Both autosomal and sex chromosomes had influence on those traits. The majority of the reviewed QTLs had big confidence intervals and carries several candidate genes for the studied traits. Fine mapping using advanced intercross lines can help to narrow down the confidence intervals and target major genes. The information provided in this article, can contribute to our understanding of the complex inheritance pattern of the traits underlying reproductive performance in chicken.

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INTRODUCTION

The application of modern biological techniques such as marker assisted selection in chicken breeding facilitates genetic improvement of egg production traits like age at first egg, egg production rate, number of eggs, and egg weight as such traits are sex limited and cannot be recorded in males. Through traditional breeding approach, the breeding values of sires are estimated based on their daughters' performances. The estimated breeding values are used for selection of best individuals for next generation. However, this method is time consuming and affects the rate of genetic progress. Furthermore, the heritability estimates for most egg production traits are low suggesting a strong environmental influence. This means that the phenotypes do not well represent the breeding values. In the presence of known genes or linked markers affecting traits of interest, marker assisted selection (MAS) could support the traditional breeding system. The problem of high generation interval, low heritability of traits, and the nature of the traits to be sex limited could be solved by selecting the best animals using molecular information at DNA level.

To apply major genes or linked markers in marker assisted selection, they must first be identified and mapped on the chicken genome. The level of phenotypic variance accounted for such genes or linked markers in egg production traits needs to be known. Quantitative trait loci (QTL) detection is an important step to identify genes that contribute to genetic variability. So far, 10817 QTLs have been deposited for different traits in chicken QTL database (https://www.animalgenome.org/cgi-bin/QTLdb/GG/index). Out of those QTLs, 2412 (22.3%) represent egg quality and 365 (3.4%) egg production traits such as number of eggs, egg weight, egg production rate, and age at sexual maturity.

Those QTLs affecting egg production traits were detected on various chromosomes [1-7].

Despite several efforts made globally to reveal genetic loci affecting those economically important traits, many of the major genes and their variants which are responsible for egg production traits in chicken have not been understood yet. There is still a need to make further investigations for detecting genomic regions explaining the majority of genetic variations in traits of interest.

Whole genome sequencing can provide comprehensive information on existing genetic polymorphisms in studied populations. However, due to cost reason, it is not always easy to perform whole genome sequencing; rather, specific regions of the genome are targeted to study effects on traits of interest.

For this, reviewing and summarization of previous findings on QTL detection and estimation of genetic and phenotypic parameters for economically important traits in chicken is very crucial to provide insight for further investigations targeting specific and most promising regions that might affect traits of interest.

Thus, the objective of this review was to provide compiled information on genomic loci associated with reproductive traits and genetic parameters estimated for those traits in chicken. Different sources such as journals, books and genome database were used to generate information. The findings were summarized in Tables. The paper is divided into eight main sections; Chicken genome, chicken as a model animal for genomic research, factors affecting egg production in chicken, heritability and correlations of egg production traits, quantitative trait loci, mapping populations for egg traits, QTLs for egg production traits and conclusion.

Chicken Genome

Chicken (Gallus gallus) was domesticated 8000 years ago in South East Asia: Thailand and Vietnam [8]. The aim of domestication was mainly for cock-fighting. Through time, man started to keep chicken for diversified uses: meat and egg production, income generation, and research purpose.

Chicken has 38 pairs of autosomal and 1 pair of sex chromosomes. The sex chromosomes of chicken are Z and W. Females have hetrogametic sex (ZW) and the males have homogametic sex (ZZ).

Chicken has a genome size of 1.2 billion bp, which is one-third of the genome size of mammals [9,10].

Chicken chromosomes are variable in size and they can be categorized into 9 cytogenetically distinguishable macrochromosomes and 30 cytogenetically indistinguishable microchromosomes. The difference in size of the chromosomes may affect many features. The microchromosomes are gene dense than the macro-chromosomes [8,10,11].

Chicken is the first agricultural animal its genome to be sequenced and the sequence information was primarily meant for boosting research in agriculture and medicine [9,12]. The consensus linkage map of the chicken genome spans 3800 cM and contains 1889 loci [10,13]. Total numbers of genes found in chicken are reported to be between 20,000 and 30,000 [14,15], and total single-nucleotides (SNPs) are 2.8 million [16].

Chicken as a Model Animal for Genomic Research

Chicken serves as a model animal for the molecular genetic analysis of all wild and domestic birds [13]. There are a number of reasons to use chicken as a model animal for genomic research. The genome sequencing is known. In chicken the red blood cells contain nucleus, therefore, there is a possibility to isolate DNA from nucleated red blood cell [8]. Chicken and human have high conserved synteny [10]. For instance human obesity related genes can be identified in chicken. Using genome comparative mapping approach, the genes can be localized in human genome.

The chicken is between the mammal and fish on the evolutionary tree [17] and shared a common ancestor with mammals 300 to 350 million years ago [18]. Therefore it is also a good model to study vertebrate evolution. The high reproduction rate and relatively low generation interval in chicken enable several generations of large families to be generated in a reasonable time frame. The availability of many lines is another reason to use chicken as a model animal for genomic research. This allows researchers to conduct line specific studies and cross different lines to produce different model animals. There is extensive diversity among domestic chickens that have been selected for different purposes. This makes chicken also good model for studying the genetic basis of phenotypic traits [16]. Chicken embryos can be easily accessed in eggs. This allows developmental study and genetic modification of embryo in vivo [9]. Chicken genes can be knocked down using new tools such as electroporation of chicken embryos and the use of RNAi [18].

Factors Affecting Egg Production in Chicken

Egg production traits in chicken are affected by a number of genes, environmental factors, and their interaction. Genetic components can be due to additive, dominance or epistatic effects of genes or gene combination. Breeders are most interested in the additive genetic components which are inherited from parents to offspring for several generations [19]. Hens start to lay eggs when they reach sexual maturity. Chicken can live and continue to lay eggs for many years, however, the productivity of many layers decline after two to three years.

Layers require balanced diet to sustain maximum egg production over time. Absence of adequate and balanced diet can affect hens' productivity. For instance, inadequate calcium consumption leads to poor egg production and lower egg shell quality.

Heritability and Correlations of Egg Production Traits

Gene variants contribute to the variability of egg production traits. Understanding the genetic contribution to the traits of interest is advantageous for further improvement of the animals. Heritability values of 0.31 to 0.69 and 0.28 to 0.60 were reported for number and weight of eggs, respectively, in outbred chicken populations [20 - 22]; whereas, a heritability of 0.03 to 0.21 and 0.18 to 0.42 were reported for the same traits, respectively, in crosses generated from inbred lines [23].

Understanding the level and direction of correlations between traits of economic importance is crucial to set appropriate breeding programs. Traits with high positive genetic and phenotypic correlations can be improved together genetically. In other words, genetic improvement for one trait can also improve the other trait. However, negative correlation between traits leads to opposite direction of improvement.

Sexual maturity of hens is negatively correlated to number of eggs, egg production rate, and body weight. Egg number and egg weight also show negative correlation. The body weight of hens positively correlates with egg weights and number of eggs [23 – 25].

Quantitative Trait Loci

Identification of quantitative trait loci (QTL) for production traits is the first step to identify the causative genes affecting traits of interest. In QTL mapping, the chromosomal regions that passed from parent to offspring are traced and individuals that inherited alternative chromosomal segments are checked if they differ with respect to the quantitative trait [26 - 28]. Since the beginning of chicken genetic research, a number of efforts have been made to detect and map QTL affecting economically important traits in chicken (Tables 1-6). Most of these QTLs have been mapped on autosomal macrochromosomes and Z chromosome implying that these chromosomes play major role in egg production than microchromosomes. Among the macrochromosomes, chromosome 1 and 4 contain the majority of the QTLs affecting egg production traits. On some chromosomes, the QTLs affected more than one trait at a time. The sizes of the confidence interval of the QTLs differ from QTL to QTL. Many of the egg production traits are represented by more than one QTL and most of the QTLs had only small effect on the traits.

Mapping Populations for Egg Traits

A QTL mapping experiment requires genetically and phenotypically different parental populations for the trait of interest [1,29,30]. If parents have extremely different phenotypic performance, e.g. low vs. high, the identification of QTLs can be expected. In that case QTL linked genotype groups in F_2 generations will show different performance for traits of interest.

The cross between layers and broilers are the most common type of mapping populations used in several QTL mapping studies in chicken [1 – 4]. The cross between White Leghorn and either Rhode Island Red [1 – 4], Broiler [5], Red Jungle fowl [6], or Cornish breeds [7] are the common crosses made between layers and broilers. Most of the previous studies used the three generation (G0, G1, G2) mapping populations for QTL detection [1 – 4, 23]. In most cases the parental lines (Go populations) are inbred and selected for one or more traits.

Table 1: QTLs detected for age at first egg (AFE)

Trait	Chr.	Position (CM)	Flanking markers (position in Mb)	a	d	V%	Cross	Reference
AFE	1	204	MCW0007 (65.9 Mb)-ADL0150 (67.1 Mb)	N.A.	N.A.	N.A.	RIR x WL	[4]
AFE	1	205	MCW0018 (63.8)	N.A.	N.A.	N.A.	Polish x RIR	[34]
AFE	3		ADL0155 (37.5 Mb)-MCW0004 (51.5 Mb)	N.A.	N.A.	N.A.	RIR x WL	[3]
AFE	15	28	MCW0031 (2.3)-MCW0226 (2.4 Mb)	7.03	N.A.	6	F_2-WL x RIR	[2]
AFE	27	70	STAT5B	N.A.	N.A.	N.A.	Beijing You chickens	[35]
AFE	Z	28	ADL0201 (32.1 Mb)-MCW0241 (34.2 Mb)	7.03	N.A.	6	F_2-WL x RIR	[2]
AFE	Z	65-137		N.A.	N.A.	N.A.	RIR x WL	[3]
AFE	Z		ADL0273 (26.1 Mb)-MCW0128(un) ADL0217 (38.9 Mb)	2.76	N.A.	6.8	RIR x WL	[3]

AFE: age at first egg; EPR: egg production rate; EN: number of eggs; EW: egg weight; a: additive effect; d: dominance effect; V: explained variance; N.A: not available; RIR: Rhode Island Red; WL: White Leghorn; BR: Broilers; RJF: Red Jungle Fowl; Mb positions are according to the ENSEMBL53 WASHUC2 Chicken Assembly.

Table 2: QTLs detected for egg production rate (EPR)

Trait	Chr.	Position (CM)	Flanking markers (position in Mb)	a	d	V%	Cross	Reference
EPR	1		MCW0145 (162 Mb)	N.A.	N.A.	N.A.	Polish x RIR	[34]
EPR	1	54	LEI0174 (64.9 Mb)	4.17	3.6	4	F_2-WL x RIR	[2]
EPR	1	205-208	LEI0174 (64.9 Mb)	N.A.	N.A.	N.A.	F_2-WL x RIR	[2]
EPR	1	128	ADL0307 (47.3 Mb)	N.A.	N.A.	N.A.	BR x BR BR x WL	[36]
EPR	1	283	MCW0068 (un)	N.A.	N.A.	N.A.	BR x BR BR x WL	[36]
EPR	1	386	LEI0139 (130.2 Mb)	N.A.	N.A.	N.A.	BR x BR BR x WL	[36]
EPR	4	78	LEI0095 (25.2 Mb)	N.A.	N.A.	N.A.	BR x BR BR x WL	[36]

AFE: age at first egg; EPR: egg production rate; EN: number of eggs; EW: egg weight; a: additive effect; d: dominance effect; V: explained variance; N.A: not available; RIR: Rhode Island Red; WL: White Leghorn; BR: Broilers; RJF: Red Jungle Fowl; Mb positions are according to the ENSEMBL53 WASHUC2 Chicken Assembly.

Table 3: QTLs detected for egg weight (EW)

Trait	Chr.	Position	Flanking markers	a	d	V%	Cross	Reference
		(CM)	(position in Mb)					
EW	1	72-122	MCW0010 (25.2 Mb)-ADL0019 (42.4 Mb)	-26.4	41.5	7.8	RJF x WL	[6]
EW	2	12	ADL0228 (un)-MCW0082 (un)	N.A.	N.A.	N.A.	WL x RIR	[1]
EW	2		MCW0247 (19.3 Mb)-ADL0217 (38.9 Mb)	N.A.	N.A.	5	RIR x WL	[3]
EW	3	233	MCW0004 (51.5 Mb)-ADL0306 (84.7 Mb)	N.A.	N.A.	N.A.	RIR x WL	[4]
EW	3		LEI0113 (106.4 Mb)	N.A.	N.A.	N.A.	Polish x RIR	[34]
EW	4	76	LEI0081 (62.1 Mb)-MCW0122 (76.4 Mb)	3.01	-0.6	17	W Lx RIR	[2]
EW	4	182-210	LEI0081 (62.1 Mb)-MCW0122 (76.4 Mb)				WL x RIR	[2]
EW	4	182-210	LEI0081 (62.1 Mb)-UMA4.034 (75.8 Mb)	2.74	-0.75	17.5	WL x BR	[5]
EW	4	206	LEI0081 (62.1 Mb)-UMA4.034 (75.8 Mb)	3.03	0.02	10.3	WL x BR	[5]
EW	4	138-141	ADL0266 (46.7 Mb)-MCW0170 (69.8 Mb)	N.A.	N.A.	N.A.	RIR x WL	[3]
EW	4	153-156	LEI0094 (51.6 Mb)	N.A.	N.A.	N.A.	RJF x WL	[6]
EW	4	173 – 230		N.A.	N.A.	14.5	RIR x WL	[3]
EW	4	186 – 197		N.A.	N.A.	16	RIR x WL	[3]
EW	4	204-207	MCW0180 (un)-MCW0170 (69.8 Mb)	N.A.	N.A.	N.A.	RIR x WL	[3]
EW	4		MCW0170 (69.8 Mb)	N.A.	N.A.	N.A.	Polish x RIR	[34]
EW	4		MCW0170 (69.8 Mb)	3.1	N.A.	16	RIR x WL	[3]
EW	4		MCW0170 (69.8 Mb)-MCW0129 (80.9 Mb)	3.2	N.A.	14.5	RIR x WL	[3]
EW	5	0	LEI0082 (10.2 Mb)	-0.05	2.11	5	WL x RIR	[2]
EW	5	32-35	LEI0082 (10.2 Mb)				WL x RIR	[2]
EW	9	1	LMU0006 (un)	-1.13	-0.59	3	WL x RIR	[2]
EW	9	53	LMU0006 (un)				WL x RIR	[2]
EW	Z	95-105	MCW0241 (34.2 Mb)-MCW0246 (un)	N.A.	N.A.	N.A.	RIR x WL	[3]
EW	Z		MCW258 (21.4 Mb)-MCW154 (35.6 Mb)	N.A.	N.A.	N.A.	RIR x WL	[3]
EW	Z		ADL0273 (26.1 Mb))-MCW0246(N.A)	1.9	N.A.	10	RIR x WL	[3]

EW: egg weight; a: additive effect: d: dominance effect; V: explained variance; N.A: not available; RIR: Rhode Island Red; WL: White Leghorn; BR: Broilers; RJF: Red Jungle Fowl; Mb positions are according to the ENSEMBL53 WASHUC2 Chicken Assembly.

Inbred animals have a number of advantages to be used for QTL mapping experiment because the parents are fixed for alterative QTL allele, there is high power to detect QTL and analysis is easy. Some of the disadvantages of using inbred animals for QTL mapping experiment are one has to wait many generations to produce highly inbred animals, it is costly, and the results of QTL cannot be directly applied in commercial breeds. First one has to check whether the QTLs are segregating in population of interest [31–33].

QTLs for Egg Production Traits

Age at first egg (AFE)

Ideal age at first egg is important for better life time performance of chickens. QTLs for age at first egg are presented in Table 1. QTLs were found on chromosomes 1, 3, 15, 27, and Z in experimental chicken populations derived from crosses between layers and broilers [2–4]. Two QTLs were located on GGA1 between the markers MCW0018 and ADL0150 [3–4,34]. GGA15 contains one QTL between the markers MCW0031 and MCW0226 [2]. This QTL has an additive genetic effect of + 7.03 days and explains 6% of the phenotypic variance. Chromosome Z contains two QTLs between the markers ADL0273 and MCW0241 [2 – 4]. The additive effects of the first and the second QTL are 7.03 and 2.76, and explained 6 and 6.8% of the phenotypic variance, respectively. In addition the STAT5B locus on chromosome 27 was associated with age at first egg [35].

Egg Production Rate (EPR)

Egg production rate refers to the number of eggs divided by the number of days during 169 to 280 days of production period. QTL for egg production rate was detected on chromosome 1 between the markers ADL0307 (47.3 Mb) and LEI0139 (130.2 Mb) in

Table 4: QTLs detected for number of eggs (EN)

Trait	Chr.	Position	Flanking markers	a	d	V%	Cross	Reference
		(CM)	(position in Mb)					
EN	1	149	ADL0019 (42.4 Mb)-ADL0150 (67.1 Mb)	-11.1	30.8	N.A.	Cornish x WL	[7]
EN	2	117	ADL0176 (37.1 Mb)-ADL0257 (46.2 Mb)	-25.9	14.8	N.A.	Cornish x WL	[7]
EN	4	200	LEI0081 (62.1 Mb)-UMA4.034 (75.8 Mb)	-3.2	2	6.2	WL x BR	[5]
EN	4		ADL0266 (46.7 Mb)-MCW0170 (69.8 Mb)	N.A.	N.A.	N.A.	RIR x WL	[3]
EN	4	210-213	UMA4.034 (75.8 Mb)				WL x BR	[5]
EN	5		MCW0090 (N.A)-MCW0038 (N.A)	N.A.	N.A.	N.A.	RIR x WL	[3]
EN	8		MCW0100 (19.1 Mb)-ADL0345 (N.A)	6.8	10.9	6	RIR x WL	[3]
EN	Z	73-105	ADL0273 (26.1 Mb)-MCW0241 (34.2 Mb)	N.A.	N.A.	N.A.	RIR x WL	[3]
EN	Z		MCW0241 (34.2 Mb)-MCW0246 (N.A)	-9	N.A.	9.8	RIR x WL	[3]
EN	Z		ADL0022 (4.2 Mb)-MCW0154 (35.6 Mb)	N.A.	N.A.	5	RIR x WL	[3]

EN: number of eggs; EW: egg weight; a: additive effect; d: dominance effect; V: explained variance; N.A: not available; RIR: Rhode Island Red; WL: White Leghorn; BR: Broilers; RJF: Red Jungle Fowl; Mb positions are according to the ENSEMBL53 WASHUC2 Chicken Assembly.

Table 5: QTLs detected for albumen weight, yolk weight, egg shell strength, egg shell thickness, egg shell weight, length of egg and shell percentage

Trait	Chr.	Position (cM)	Flanking markers	a	d	v%	Cross	Reference
Albumen weight	3	214-223	MCW0139	N.A	N.A	25,3	GIP x RIR	[37]
Albumen weight	4	4	LEI0081-UMA4.034	2.48	-0.67	16.1	WL x BR	[5]
Albumen weight	4	209	UMA4.0345	2.23	-0.69	18.5	WL x BR	[5]
Albumen weight	4	99-100	MCW0170	N.A	N.A	3.3	GIP x RIR	[37]
Yolk weight	3	213-223	MCW0139	N.A	N.A	26.2	GIP x RIR	[37]
Egg shell Strength	1	29	MCW0200	-0.01	0.25	5	WL x RIR	[2]
Egg shell Strength	4	36	LEI0125-LEI0076	-0.01	0.35	4	WL x RIR	[2]
Egg shell Strength	7	16	MCW0183- LEI0158	0.19	N.A	4	WL x RIR	[2]
Egg shell Strength	Z	47	MCW0154- LEI0254	0.21	N.A	3	WL x RIR	[2]
Egg Shell thickness	1	29	MCW0200	0.61	11.8	5	WL x RIR	[2]
Egg Shell thickness	1	263-267	MCW0145	N.A	N.A	21.9	GIP x RIR	[37]
Egg Shell thickness	4	182	MCW0114	N.A	N.A	7.5	GIP x RIR	[37]
Egg Shell thickness	7	29	MCW0092-ADL0169	7.75	-2.3	4	WL x RIR	[2]
Egg Shell thickness	Z	36	LEI0229	8.72		2	WL x RIR	[2]
Egg Shell Weight	1	27	LEI0088- MCW0200	N.A	0.21	4	WL x RIR	[2]
Egg Shell Weight	1	256-267	MCW0145	N.A	N.A	31.1	GIP x RIR	[37]
Egg Shell Weight	4	41	LEI0125-LEI0076	0.15	0.2	5	WL x RIR	[2]
Egg Shell Weight	5	0	LEI0082	-0.05	2.11	5	WL x RIR	[2]
Egg Shell Weight	Z	36	LEI0229	8.72	N.A	2	WL x RIR	[2]
Egg Shell Weight	Z	47	MCW0154- LEI0254	0.21	N.A	3	WL x RIR	[2]
Egg Shell Weight	Z	96	LEI0075- LEI0123	12	N.A	3	WL x RIR	[2]
Long Length of Egg	4	36	LEI0125- LEI0076	-0.01	0.35	4	WL x RIR	[2]
Long Length of Egg	4	41	LEI0125- LEI0076	0.15	0.2	5	WL x RIR	[2]
Long Length of Egg	4	81	MCW0122	0.54	-0.53	5	WL x RIR	[2]
Long Length of Egg	7	15	MCW0183- LEI0158	-0.14	-1.16	4	WL x RIR	[2]
Short Length of Egg	4	75	LEI0081- MCW0122	0.83	0.04	16	WL x RIR	[2]
Percentage shell	4	209	UMA4.034	-0.23	0.19	6.7	WL x BR	[5]

a: additive effect; d: dominance effect; GIP: Green-legged Partrigenous breed; V: explained variance; N.A: not available; RIR: Rhode Island Red; WL: White Leghorn; BR: Broilers; RJF: Red Jungle Fowl; Mb positions are according to the ENSEMBL53 WASHUC2 Chicken Assembly.

populations derived from a cross of White Leghorn with either Rhode Island Red or broiler [2, 36]. The additive and dominance genetic effects and variance explained by the QTL were 4.17, 3.6, and 4%, respectively. Another QTL for egg production rate was reported on chromosome 4 at 25.2 Mb where the marker LEI0095 is located (Table 2).

Egg weight (EW)

The weight of eggs is correlated with body weight at hatch. Individuals hatched from heavier eggs expected to have higher body weight at hatch. QTLs were reported for egg weight on chromosomes 1, 2, 3, 4, 5, 9, and Z in chicken populations

Table 6: QTLs detected for egg shell color, lightness, redness, and yellowness

Trait	Chr.	Position (cM)	Flanking markers	a	d	v%	Cross	Reference
Egg shell color	2	230	BCL2-ADL0267	2.6	-2.8	5.2	WL x BR	[5]
Egg shell color	2	254	ADL0267-LEI0147	2.9	-3	5.3	WL x BR	[5]
Egg shell color	4	219	UMA4.034-ADL0260	2.7	-2.9	5	WL x BR	[5]
Egg shell color	5	56-57	MCW0032	N.A	N.A	7.4	GIP x RIR	[37]
Lightness	6	0	LEI0192	1.18	-1.17	4	WL x RIR	[2]
Lightness	11	19	LEI0072- LEI0214	-1.16	3.19	10	WL x RIR	[2]
Redness	6	0	LEI0192	-1	0.9	6	WL x RIR	[2]
Redness	11	19	LEI0072- LEI0214	0.84	-2.56	19	WL x RIR	[2]
Yellowness	6	0	LEI0192	-1.51	1.02	4	WL x RIR	[2]
Yellowness	11	19	LEI0072- LEI0214	0.97	-3.74	13	WL x RIR	[2]

a: additive effect; d: dominance effect; GIP: Green-legged Partrigenous breed; V: explained variance; N.A: not available; RIR: Rhode Island Red; WL: White Leghorn; BR: Broilers; RJF: Red Jungle Fowl; Mb positions are according to the ENSEMBL53 WASHUC2 Chicken Assembly.

derived from crosses between White Leghorn and either Rhode Island Red [1 - 4], Broiler [2], Red Jungle fowl [6] or Cornish breeds [7]. The flanking markers of the QTLs are MCW0010 and ADL0019 (GGA1), MCW0247 and ADL0219 (GGA2), MCW0004 and LIE0113 (GGA3), ADL0266 and MCW0129 (GGA4), LEI0082 (GGA5), LMU0006 (GGA9), and MCW258 and MCW154 (GGAZ). The additive and dominance genetic effects ranged from -1.13 to 3.2 and -0.75 to 2.11 g, respectively. The QTLs explained 3 to 17.5% of phenotypic variances (Table 3).

Number of Eggs (EN)

QTL affecting numbers of eggs were previously identified on chromosomes 1, 2, 4, 5, 8, and Z in an experimental chicken population derived from a cross of White Leghorn with either Rhode Island Red, broiler or Cornish breeds [3 - 5, 7]. These QTLs were found between the markers ADL0019 and ADL0150 (GGA1), ADL0176 and ADL0257 (GGA2), ADL0266 and UMA4.034 (GGA4), MCW0090 and MCW0038 (GGA5), MCW0010 and ADL0345 (GGA8), and ADL0022 and MCW0154 (GGAZ). The additive and dominance genetic effects of the QTL affecting number of eggs ranged from -25.9 to 6.8 and 2 to 30.8, respectively (Table 4).

QTLs for Egg Quality Traits

Egg quality traits such as shell thickness (ST), shell weight (SW), shell strength, (SS), albumen weight (AW), and yolk weight (YW) are affected by several genes. QTLs affecting those quality traits were discovered on chromosomes 1, 3, 4, 5, 6, 7, 11, and Z in chicken populations derived from crosses between White Leghorn and either Rhode Island Red [2], or Broiler [5] and between Green-legged Partrigenous and Rhode Island Red breeds [37]. Additive genetic effects of the QTLs ranged from -0.23 to 12 and the dominance effects ranged from -2.3 to 11.8. The variance explained by the QTLs ranged from 2.0 to 31.1% (Table 5).

Similarly, egg quality traits such as shell color (SC), lightness, redness, and yellowness, are affected by several genes. QTLs affecting those quality traits were discovered on chromosomes 2, 4, 5, 6, and 11 in chicken populations derived from crosses between White Leghorn and either Rhode Island Red [2], or Broiler [5] and between Green-legged Partrigenous and Rhode Island Red breeds [37]. Additive genetic effects of the QTLs ranged from -1.51 to 2.9 and the dominance effects ranged from -3.74 to 3.19. The variance explained by the QTLs ranged from 4.0 to 19% (Table 6).

Candidate Genes

Candidate genes are genes which map in QTL region. In most cases, a QTL region contains several candidate genes that might have direct or indirect influences on quantitative traits [38–39]. Previous studies discovered a number of candidate genes associated with economically important traits in chicken (Table 7).

Candidate genes like chicken prolactin (PRL), (PEPCK-M), autosomal recessive dwarf (adw), PRLpro2, CR523443, vasoactive intestinal peptide receptor-1 (VIPR-1), ovocalyxin-32 (OCX-32), gonadotropin-releasing hormone receptor (GnRHR), and neuropeptide Y (NPY), were reported as a potential genetic loci associated directly or indirectly with egg production traits [40 – 49]. The chicken CLOCK gene which regulates the circadian rhythm can also affect egg production. The gene HPGDS (Hematopoietic prostaglandin-D synthase) has shown different expression levels between layers and broilers [45]. The gene ovocleidin-116 was associated with shell thickness and egg shape [50]. Hens' growth is directly related to egg production; therefore, candidate genes associated with growth are also interesting molecular tools for marker assisted selection. Candidate genes such as apoVLDL-II, PIT1, Insulin (INS), Spot14α, and the Insulin-like growth factor binding protein 2 (IGFBP2) are known to be associated with growth in chicken [41, 51 – 54].

Marker Phenotype Association

Association between a given marker and phenotype exists when there is a significant mean difference in the phenotype between animal groups carrying different genotypes of the marker. Those molecular markers which are known to directly affect phenotypic traits or those linked to a QTL can be used in marker assisted selection (MAS). Such markers serve as labels of genomic regions affecting the trait of interest. They are unaffected by environmental conditions. Therefore, selection for linked markers can enhance the speed and effectiveness of

Table 7: Description and chromosomal location of candidate genes associated with egg production

Gene	Description	Associated trait	Chr.	Position in Mb	Gene ID	Reference
adw	Autosomal recessive dwarf	Number of eggs	1	N.A.	N.A.	[48]
BDH	3-Hydroxybutyrate dehydrogenase (heart, Mito.)	Number of eggs	9	13.7	424891	[40, 45]
CR523443a candidate gene for QTL	ST53 wk in the chicken	Shell thickness	4	N.A.	2937322	[44]
GnRHR	gonadotropin-releasing hormone receptor	Number of eggs	10	22.1	427517	[46]
NCAM1	Neural cell adhesion molecule 1	Number of eggs	24	6.0	770798	[40, 45]
NPY	neuropeptide Y	Number of eggs	2	31.4	396464	[47]
OCX-32	ovocalyxin-32	Number of eggs	9	N.A.	395209	[46]
OC-116	ovocleidin-116	Shell thickness, Egg shape	4	47.5	N.A.	[50]
PCDHA@	Protocadherin alpha cluster carboxykinase	Number of eggs	N.A.	N.A.	100126833	[40, 45]
PGDS	Prostaglandin-D synthase, hematopoietic	Number of eggs	4	38.3	395863	[40, 45]
PLAG1	Pleiomorphic adenoma gene 1	Number of eggs	2	114.9	429484	[40, 45]
PRL	chicken prolactin	Number of eggs , broodiness	2	59.7	396453	40, 45]
PRLpro2	Prolactin and prolactin receptor gene	against broodines	2	59.7	N.A.	[42]
SAR1A,	SAR1a gene homolog 1 (S. cerevisiae)	Number of eggs	6	12.5	423711	[40, 45]
SCG2	Secretogranin II (chromogranin C)	Number of eggs	9	9.2	424808	[40, 45]
STMN2	Stathmin-like 2	Egg production	2	125.4	396095	[40, 45]
VIPR-1	Vasoactive intestinal peptide receptor-1	against broodines	2	N.A.	395329	[49]

Where: N.A: not available/unknown

progress in animal breeding [55]. When a molecular marker is in association with phenotypic traits, either the marker is a causative polymorphism (direct marker) or it is in linkage disequilibrium (LD) with the causative polymorphism (indirect marker) [14]. Linkage disequilibrium is a situation where two markers are always (with high probability) inherited together. On the opposite, in Linkage equilibrium, markers are inherited independently. Due to the recombination event, the linkage disequilibrium between markers and causative polymorphisms might be broken down [14]. This condition may not always guarantee the utilization of associated markers in MAS.

Previous studies discovered a number of markers which are strongly associated with economically important traits in chicken. For instance, ADL0023 which is located on GGA5 at 104 cM, is associated with number of eggs and egg weight [56]. LEI0146 and MCW0043 which are located on GGA1 are associated with autosomal dwarf locus [57]. Markers like ADL0146, ADL0290, and ADL0298 are associated with immune response in chicken [58].

The degree of association between genes or markers with economically important traits can be affected by sample size of the animals, breed, direction of cross, number of markers used, the quality of the phenotypic data, and statistical model. Therefore, the above mentioned candidate genes or regions need to be tested in populations of interest before they can be applied in marker assisted selection.

Genomic Selection

In a traditional animal breeding program, parents are selected based on their breeding values which are estimated from phenotypic and pedigree records. The lower accuracy of the breeding value estimation using traditional animal breeding can be improved by information on variations at DNA level [59]. Selection at DNA level allows faster genetic gain than using only phenotypic information [60]. Several efforts have been made in the past to use marker assisted selection (MAS). However, implementation of this method remained limited and enabled only a small increase in genetic gain [59].

The availability of several thousands of SNP markers in livestock genome makes it possible to use genomic selection for breeding value estimation. Genomic or whole genome selection is a new and powerful method of genetic improvement. It utilizes genome-wide dense markers to predict the total breeding values of animals [59, 61]. In genomic selection, the total breeding values of animals can be more accurately predicted. For instance, using a simulation study, an accuracy of 0.85 for breeding value estimation was previously reported [59, 62]. Unlike in marker assisted selection (MAS) where the effects of only few QTLs are considered, in genomic selection the effects of all genes in the genome can be used to select potential parents for next generation. Genomic selection is the future of genetic improvement in both plant and animals. It increases genetic gain by increasing the accuracy of selection

and by reducing generation intervals [60, 63]. In comparison to traditional breeding, if established genomic selection requires lower number of animals for predicting breeding values. The breeding values estimated using genomic selection will be more reliable than values obtained using the traditional breeding method, as the former method employs genomic information at higher accuracy.

Some of the limitations of genomic selection are the need of large number of markers and the higher cost of genotyping [59]. Furthermore, the method is new, not fully tested and proved. In a first phase, a high number of animals genotyped are needed to estimate SNP effects at high precision. Genomic selection can be done only for those species, where dense marker maps are available.

CONCLUSION

The compiled information in this review article showed that reproductive traits in chicken are genetically correlated, have low heritability and are affected by several quantitative trait loci (QTLs) that are located either on the same or different chromosomes. Both autosomal and sex chromosomes had influence on those traits. The reviewed QTLs had different degree of influence on the phenotypic variance of the studied reproductive traits. In most cases, a single trait was affected by more than one QTL and some QTLs did affect more than one trait. Many of the reviewed QTLs had big confidence intervals and carry several candidate genes. This shows that further fine mapping of the QTL regions is required to narrow down the intervals and identify the major genes. The high accumulation of recombination events in an advanced intercross population makes those animals of choice for fine mapping and candidate gene identification. Most of the reviewed QTLs were detected in the cross between commercial lines. So, those QTLs need to be confirmed in production populations before they can be recommended for marker assisted selection.

Generally, the compiled information provided in this review article can enhance our understanding on the genetic determination of reproductive traits, mode of inheritance, and magnitude of effects which can further be used to dissect the genomic components to identify the underlying DNA variants.

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