

# The study of candidate genes in the improvement of egg production in ducks – a review

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**ABSTRACT** Duck is the second-largest poultry species aside from chicken. The rate of egg production is a major determinant of the economic income of poultry farmers. Among the reproductive organs, the ovary is a major part of the female reproductive system which is highly important for egg production. Based on the importance of this organ, several studies have been carried out to identify candidate genes at the transcriptome level, and also the expression level of these genes at different tissues or egg-laying conditions, and single nucleotide polymorphism (SNPs) of genes associated with egg production

in duck. In this review, expression profile and association study analyses at SNPs level of different candidate genes with egg production traits of duck were highlighted. Furthermore, different studies on transcriptome analysis, Quantitative Trait Loci (QTL) mapping, and Genome Wide Association Study (GWAS) approach used to identify potential candidate genes for egg production in ducks were reported. This review would widen our knowledge on molecular markers that are associated or have a positive correlation to improving egg production in ducks, for the increasing world populace.

**Key words:** egg production, candidate genes, expression profile, single nucleotide polymorphism (SNPs), transcriptome sequencing, QTL mapping, GWAS

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## INTRODUCTION

Muscovy duck is native to tropical areas of Central and South America (Stahl, 2008), with a strong adaptation ability, fertility, and high meat yield (Cui et al., 2019). Different varieties of Muscovy duck have been identified which include Jiaji Duck that is formerly raised at Jiaji Town, Qionghai Country, Hainan Province (Gu et al., 2020), Black Muscovy (Hu et al., 2021), and White Muscovy (Bao et al., 2020). However, in China, black and white Muscovy ducks are vastly raised.

The Domestic Muscovy duck is one of the most economically important poultry species across the globe due to its distinct meat quality and low-calorie content (Ye et al., 2019a). Aside from Muscovy duck, almost all other domesticated ducks descended from Mallard

(*Anas Platyrhynchos*) (Veeramani et al., 2016). Moreover, Muscovy duck does not require swimming water for survival, and optimum hatchability performance due to its tolerant to hot weather is much better than Pekin duck (Zeng et al., 2013), and this has made it possible to rear them in either traditional extensive or cage system (Harun et al., 1998). However, the long incubation period (35 d) and excess broodiness have led to a decline in egg production, and low development of the Muscovy duck industry (Jiang et al., 2010). Persistent nesting, tilting head backward, clucking, and nest defense are distinct incubation of the Muscovy duck (Wu et al., 2014d). The peak of egg production of Muscovy is between 35 and 53 wk (Ye et al., 2017). Despite all these factors, these ducks have been raised on a large scale due to the high demand for duck eggs and meats by consumers couple with continuous improvement of the standard of living. More so, it has been reported by Statistics of National Waterfowl Industrial Technology System of China in 2019 that there were 187 million laying ducks in China, and the total output of duck eggs was 3.0934 million tons.

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Domesticated Muscovy duck is one of the poultry species categorized as a local bird in Africa and one of the most famous waterfowl species in Nigeria (Adeola et al., 2020). Moreover, it is one of the most famous types of duck in India due to its outstanding meat quality and taste (Kameshpandian et al., 2018). Due to their high population in India, they are called by different names which include Moti, Kadna Hans, and China han in Odisha (Padhi, 2014) and Chinae haras, Cina hanh, Bor China, and Bhatt China in Northeast India (Alyethodi et al., 2010; Banerjee, 2013).

The reproductive performance which is an important economic trait of poultry species is mainly determined by egg production (Bao et al., 2020). The key objective of duck breeders is to increase egg production, although this trait is affected by many factors ranging from nutrition, environment, disease, gene expression, and others (Hu et al., 2021) as shown in Figure 1 (Although, we reviewed only about the genetic factors). Using traditional breeding techniques, reproductive traits of laying duck have been progressively improved although, an obviously significant improvement has not been recorded (Zhu et al., 2017).

Egg production is a polygenic trait that is affected by both genetic and environmental factors. It involves a multifactorial interaction of genes that control energy metabolism, protein synthesis, and storage processes, this phenomenon depends on different organs involved in reproduction (Su et al., 1999). Moreover, this is regulated by several physiological processes that require the coordination of the hypothalamus-pituitary-gonadal (HPG) axis for successful procreation (Ye et al., 2019b). This axis regulates the reproductive and endocrine systems in laying hens (Padmanabhan et al., 2002), and also initiates the maturation of the ovary (Ouyang et al., 2020). In poultry species, the hypothalamus regulates reproduction activity through the secretion of gonadotropin-releasing hormone-1 (GnRH-1) that triggers the adenohypophysis (anterior pituitary gland) to enable the release of Luteinizing hormone (LH) and follicle stimulating hormone (FSH). These gonadotropins enable the gonads to stimulate

gametogenesis and sex steroid hormone secretion from the specialized cell in the left ovary (Mishra et al., 2020; Figure 2). The ovary is a major part of the female reproductive system which is highly important for the regulation of oocyte development, follicle maturation, and release of sex hormones for ovulation (Eppig et al., 2002), and also an important organ that affects egg-laying (Natesampillai et al., 2008; Xu et al., 2018). Estrogen that is mainly secreted by granulosa cells in the ovary also transfers endocrine signals to other tissues (Nelson and Bulun, 2001). Based on the role of the ovary in reproduction, several studies have been carried out using this organ to identify candidate genes at the transcriptome level, expression level, and single nucleotide polymorphism (SNPs) of genes associated with egg production in ducks (Ni et al., 2007a; Asiamah Amponsah et al., 2019; Asiamah et al., 2022; Figure 1).

In this review, we focus on reports of different studies on candidate genes responsible for egg production in ducks. This would widen our knowledge on molecular markers that are being used to improve egg production for the increasing world populace.

## STUDIES ON EXPRESSION PROFILE AND SINGLE NUCLEOTIDE POLYMORPHISM OF CANDIDATE GENES ON EGG PRODUCTION

Having identified Muscovy ducks as one of the poultry species which has potentials for the production of eggs and meat, the low rate of egg production can be increased through genetic improvement through marker-assisted selection. Marker-assisted selection is based on the relationship that exists between DNA variation and specific genes that control a specific trait of interest. This has become an important technique in animal breeding for selecting high-laying performance ducks for genetic improvement. A candidate gene approach is useful for the understanding of the relationship that exists between various forms of a particular gene and quantitative trait loci (QTL) that are involved

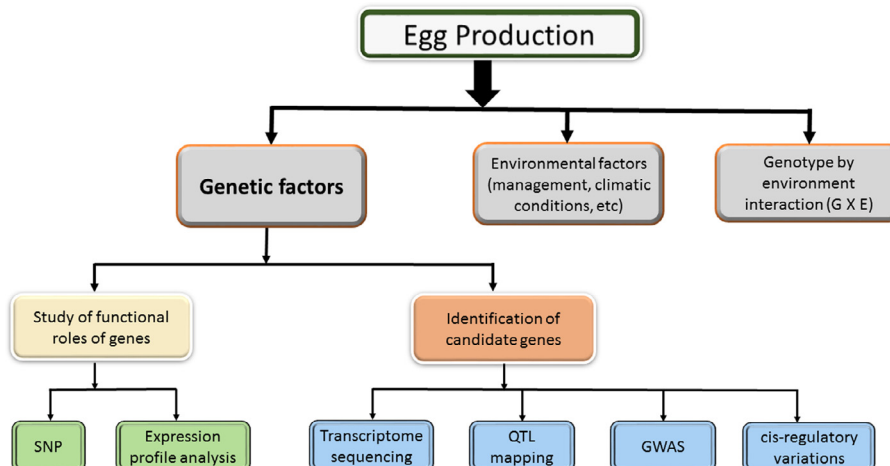
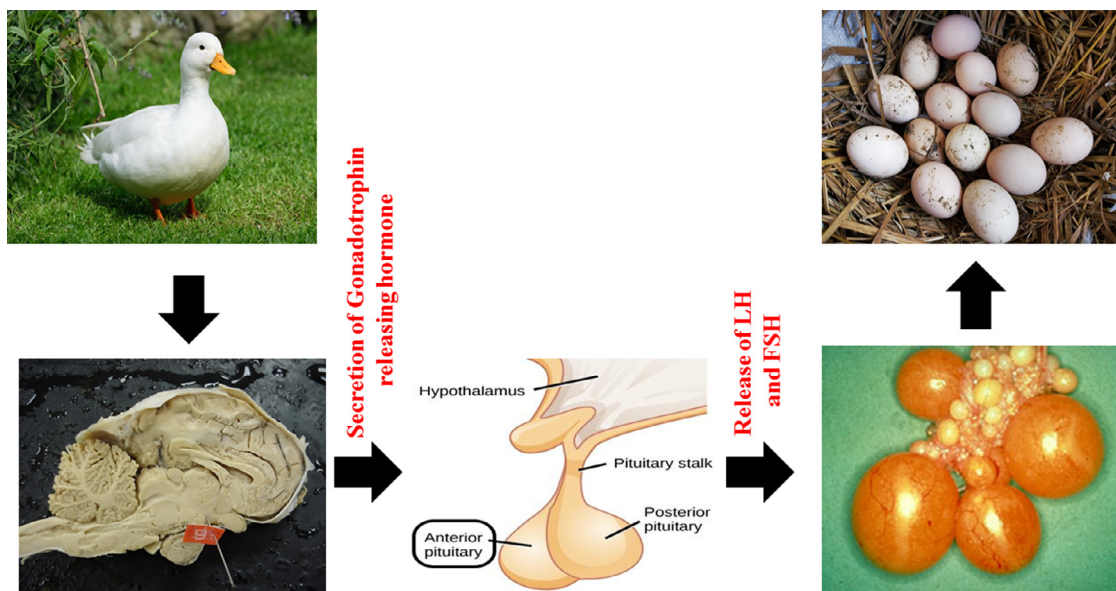


Figure 1. Approaches used to study/identify candidate genes responsible for egg production.



**Figure 2.** A chart showing the processes involved in egg production along HPG axis in poultry birds.

in the variation of economic traits of interest (Qin et al., 2015; Yuan et al., 2015).

Recently, the potential role of expressions of insulin-like growth factor-1 (**IGF-1**), prolactin receptor (**PRLR**), **FSH**, very low-density lipoprotein receptor (**VLDLR**), low-density lipoprotein receptor-related protein (**LRP**), estrogen receptor 1 (**ESR1**), luteinizing hormone receptor (**LHR**), and estrogen receptor 2 (**ESR2**) with egg traits have received serious attention (Yao et al., 2010; Wang et al., 2016; Asiamah Amponsah et al., 2019; Cui et al., 2019; Asiamah et al., 2022).

SNP is the difference that occurs among individuals at a single position in a DNA sequence. Due to their abundance and a high potential for automation, SNPs are the most commonly used molecular markers in genetic studies (Kumar et al., 2012). Moreover, SNPs have been used to identify genetic factors in different fields (Liao and Lee, 2010), including studies in animal and crop breeding (Lagudah et al., 2009; Schennink et al., 2009).

### Follicle-Stimulating Hormone

**FSH** plays a critical role in the regulation of several reproductive activities in avian. This gene stimulates the reproductive gland function of males and females by binding to its receptor (**FSHR**), which is located in the testis (sertoli cells) and ovary (granulosa cells), respectively (You et al., 1996; George et al., 2011). In a recent study, there was a significantly high expression of **FSH** in the egg-laying period compared with the pre-laying period (Huang et al., 2015). The SNP of the **FSH** gene were determined to be related to the reproductive traits of chickens (Li et al., 2011; Kang et al., 2012). In a study by Xu et al. (2017), molecular characterization, expression profile, and association study of **FSH** on egg production in Muscovy duck were studied. From their findings,

3 different Muscovy duck **FSHR** transcripts (**FSHRTV1**, **FSHRTV2**, and **FSHRT**) were identified. Based on the expression profile of **FSH** mRNA in 14 different selected tissues, the ovary had the highest expression level of **FSH** when compared to other tissues while obvious mRNA expression of **FSH** was observed in lung, liver, and abdominal fat (Xu et al., 2017). Also, the study by Liu et al. (2021c) on the expression level of **FSH** in 3 stages of laying of Peking and Black Muscovy duck, **FSH** decreased in the peak laying period of Peking duck while the expression level of **FSH** in the Black Muscovy duck at the peak stage of laying was extremely significant compared to early and late stages of laying (Liu et al., 2021c). Sixteen SNPs were identified within 2,860 bp region of the Muscovy duck **FSHR** gene (Xu et al., 2017). However, 4 variations (TS59C, T409G, C424G, and C428T) at the 5' flanking region and 8 (A112G, T125C, T13C, C72T, T231C, A54T, T42C, and A227G) in the intronic regions were detected among those identified SNPs. Moreover, 4 SNPs (C608T, A176G, C320T, and C1044G) were identified at the coding region while only one SNP (C1044G) caused a single amino acid substitution from leucine (L) to valine (V) (Xu et al., 2017). Based on the association analysis of 9 SNPs to 3 different egg production traits (age at first age [**AFE**], the number of the egg at 33 wk [**E33W**], and the number of the egg at 59 wk [**E59W**]), only 2 SNPs (C320T and A227G) were found in the exon and intron regions, respectively, these SNPs were significantly associated with Muscovy egg production traits (Xu et al., 2017).

### Growth Hormone

Growth hormone (**GH**) is secreted by the hypothalamic-pituitary-gonadal (**HPG**) axis and released into the bloodstream and participates in several differentiation processes in different tissues which includes the

stimulation of growth and development (Martínez-Moreno et al., 2011). Due to the function of *GH* in reproduction, Wu et al. (2014d) researched the expression, polymorphism, and association of this gene on egg production in White Muscovy duck. Only one polymorphism with genotypes AA, AG, and GG was found at intron 3 of the *GH* gene using Polymerase Chain reaction-Single strand conformation polymorphism (PCR-SSCP) method. Based on the expression profile using 12 different tissues (pituitary, hypothalamus, muscular stomach, glandular stomach, ovary, kidney, liver, heart, lung, duodenum, pancreas, and spleen), the mRNA level of *GH* in the pituitary recorded the highest expression among other tissues. Moreover, the polymorphic variants of *GH* had no significant difference in age at first laying (Wu et al., 2014d).

### **Dopamine Receptor 2 and Insulin Like Growth Factor 2**

Dopamine (*DA*) is an important neurotransmitter that exists in the nerve center and its peripheral tissue. Dopamine receptor 2 (*DRD2*) could assist in the secretion of reproductive hormones through *FSH* and *LH* in chicken (Youngren et al., 1996, 1998). In a study, it was reported that *IGF2* is highly expressed in the dominant follicle in mammals thereby supporting key roles in follicular development (Mao et al., 2004). Moreover, *IGF2* might regulate ovarian development through stimulation of *FSH* (Baumgarten et al., 2015).

Ye et al. (2017) investigated the expression profile and polymorphism of *IGF2* and *DRD2* with laying traits of Muscovy duck. Based on their study, the highest expression levels of *IGF2* were found in the kidney and ovary while *DRD2* expression had the highest in the ovary. Moreover, 5 SNPs (A-1864G, C-1704G, A-584G, A-227G, and A-183G) were identified in the 5' flanking region of *IGF2* while 28 SNPs were found in *DRD2*. However, only 2 SNPs and 11 SNPs of *IGF2* and *DRD2*, respectively, based on mixed pool sequencing results were considered most likely associated with egg-laying traits in their study. Moreover, 3 genotypes (AG, GG, and CC) were identified in A-18764G SNP with individuals with GG genotype had 6 to 7 eggs more than GG genotype individuals at E59W. Furthermore, the GG genotypes of C+3301G and G+3545G of the *DRD2* gene were advantageous for earlier egg-laying (Ye et al., 2017).

### **Low-Density Lipoprotein Receptor-Related Protein**

Low-density lipoprotein receptor-related protein (*LRP*) is one of the multitissue endogenous receptors which include *LRP5*, *LRP6*, *LRP8* gene are related to ovaries and follicles, and *LPR4*, *LPR5*, *LPR6*, *LPR8* gene can affect the reproduction of female animals through the regulation of the ovarian or follicular development (Magoori et al., 2003; Yao et al., 2010). The

expression of *LRP1* in Peking duck during the late laying stage was significantly higher than that in the early laying stage. However, the expression of *LRP1* was extremely significantly related to the decrease of laying in the peak laying stage of Black Muscovy duck (Liu et al., 2021c). Further, the *LRP8* gene is found related to duck reproductive potential and egg quality (Wang et al., 2013). Six nucleotide mutation sites in the coding region of the *LRP8* gene were found linked to egg production of which c.528C > T genotype were associated with egg production, age at first laying, and body weight at maturity (Wang et al., 2013). However, the c.1371A > G genotypes were only related to egg production. Moreover, the egg production was associated with 2 haplotype sites, which include c.528C > T and c.1371A > G that were associated with egg weight and egg yolk weight (Wang et al., 2013).

### **Estrogen Receptor**

Estrogen receptor (*ESR*) is an essential member of large family steroid hormone receptors which has 2 subtypes. This gene has been reported to play an important role in the ovary during the egg-laying stages and might be closely related to egg production in ducks (Wu et al., 2014b; Khristi et al., 2018). As reported by Couse et al. (2005), *ESR2* is crucial in granulosa cell differentiation and the response of ovulation to gonadotropins. The expression of *ESR1* was slightly higher in the peak laying stage than early and late laying stages in Black Muscovy duck (Liu et al., 2021c). However, the early laying stage had a significant expression of *ESR1* than that of the peak laying stage, although, the late laying stage was extremely significantly higher than that in the peak laying stage in Peking duck (Liu et al., 2021c). Previous reports confirmed that SNPs of *ESR1* (T1101C located on exon 4) gene were related to egg production in duck (Niu et al., 2017). *ESR2* participated in the regulation of reproductive hormone (Zou et al., 2020). In lieu of this, the functional roles of *ESR2* was investigated (Asiamah et al., 2022). Based on their study, 23 SNPs was identified and only SNPs g.56805646 T>C and exon 3-20 G>A were significant ( $P < 0.05$ ) related to egg weight. It is worth knowing that the ducks with CT and AG genotypes recorded significant ( $P < 0.05$ ) higher egg weight. In addition, the mRNA expression of *ESR2* was significantly more ( $P < 0.05$ ) in the ovary than the hypothalamus and pituitary.

### **Prolactin Receptor**

In general, the reactions of the 2 *PRLRs* with prolactin (*PRL*) can convey information (Goffin et al., 1998; Dalrymple and Jabbour, 2000), by controlling the estrus of the corpus luteum that regulates the estrus and nest behavior in poultry species (Grosdemouge et al., 2003). *PRLR* is also important for the regulation of follicular development which then enables the *IGF* gene family to control growth, follicle maturation, and atresia, selection

of dominant follicle, egg maturation, production of steroid hormones, and activity of corpus luteum (Armstrong and Hogg, 1996). Prolactin and its receptor have been reported to regulate follicle development and egg production (Wang et al., 2011b; Asiamah Ampon-sah et al., 2019). The expressions of *PRLR* were extremely significantly associated with an increase in laying at the peak laying stage which infers that *PRLR* might promote egg production in Black Muscovy duck (Liu et al., 2021c). Furthermore, the polymorphism of the *PRL* gene has shown that *PRL* might be a candidate gene that controls egg-laying parameters and reproduction in ducks (Wang et al., 2011b; Bai et al., 2019). Liu et al. (2012) reported that exon 6 of *PRLR* was significantly associated with egg production and age at first egg.

### Luteinizing Hormone Receptor

*LHR* belongs to the uncommon members of the G protein-coupled receptor (McFarland et al., 1989), which controls the development of follicles and secrete estrogen by coordinating the role of luteinizing hormone (Zhang et al., 1997). In laying birds, there is a periodic fluctuation in the expression levels of *LH* and *LHR* with ovulation activity (Liu et al., 2021c). Despite this, there was a gradual increase in expression of *LHR* during follicle development before ovulation, while there is a decline in the granulosa cells of the biggest follicle before ovulation, this reduction might be mediated by the steroids (Liu et al., 2021c). In a report by Yamamura et al. (2001), the high levels of *LH* might inhibit the expression of *LHR*. Different studies have reported that high expression of *LHR* might lead to high egg yield (Liu and Zhang, 2008). Due to the extremely significant expression of *LHR* in the peak laying stage of Peking duck and Black Muscovy duck, it was inferred that the *LHR* gene plays an important role in the regulation of egg-laying in Peking duck and Black Muscovy duck (Liu et al., 2021c). Moreover, expression of *LHR* in the ovary of Shaoxing duck increased consecutively on the first day, 30th day, 60th day, and 90th day which shows that *LHR* might be responsible for the regulation of egg production in Shaoxing duck (Ni et al., 2007a, b).

### Melatonin Receptor Genes

In poultry species, melatonin (N-acetyl-5-methoxytryptamine) which is mainly synthesized in the pineal gland participates in reproduction activities in poultry birds (Kumar Kharwar and Haldar, 2011; Yadav and Haldar, 2013; Trivedi and Kumar, 2014). In birds, 3 melatonin receptor subtypes namely; *MTNR1A*, *MTNR1B*, and *MTNR1C* have been cloned (Reppert et al., 1995; Li et al., 2013). In a recent study by Feng et al. (2018), seven novel polymorphism of melatonin (*MTNR1A*: g. 268C>T, *MTNR1B*: g. 41C>T, and g. 161T>C, *MTNR1C*: g. 10C>T, g. 24A>G, g. 108C>T, g. 363T>C) were detected in Shaoxing duck. Based on their

findings, there was a strong association between g. 268C>T of *MTNR1A* gene with age at first egg, the total number of eggs at 34 wk of age, and age at first egg. Moreover, there was a significant reduction of the mRNA expression of *MTNR1C* in the late-matured group when compared with the early-matured group. This shows that melatonin receptors might influence the age at the first egg and, also imply their function in the sexual mature of ducks (Feng et al., 2018).

### Very Low Density Lipoprotein Receptor Gene

*VLDR* belongs to the family of the *LDLR* gene (Nykjaer and Willnow, 2002). Wang et al. (2011a) reported that the *VLDR* gene was first isolated from the cDNA library of rabbit's heart and later cloned in chicken, human, mouse, cattle, and monkey. In similar to the *LDLR* gene, the *VLDR* gene has 5 functional domains (Willnow, 1999). This gene plays a significant role in different cellular processes which include cell proliferation, migration, and differentiation (Hussain, 2001). In chicken reproduction, *VLDR* gene plays a distinct role through the development of oocytes and deposition of yolk lipoprotein (Barber et al., 1991; Shen et al., 1993). Also, in the zebra finch, it was reported that expression of *VLDLR* mRNA has a major function in ascertaining variation among individuals in reproductive phenotype (for instance, follicle or egg size) (Han et al., 2009). Moreover, the phylogenetic tree showed that the evolutionary origin of duck *VLDR* proteins is closer to chicken and zebra finch than to other species (Wang et al., 2011a). Due to its role in reproduction, Wang et al. (2011a) studied its expression profile in 12 different tissues and also investigated its association with egg performance in duck using SNP. Based on their findings, it was reported that 2 *VLDLR* splice variants namely; *VLDLR-a* (with an O-linked sugar domain) and *VLDLR-b* (without) were present in the heart of the duck. The muscle tissue of duck has a high expression of *VLDLR-a*. However, there was significant expression of *VLDLR-b* in the ovary, pituitary gland, liver, spleen, lung, kidney, and intestine (Wang et al., 2011a). Based on their association analysis, the 2 haplotypes were significantly associated with 2 egg production traits namely, age at first egg, and body weight at first egg (Wang et al., 2011a). However, ducks with haplotype AT had a higher egg production at 210, 300, and 360 d egg production, and an earlier age for starting laying while those with haplotype CG had only higher body weight at the first (Wang et al., 2011a). In addition, a study by Liu et al. (2021c) on the expression of *VLDLR* in 3 different stages of egg-laying in Peking and Black Muscovy duck observed that there was an increase in the expression of *VLDLR* in the late laying stage of Peking duck nevertheless, it was not significantly different from the early and peak laying stages. However, this gene was extremely significantly associated with the increase of laying in the peak laying stage of black Muscovy duck (Liu et al., 2021c).

## Ovoinhibitor

According to Kinoshita et al. (2004), ovoinhibitor (*OIH*) is the major proteinase inhibitor present in egg white. This gene is secreted in the tubular gland cell of the oviduct, which is controlled by estrogen and progesterone (Liu et al., 1971). In the reproductive trait of turkey, *OIH* has been reported to control the microenvironment for the sperm in the epididymis and ductus deferens (Słowińska et al., 2014). Moreover, it was predicted that *OIH* might be related to the reproductive performance of birds. Based on this, Wu et al. (2018) studied the role of *OIH* in the ovaries of two breeds of duck namely; Jingjiang (JJ) and Shaoxing (SX) ducks at different laying stages, and also identified the SNP of the *OIH* gene associated with egg-laying traits. In their findings, the relative expression of *OIH* mRNA spontaneously increased during the laying period (from the first egg to 500 d of age). Nevertheless, there was a significant difference in the relative expression level of *OIH* mRNA in the ovaries between the 2 breeds from age at first egg and 180 d of age, although not at 500 d of age. Based on their SNPs study on the *OIH* gene, one novel mutation (G-A at the 389-nucleotide position 389G>A) was discovered at exon 5–6 using PCR-RFLP methods. Based on their association analysis, the egg production of the AG genotype ducks was significantly small at first egg compared with AA and GG counterparts in the JJ line I. However, the number of the egg at 72 wk was significantly different among AG, GG, and AA genotypes in JJ line II (Wu et al., 2018).

## TRANSCRIPTOMIC STUDIES ON EGG PRODUCTION IN DUCK

Since the invention of next-generation sequencing, a powerful, highly reproducible, and cost-efficient tool for transcriptomic studies (Li et al., 2014; Morozova and Marra, 2008). This technology allows the usage of RNA-seq for examining the functions of genes by discovering the gene expression in animal samples (Yu et al., 2016). Moreover, RNA-Seq allows the detection of differences in gene expression profiles among individuals in various developmental states (Tao et al., 2017). Due to its ability to sequence the complete set of transcripts in a cell or a tissue, it provides an effective method for identifying different phenotype-associated differentially expressed genes (DEGs) (Wang et al., 2017).

The application of transcriptomic studies on the ovaries has led to the discovery of DEGs related to egg production, and this would assist in the breeding of potential egg-laying ducks to meet the need of the increasing population and to improve the economic situation of farmers (Zeng et al., 2015; Zhu et al., 2017). Different studies have been carried out to identify potential genes responsible for egg production in different types of duck which include White Muscovy (Bello et al., 2021), Black and White Muscovy (Bao et al., 2020), Black Muscovy (Hu et al., 2021), Leizhou black (Zou et al., 2020), Longyun Shan-ma (Sun et al., 2020), Peking

(Ren et al., 2018), Jinding (Tao et al., 2017), and Shan Ma (Zhu et al., 2017) ducks as shown in Table 1.

Our recent study on transcriptome analysis of hypothalamus and ovaries of White Muscovy duck at 59 wk of laying revealed 10 potential genes that might be responsible for egg production (Bello et al., 2021). Based on our findings, 596 and 2,259 DEGs were found in the hypothalamus and ovary, respectively (Bello et al., 2021). It is already an established fact that the ovary of poultry birds has concourse effects of different genes that firmly control ovarian follicle and hormone secretion (Quan et al., 2019; Zou et al., 2020).

Black and White Muscovy duck are vastly raised in China. Bao et al. (2020) examined the transcriptome profiling of the ovary tissues between these 2 ducks using high and low egg production. Based on their findings, 113, 619, and 87 DEGs were identified in the Black high (BH) and White high (WH), Black low (BL) and BH, and BL and White low (WL), respectively. Based on their DEGs within the BH and BL, several genes such as *TGF $\beta$ 2*, *NGFR*, *CEBPD*, *CPEB2*, *POSTN*, *SMOC1*, *FGF18*, *EFNA5*, and *SDC4* that might be involved in the egg production of Muscovy duck were identified (Bao et al., 2020).

Hu et al. (2021) studied the transcriptome of the ovary of black Muscovy duck at 3 different stages of laying namely; early (BE), peak (BP), and late laying (BL) stages. Based on their findings, a total of 1683 DEGs were identified from 3 comparison groups (BE-vs-BP, BE-vs-BL, and BP-vs-BL). However, only 11 genes were co-expressed among the 3 comparison groups (Hu et al., 2021). In their study, several genes that might affect egg production in Black Muscovy duck were found, these genes include homeobox A10 (**HOXA10**), High-temperature requirement factor A3 (**HtrA3**), Steroidogenic acute regulatory protein (**StAR**), Zona pellucida glycoprotein 2 (**ZP2**), and tyrosine aminotransferase (**TAT**).

In a recent study by Zou et al. (2020), 1,027 DEGs of which 495 and 532 genes were upregulated and downregulated, respectively were identified between the high yield group (HG) and low yield group (LG) of Leizhou ducks. However, only 25 genes and 25 genes were related to reproduction and reproductive processes, respectively. Prolactin (*PRLR*), Estrogen 2 (*ESR 2*), and Bone morphogenetic protein receptor beta (*BMPRI1B*) were found to be expressed in the ovarian tissues with significant expressions in HG and LG, respectively (Zou et al., 2020). The roles of *PRLR* and *ESR* in egg production have been discussed earlier in section 2 of this review.

A study by Sun et al. (2020) using the ovarian transcriptome to identify DEGs and signaling pathways responsible for egg production in higher and lower laying ducks at the late laying period (71 wk). Based on their study, a total of 343 DEGs comprising of 269 upregulated and 74 downregulated were identified. Out of the top 20 DEGs (17 upregulated and 3 downregulated expressed genes), one (LOC101793233), 4 (IL411, DUOX2, ASS1, and PTGS2), 2 (C1S and IL8), one (PRG4), and 12 (LOC101791385, F13A1, LOC101800358, LOC101795022, DDX60, TPM2, STC1, STAT1, COL1A1, LOC101790957, LOC10601

**Table 1..** Different transcriptomic studies to identify potential candidate genes responsible for egg production in ducks.

Breeds of duck	Tissue used	Stage of laying considered	Group comparison	Egg production parameters considered	Number of DEGs identified	Potential candidate genes and their functions	Expression level	Transcriptome studies involved
White Muscovy	Hypothalamus and ovary	59 wk	Highest producing (HP) and lowest producing (LP)	Age at first egg (AGE), number of eggs at 300 d (N300D), and number of eggs at 59 wk (N59W)	596 (Hypothalamus) 1,502 (Ovary)	<b>PR2X1</b> Inhibition of sperm transport that might affect ovulation of eggs (White et al., 2013) <b>LPAR2</b> Influences the uterine cycle during estrous cycle and early pregnancy (Seo et al., 2008) <b>ADORA1</b> Plays an important role in cell proliferation and hormone secretion (Wang et al., 2015) <b>FN1</b> Support of cell adhesion (Goossens et al., 2009) <b>AKT3</b> Fundamental regulator of many cytokines- and hormones-driven processes (Fabi and Asselin, 2014) <b>ADCY5</b> Affect the development of ovarian morphological-related (Liu et al., 2021a) <b>ADCY8</b> <i>mRNA expression of this gene control endocrine system in the HPG axis (Farmanullah et al., 2020)</i> <b>MAP3K8</b> <i>Target gene of miRNA-509-3p that promote the secretion of estradiol (Zeng et al., 2016)</i> <b>PXN</b> Involved in focal adhesions (Zeng et al., 2016) <b>PTTG1</b> Key role in organ development, regulation of cell cycle (Wu et al., 2014a)	Upregulated in hypothalamus Downregulated in hypothalamus Downregulated in hypothalamus Upregulated in ovary Upregulated in ovary Upregulated in ovary Upregulated in ovary Downregulated in ovary	(Bello et al., 2021)
Black Muscovy	Ovary	Early, peak and late laying	Late laying (BL) vs early (BE) BL vs peak (BP), and BP vs BE	NIL	101 (BE vs BL) 1090 (BP vs BL) 990 (BE vs BP)	<b>HOXA1</b> Promotes the development of uterus and the adhesion of embryo <b>HtrA3</b> Involved in ovarian development (Singh et al., 2011) <b>STAR</b> <i>Participates in steroid hormone synthesis (Woodruff and Shea, 2007)</i> <b>ZP2</b> <i>Play a key role in the process of oogenesis, fertilization and preimplantation development (Woodruff and Shea, 2007)</i> <b>TAT</b> For the development and differentiation of chicken oviduct (Lim and Song, 2016)	Up (BE vs BL group) BP = 6.5 by BE group Value of FKPM of BP = 5 higher than BL Up-regulated in BE group compared with BP group Relative expression significantly increased in BL group compared with BP group	(Hu et al., 2021)
Black and White Muscovy	Ovary	216–280-day-old	Black high (BH) vs White high (WH) Black low (BL)	Number of eggs produced	113 (BH vs (WH) 619 (BL vs BH) 87 (BL vs WL)	<b>TGFβ2</b> Play a key role in the regulation of development of germ cells of ovaries (Hattori Ma et al., 2002)	Highly expressed in high-laying As above As above	(Bao et al., 2020)

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Table 1. (Continued)

Breeds of duck	Tissue used	Stage of laying considered	Group comparison	Egg production parameters considered	Number of DEGs identified	Potential candidate genes and their functions	Expression level	Transcriptome studies involved
			vs Black high (BH), and Black low (BL) vs White low (WL)			<p><b>NGFR</b> Important in regulating the growth, development and function of reproductive organs (Vera et al., 2014)</p> <p><b>CEBPD</b> Higher proliferation rate in calf endometrium under the influence of steroid hormones (Becker et al., 2011)</p> <p><b>CPEB2</b> Promote meiotic maturation and embryonic development of porcine oocytes (Prochazkova et al., 2018)</p> <p><b>POSTN</b> Follicular granulosa cell proliferation (Ozegowska et al., 2019; Kulus et al., 2019)</p> <p><b>SMOC1</b> It helps in reproductive trait development of fetal (Pazin and Albrecht, 2009)</p> <p><b>FGF18</b> Participates in follicular development (Zhang et al., 2006)</p> <p><b>EFNA5</b> Steroid production during follicular development (Worku et al., 2018)</p> <p><b>SDC4</b> Upregulation of <i>SDC4</i> gene in ovulatory follicles may affect ovulation period (Lussier et al., 2017)</p>	<p>Ovarian tissues of high- and low-laying duck and white Muscovy ducks</p> <p>As above</p> <p>As above</p> <p>Expressed in the ovarian tissue of high yield black</p> <p>As above</p> <p>Ovarian tissue of HL-was significantly up-regulated</p>	
Leizhou black	Ovary	High yield and low yield egg laying ducks	High yield (HG) vs low yield (LG) group	Number of eggs (NE), age at first egg (AFE) and weight at first egg, and egg weight (EW)	1,027 (HG vs LG)	<p><b>ESR2</b> Allow normal follicular development (Wu et al., 2014b)</p> <p><b>PRLR</b> (Already discussed in the first section)</p> <p><b>BMPR1B</b> Determinant of ovulation rate (Polley et al., 2010)</p>	<p>Expression was higher in HG than I have LG</p> <p>Not reported in this study (check Introduction)</p> <p>Not reported</p>	(Zou et al., 2020)

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Table 1. (Continued)

Breeds of duck	Tissue used	Stage of laying considered	Group comparison	Egg production parameters considered	Number of DEGs identified	Potential candidate genes and their functions	Expression level	Transcriptome studies involved
Longyan Shan-ma	Ovary	Number of egg produced and egg weight from point of lay to 71 wk	High egg number (HEN) vs low egg number (LEN)	71 wk of laying	343 (HEN vs LEN)	<b>ITGB5</b> Important role in ovarian; development (Herrera et al., 2005), follicular development (Hatzirodos et al., 2014), and follicular selection in cattle (Liu et al., 2009) QTL for egg albumen quality in egg layers (Antosik et al., 2016) <b>ITGB2</b> mRNA level of ITGB2 is associated with ovarian follicle size in pigs (Akison et al., 2010) <b>ITGA8</b> Regulating the recruitment of mesenchymal cells into epithelial structures	Not reported Not reported Highly downregulated on ovarian follicle	(Sun et al., 2020)
Peking	Ovary follicle	60-day-old young (YD), 160-day-old first-laying (FL), and 490 day old stop-laying (OD)	YD vs FL FL vs OD	NIL	593 (FL vs YD) 518 (OD vs FL)	<b>EPOX</b> Member of the cytochrome P450 superfamily of enzymes (Craig et al., 2011) 3 $\beta$ -HSD, StAR, CYP17 3 $\beta$ -HSD were also identified as key genes	High expression in laying ducks	(Ren et al., 2018)
Jinding	Ovary	High (HEP) and low egg producing (LEP) duck	HEP vs LEP	Number of egg produced between 169 and 310 d	843 (HEP vs LEP)	<b>MC5R</b> It plays a key role in female reproductive system (Lantang et al., 2015) <b>APOD</b> It might regulate remodeling of the fallopian tube (Jeong et al., 2015) <b>ORAI1</b> It is involved with the calcium signaling pathway <b>DYRK4</b> Important in cell differentiation, survival, proliferation and development (Papadopoulos et al., 2011) <b>GRAMD1B</b> It has been identified as candidates gene in female fertility (Höghlund et al., 2015)	More than 80-fold greater in the HEP than LEP Significantly greater in HEP group than LEP Upregulated (HEP vs LEP) Significant differences between HEP and LEP Not reported	(Tao et al., 2017)
Shan Ma	Ovary	Peak (180 d) and late stage (520 d)	Peak vs Late	NIL	2,002 (peak and late)	<b>FSH<math>\beta</math></b> , <b>PLA2G2E</b> , <b>GNAQ</b> , <b>MAP2K4</b> and <b>CALM3B</b> are involved in <i>GnRH</i> signaling “an important pathway related to egg production in poultry birds (Bédécarrats et al., 2009)	Not reported	(Zhu et al., 2017)

**Table 2.** List of several studies on QTL, GWAS, selection signature, and cis-regulatory on egg production traits in ducks.

Approaches	Egg production traits	Candidate genes revealed	Location on QTL region	Expression level	References
Transcriptome, proteome quantitative trait loci (QTL)	Duck egg shell and albumen formation	<b>LPCAT3</b> Regulate membrane fluidity and phospholipid dependent signaling (Demeure et al., 2011) Associated with the bacterial-resistance ability of duck eggs <b>ORM1</b> It is the most highly expressed gene during albumen formation in ducks key acute phase plasma protein (acute-phase reactant) (Pruitt et al., 2009) Responsible for albumen differences in duck and chickens albumen <b>SPINK7</b> Function as carbohydrate-binding and involved in steroid hormone process (Compere et al., 1981) Involved in some initial phase <b>BP1FB3</b> <b>MCTP1, MDN1, TMC3, OCX-36</b>	Albumen height/haugh unit QTL region Not reported Not reported Eggshell quality-related QTL regions (thickness, stiffness, weight, yellowness, and strength)	Not reported Greatly increased in the active duck magnum (high expression level in the quiescent duck magnum) Not reported Greatly expressed between the two functional states	(Zhang et al., 2020) (Zhang et al., 2020)
Preteomics	Egg shell	<b>CEP162, APPL1, DAG, REG4</b>	Egg shell color region Egg shell strength QTL region	Not reported	(Zhu et al., 2019)
GWAS	Egg internal quality	<b>EHF, ZDHHC13, MUC6, CHID1, CRACR2, LRR MUC6</b> Orthologus of ovocumin (Lang et al., 2006) The ovumucin is around 3.5% of ovalbumin (Carey, 1990). Major role in gelation of fresh eggs (Nishinari et al., 2000) <b>PAR2, PRR5L, LDLRAD3, PAMR1, ELF5, ABTB2, SHANK2, TSPAN4, LRRC56, AKAP6, ELF5, AKAP6, ARHGAP5, and STRN3</b> were found close to the significant SNPs <i>LPLRAD2</i> as a candidate gene associated with egg quality traits in dwarf layer (Zhang et al., 2011) All these SNPs are synonymous	Chromosome 5	Notably higher in oviduct than in other tissues	(Liu et al., 2021b)
Combination of GWAS and signature of selection Combination of GWAS and signature of selection	Feed conversion ratio (FCR) of egg production traits	<b>LOC106017218, CRBN, TRNT1, IL5RA, and CNTN4</b> <b>MMS22L, KLHL32, LOC106017657, NDUFAF4, GPR63, FHL5, LOC106017656, FUT9, and MANEA</b> <b>GDF2, RBP3, ZNF488, ANTXRL, ANXA8L1, LOC106017915, LOC101795151, LOC101795347, LOC101795539, ZFAND4, ALOX5, LOC101797666, BLOC1S2, LOC101797254, PKD2L1, LOC106018867, and SCD</b> <b>CNTN4</b> <b>TRNT1 and CRBR</b> <b>MANEA</b> <b>FHL5</b> <b>GPR63, NDUFAF4, KLHL32 and MMS22L</b> <b>SCD</b> Regulates lipid metabolism <b>LOC101795347</b> Annotated as lncRNA <b>ZNF488, ANTXRL, ZFAND4, ALOX5</b>	Chromosome 13 Chromosome 3 Chromosome 6 Chromosome 3 Chromosome 6	Not reported Highly expressed in nervous tissues (CPM> 96 in the hypothalamus, CPM>29- pituitary gland) Expressed in all investigated tissues As above Highly expressed in the ovary and the follicular membrane Relatively expressed in the ovary and the follicular membrane Highest expression level in the hypothalamus Highest expression level in the oviduct (an essential organ for egg formation) Moderately expressed in the ovary, oviduct, and the follicular membrane	(Liu et al., 2021b)
Cis-regulatory	Mallard egg color Blue eggshell	<b>ABCG2</b> <b>ABCG2</b>	Not provided Not provided	Not provided Not provided	(Liu et al., 2021a) (Chen et al., 2020)

8024, and LOC101802453) DEGs are an essential role in cell-cell adhesion, encoding oxidases or synthases, immune response, follicle development, and encoding structural proteins or subunits, respectively (Sun et al., 2020).

Due to the importance of follicles in duck reproductive performance, Ren et al. (2018) researched the differentially expressed key genes that are related to the development of follicles in Peking ducks (*Anas Platyrhynchos*) at 3 different stages of life (young, laying, and old). Based on their findings, 593 and 518 coding genes were expressed between young and laying ducks and laying and old ducks, respectively (Ren et al., 2018).

In a comparative transcriptomic study of the ovaries of Jinding ducks at 2 different egg production levels (high and low), Tao et al. (2017) reported that 367 downregulated and 476 upregulated DEGs were identified in high and low egg-producing ovaries, respectively. However, among the top 24 DEGs, only 4 DEGs (MCR5R, APOD, ORAI1, and DYRK4) were more active in the ovaries of the high egg-producing ducks, which indicated that these genes might play vital roles in egg production (Tao et al., 2017).

The ovarian transcriptome in Shan Ma ducks at 2 stages of egg production was studied by Zhu et al. (2017). A total of 2,002 DEGs comprising 790 upregulated and 1,212 downregulated were detected. The annotation of the genes revealed that 1,645 genes were already annotated, of which 999 and 646 genes were downregulated and upregulated, respectively (Zhu et al., 2017). However, only the top 10 up- and downregulated DEGs in the ovaries of peak and late

stages, respectively that might be related to reproductive processes were presented in their findings.

The summary of breeds of duck used, stages of laying considered, egg production parameters considered, number of DEGs, potential candidate genes and their functions, expression level of these potential genes in tissues considered are presented in Table 1.

### QTL, GWAS, SELECTION SIGNATURE, OR COMBINATION OF APPROACHES TO IDENTIFY GENES

Genome wide association studies with phenotypic traits have revealed multiple QTL regions using different of markers, that is, microsatellites or SNPs, and these QTLs have narrowed down genome regions of candidate gene study (Tuiskula-Haavisto et al., 2002; Mondal et al., 2004; Hansen et al., 2005). However, there are little reports on QTLs studies related to egg production traits in ducks. Based on this, a study incorporated transcriptome, proteome and QTL analyses to identify advantageously significant genes that contribute to egg-shell and albumen formation in duck (Zhang et al., 2020). In another study by Liu et al. (2021b), GWAS was utilized to reveal the genetic variations for egg internal quality in ducks. GWAS and selective sweep analysis reveal genetic loci responsible for feed conversion ratio (FCR) of egg production performances in ducks (Liu et al., 2021b). The identified SNPs at the cis-regulatory region of *ABCG2* gene are related to egg color in Mallard (Liu et al., 2021a) and the 2 cis-regulatory

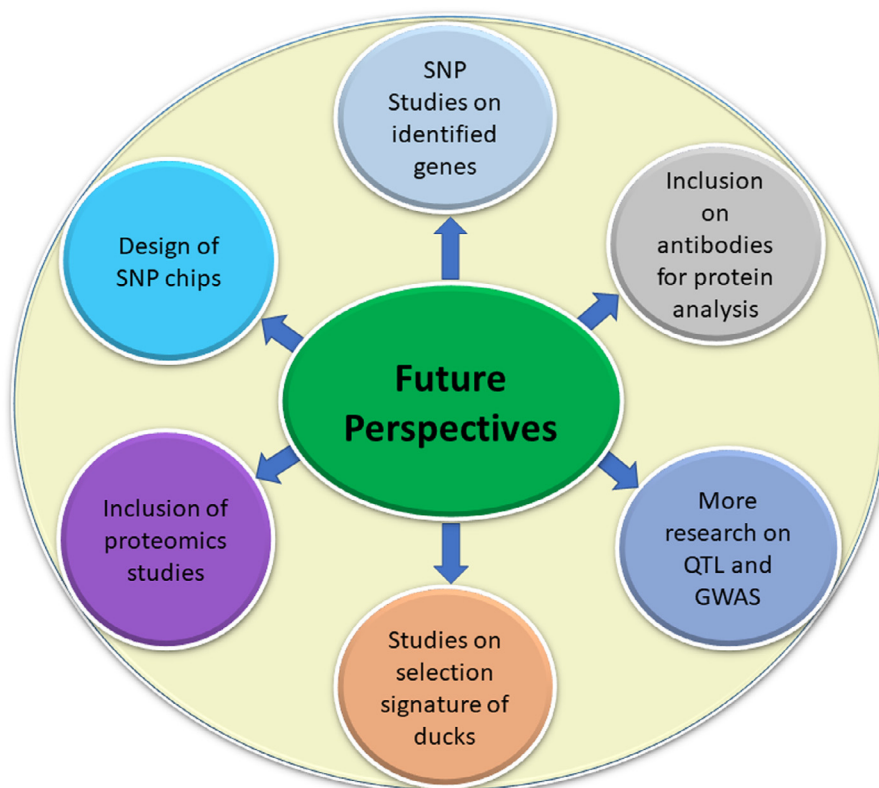


Figure 3. Perspectives towards the improvement of egg production in ducks.

SNPs upstream of *ABCG2* can cause blue eggshell phenotype in duck (Chen et al., 2020). The summarize findings from several studies using QTL, GWAS and selection signature, and cis-regulatory are presented in Table 2.

## CONCLUSIONS

The number of eggs produced by ducks is below the demand of the increasing human population across the globe; this necessitates the need to improve the egg production from this waterfowl bird as the protein requirement of human beings and economic income of duck farmers might be increased through this poultry specie. In our own opinion, the following remarks would be useful to improve research on candidate genes responsible for egg production in ducks, and the highlighted remarks are summarized in Figure 3 below.

- Future studies should look into the polymorphic studies of other identified genes in association with egg production traits of ducks.
- Future studies should incorporate antibodies for protein expression of the candidate genes in reproductive tissues of ducks to reveal the reliability of the qRT-PCR.
- More studies on QTL and GWAS could be done to identify different SNP markers of genes that might be responsible for egg production in ducks.
- Proteomics study of these genes would be helpful to understand the rising need for genetic improvement of egg production in duck.
- There is a need to deeply study the correlation that exists between the genes at different QTL regions in ducks.
- There is need to design a SNP chips for GWAS study.

## DISCLOSURES

The authors declare that they have no competing interests relevant to this publication.

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