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Genetic effects of polymorphisms of candidate genes associated with ovary development and egg production traits in ducks

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ABSTRACT

Duck eggs are highly nutritious, and demand for consumption has markedly increased in the growing human population, resulting in the need to increase production. Egg production is dependent on the reproductive performance of animals, a trait that is not highly heritable. Improving reproductive performance, therefore, is an essential aim of breeders performing genetic selection to increase egg production. The ovary has received much attention by breeders because of its importance in the production and release of eggs. The ovary, therefore, has been intensely studied to identify the candidate genes and the polymorphisms associated with egg-laying traits. The expression of these genes in the ovary indicates the potential for involvement in ovarian follicular development. The expression of the growth hormone, follicle-stimulating hormone receptor, prolactin, ovoinhibitor, melatonin receptor, and insulin-like growth factor-2 genes in the ovary has been studied, and polymorphisms have been identified that are related to egg-laying traits. The single nucleotide polymorphisms of these genes help with the identification of novel genetic markers that assist in selecting the ducks with the most desirable genotypes for egg production. This approach to genetic selection is more effective than the traditional method used to select animals for egg production. With this review, therefore, there is a summarization of genetic effects of polymorphisms in candidate genes related to ovarian development and egg production traits in ducks.

1. Introduction

In recent times, egg production has been the most important economic trait in poultry because of the desirable nutritional content of eggs in diets of humans. Duck eggs are reported to contain greater concentrations of seven of eight minerals, seven of nine vitamins and 11 of 18 amino acids examined than chicken eggs (Metzer, 2012). The human population is also increasing, which leads to an increased demand for animal products. Thus, animal production, including egg production, should be increased to meet the consumption demands of the growing human population (Huang et al., 2012). Egg production is mainly dependent on the reproductive performance of poultry, which is a trait with low heritability. Endocrine and environmental factors, including feeding allowance and length of photoperiod can affect egg production (Lewis and Gous, 2006). Using traditional breeding and selection methods, the reproductive performance of egg-laying ducks has progressively been enhanced, but additional improvement for maximum performance is very slow (Zhu et al., 2017). The ovary is the female reproductive organ that produces and releases eggs and serves as an

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Table 1
Functions of identified genes in poultry production.

Genes	Functions	Reference
Growth hormone	• stimulates tissue differentiation growth and development • enhances growth and maturation of follicles • enhances the activities of the hormones in the ovarian follicles • regulates steroidogenesis and gametogenesis • enhances proliferation in sexual maturation • enhances AFE and HDR	(Hrabia et al., 2011; Komisarek et al., 2011; Martínez-Moreno et al., 2011; Ahumada-Solórzano et al., 2012; Hull and Harvey, 2014)
Prolactin	• development of breast gland • development of embryos • induces and maintains incubation behaviour • regulates follicular development • enhances egg production • increases the rate of broodiness	(Reddy et al., 2002; Jiang et al., 2005; Wong et al., 2005; Bhattacharya et al., 2011)
Melatonin	• helps in ovarian function • activates the growth of small white and yellow follicles • regulates avian reproduction • enhances egg production	(Wang et al., 2008; Sundaresan et al., 2009; He et al., 2014)
OIH	• inhibits the activities of other proteinases in the egg white and blood plasma • maintains a microenvironment for sperm • degrades egg yolk proteins • aids reproductive performance	(Laskowski and Kato, 1980; Słowińska et al., 2014; Gao et al., 2017)
FSH	• normal ovarian follicle development • improves differentiation of Sertoli cells • enhances sperm production • arouses the function of the male and female reproductive gland • upregulates FSHR	(Xie et al., 2004; Grzegorzewska et al., 2009; Li et al., 2011; Johnson, 2014)
IGF-2	• growth differentiation and proliferation • reproduction • regulates ovarian follicle development • support key functions for follicle development	(Mao et al., 2004; Kaneda et al., 2007; Baumgarten et al., 2015)

endocrine gland that produces and secretes important reproductive hormones (Zhu et al., 2017). Thus, duck breeders have focused on the ovary to research egg production and examine the main genes as well as other associated differentially expressed genes (DEGs) that regulate egg production.

Several candidate genes have been identified in ducks as being highly expressed in the ovary and that are associated with egg-laying traits. Among these are the growth hormone (GH) (Wu et al., 2014), prolactin (PRL) (Bai et al., 2019), insulin-like growth factor-2 (IGF-2) (Ye et al., 2017), melatonin receptor (MTNR) (Feng et al., 2018), ovoinhibitor (OIH) (Wu et al., 2018), and follicle-stimulating hormone receptor (FSHR) (Xu et al., 2017) genes. These hormones and relevant receptors have important functions in the differentiation, growth, and development of several tissues involved in egg production, while inhibiting the activities of proteins such as proteinases in egg yolk and blood plasma that are involved in regulation of ovarian follicular development (Table 1) (Laskowski and Kato, 2003; Bhattacharya et al., 2011; Li et al., 2011; Martínez-Moreno et al., 2011; He et al., 2014; Baumgarten et al., 2015; Gao et al., 2017; Yadav et al., 2018).

The detection of single nucleotide polymorphisms (SNPs) has helped with the identification of novel genetic markers to more precisely select animals for enhanced egg-production performance. This knowledge improves upon the traditional method of selection to enhance the production of eggs with great nutrient content. The SNPs can also be used to aid in studying and selecting the most desirable genotypes of animals for production traits (Kulibaba and Podstreshnyi, 2012). The identification of SNPs in candidate genes and the correlation with egg-laying traits is an important technique used to genetically improve animal selection and production (Feng et al., 2018). Various SNPs of genes have been identified that are related to egg-laying traits in chickens and geese, with a few studies conducted in ducks (Kang et al., 2012; Li et al., 2013; Kulibaba, 2015; Alsiddig et al., 2017; Mohamed et al., 2017).

This review, therefore, summarizes the results of studies of the genetic effects of polymorphisms of candidate genes associated with ovarian development and egg production traits in ducks.

2. Genes associated with ovarian development in egg-laying ducks

The heritability of reproductive performance is very low. The traditional breeding selection method, which depends largely on experience of duck breeders, has increasingly improved reproductive performance but there are several uncertainties as to whether this approach will continue to be successful for this purpose (Zhu et al., 2017). Apart from egg production, the ovary also functions in ovulation regulation, and hormone production and secretion to affect reproductive capacity (Pan et al., 2014). The important functions of the ovary has resulted in there being a large amount of animal breeding research focused on the identification of major

genes involved in regulation of reproduction such as in the tissues involved in the regulation of the hypothalamus-pituitary-gonadal (HPG) and growth hormone/insulin-like growth factor (GH/IGF) endocrine axes (Pierantoni et al., 2002; Rocha et al., 2007), which are integral in controlling egg production of ducks and other poultry. There has been identification of some genes in the ovary of egg-laying ducks that are in the egg production phase that enhance growth and development.

Results from a study where there was examination of the expression of the GH gene in several tissues indicated GH was greater in egg-laying ducks that are in egg production than those that are nesting (Wu et al., 2014). The polymorphism and genotype of GH for egg production traits in egg-laying ducks indicates the GH gene is expressed to a great extent in the ovaries of egg-laying ducks. In chickens, there was a greater abundance of GH mRNA in developing follicles (Hrabia et al., 2008, 2011). Even though the IGF-1 gene is highly expressed in the liver, it was also expressed in ovarian, heart, hypothalamic, and pituitary gland tissues of the Muscovy duck (Wu et al., 2016). The synthesis and secretion of IGF-1 is regulated by GH and controlled by the HPG and GH/IGF axes (Gong et al., 2007; Wu et al., 2014), indicating IGF-1 is important in the reproduction rate of ducks. In mammals and fish, IGF-1 stimulates steroid hormone production and the proliferation of granulosa cells for gonadal development and reproduction (Shimizu et al., 2008). The IGF-2 gene expression is related to ovarian follicular development in zebrafish, rats and chickens (Kim et al., 2004; Wang et al., 2005; Irwin and Van Der Kraak, 2012). Results for a recent study in the Muscovy duck indicated that the IGF-2 gene was more highly expressed in the ovary than in all other tissues examined (Ye et al., 2017). This finding indicates IGF-2 has functions in follicle development and regulation of egg production in egg-laying ducks (Ye et al., 2017). A correlation between abundance of IGF-2 mRNA transcript in the ovary and egg production in chickens was reported (Kim et al., 2004). The gene for dopamine receptor 2 (DRD 2) was expressed in the ovary of egg-laying ducks indicating DRD2 may have a function in egg production (Ye et al., 2017). Previously, it was reported in humans and grey mullet that the protein encoded by the DRD2 gene in the ovary might be involved in regulation of follicle development and reproductive functions (Morton et al., 2006; Nocillado et al., 2007). The expression of the melatonin receptor (MTNR) gene that encodes for the MTNR protein that regulates gonadal maturation was identified to occur in the ovaries of Shaoxing egg-laying ducks (Feng et al., 2018). The activation of the MTNR stimulates the production of GnIH and GnRH and suppresses the secretion of LH to control the development of gonads (Rozenboim et al., 2002; Chowdhury et al., 2010; Surbhi Kumari et al., 2015). Follicle stimulating hormone (FSH) regulates ovarian follicular development by inducing the production of the steroid hormone and maturation process in birds (Grzegorzewska et al., 2009; Li et al., 2011; Johnson, 2014). The FSHR gene was expressed in the ovaries of Muscovy duck, indicating that the gene product may be involved in ovarian follicular development in ducks (Xu et al., 2017). The FSHR gene has been reported to be highly expressed in embryonic gonads or the ovary, especially the granulosa cells of birds (Grzegorzewska et al., 2009; Kang et al., 2010).

3. Single nucleotide polymorphisms detected in genes related to egg-laying and reproductive traits

The SNPs are alterations in the prevalent DNA sequence when one base in a gene is changed, that is, if one nucleotide differs from the normal sequence. For example, the SNP may result in substitution of the nucleotide thymine (T) with nucleotide guanine (G) in a specific location in the DNA (Fig. 1) (Brookes, 2007). When SNPs occur in the coding region of a gene, the change produces distinct variants or alleles that can lead to functional differences in the encoded protein (Collins et al., 1998). Due to the differences, SNPs normally occur in non-coding areas to exert an effect on gene splicing, non-coding RNAs and transcription factor binding (Barreiro et al., 2008).

The DNA polymorphism analysis is applicable in sex determination, paternity tests of individuals, species identification, disease detection, phylogenetic analysis, and marker-assisted selection among others (Huang, 2014). Understanding and utilizing the knowledge about DNA polymorphisms has helped with identification of novel genetic markers that can be used to accurately select animals for greater production performance compared to use of traditional breeding methods. The knowledge about specific SNPs is utilized in poultry breeding to determine the exact markers of the genotypes that are associated with greater egg production (Kulibaba and Podstreshnyi, 2012).

Several genes have been identified as being involved in the egg-laying and reproductive traits of egg-laying ducks. Among them are the GH, PRL, MTNR, DRD-2, OIH, IGF-1, IGF-2, and FSH genes, which are ideal candidate genes for genetic marker screening of egg-laying ducks. Various polymorphisms in these genes have been identified as being associated with egg-laying performance and reproductive traits based on screening for genetic markers. Thus, these SNPs can be used as novel molecular markers for duck egg production (Wu et al., 2014; Xu et al., 2017; Ye et al., 2017; Feng et al., 2018; Wu et al., 2018; Bai et al., 2019).

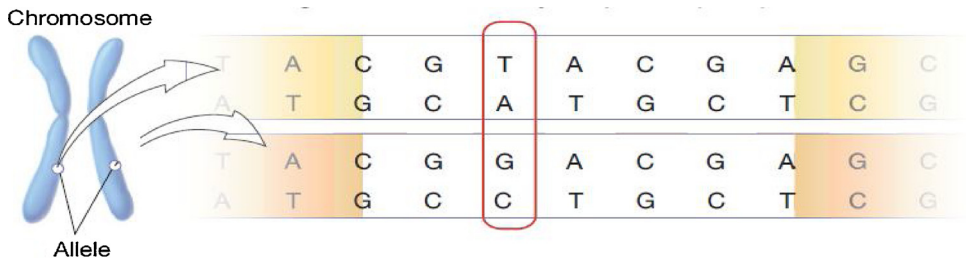

Fig. 1. Single Nucleotide Polymorphism (Brookes, 2007).

Table 2
Least squares analysis of the association of SNPs of identified genes with egg-laying traits in ducks.

Gene (SNP)	Traits	Least-squares mean ± SEM			Reference
GH (g.3270A > G)		AA (n = 268)	AG (n = 280)	GG (n = 72)	(Wu et al., 2014)
	AFE	182.54 ± 8.10 [a]	181.69 ± 7.30 [a]	184.63 ± 8.40 [a]	
	Peak clutch in days	56.56 ± 17.54 [a]	55.20 ± 15.51 [ab]	46.05 ± 14.84 [b]	
	Average clutch in days	27.26 ± 7.85 [a]	26.17 ± 6.36 [ab]	20.40 ± 8.95 [b]	
	E300D	90.38 ± 16.18 [a]	88.48 ± 17.01 [ab]	85.83 ± 17.32 [b]	
PRL (A-412 G)		AA (n = 162)	AG (n = 358)	GG (n = 280)	(Bai et al., 2019)
	E300D	142.26 ± 8.06[a]	143.87 ± 9.76[ab]	145.56 ± 10.33[b]	
	Egg weight (g)	70.69 ± 4.16[a]	69.00 ± 3.37[b]	68.66 ± 3.33[b]	
OIH (389 G > A)		AA (n = 34)	GG (n = 130)	AG (n = 86)	(Wu et al., 2018)
	AFE (d)	149.00 ± 3.88[a]	146.38 ± 2.09[a]	136.00 ± 1.22[b]	
	Weight at first egg (g)	1408.85 ± 43.99	1364.9 ± 24.02	1427.88 ± 23.30	
	Body weight of hatch (g)	44.01 ± 0.79	44.18 ± 0.58	43.31 ± 0.67	
	Egg weight (g)	67.29 ± 0.97	66.26 ± 0.85	64.26 ± 0.73	
	E72W	199.69 ± 8.13[c]	268.22 ± 7.68[b]	315.79 ± 7.28[a]	
FSHR (C320 T)		TT (n = 6)	CT (n = 61)	CC (n = 156)	(Xu et al., 2017)
	AFE	270.08 ± 25.87[a]	270.57 ± 8.12[a]	275.52 ± 4.70[a]	
	E33W	14.75 ± 7.07[a]	19.02 ± 2.22[a]	14.86 ± 1.28[a]	
	E59W	66.53 ± 14.24[ab]	73.34 ± 4.36[b]	59.86 ± 2.59[a]	
FSHR (A227 G)		AA (n = 106)	AG (n = 93)	GG (n = 24)	
	AFE	285.73 ± 5.82[a]	261.97 ± 5.95[b]	274.07 ± 13.76[ab]	
	E33W	14.04 ± 1.64[a]	17.43 ± 1.68[a]	17.97 ± 3.88[a]	
	E59W	61.33 ± 3.38[a]	65.03 ± 3.47[a]	68.31 ± 7.92[a]	
IGF2 (A−1864 G)		AA (n = 204)	AG (n = 308)	GG (n = 172)	(Ye et al., 2017)
	AFE	276.60 ± 1.41[a]	275.67 ± 1.15[a]	276.77 ± 1.54[a]	
	E59W	75.35 ± 1.92[a]	76.01 ± 1.57[a]	69.18 ± 2.10[b]	
	E300D	21.43 ± 1.04[a]	21.91 ± 0.85[a]	20.84 ± 1.14[a]	
IGF2 (C-1704 G)		CC (n = 158)	CG (n = 310)	GG (n = 216)	
	FEA	276.50 ± 1.61[a]	276.43 ± 1.15[a]	275.72 ± 1.37[a]	
	E59W	68.92 ± 2.19[b]	75.33 ± 1.56[a]	76.11 ± 1.87[a]	
	E300D	20.97 ± 1.19[a]	21.18 ± 0.85[a]	22.33 ± 1.01[a]	
MTNR1A (g.268C > T)		CC (n = 461)	CT (n = 282)	TT (n = 42)	(Feng et al., 2018)
	AFE	146.51 ± 15.18[ab]	143.74 ± 15.10[b]	146.55 ± 15.30[a]	
	E34W	75.99 ± 5.00	77.49 ± 4.94	74.95 ± 3.73	
	E72W	303.23 ± 12.93	302.64 ± 11.43	298.19 ± 15.49	
	Egg weight (g)	70.45 ± 5.17	69.61 ± 5.56	68.57 ± 8.20	
MTNR1C (g.108C > T)		CC (n = 499)	CT (n = 250)	TT (n = 36)	
	AFE	146.50 ± 15.75[a]	144.28 ± 14.28[ab]	140.56 ± 12.03[b]	
	E34W	75.09 ± 5.34[b]	78.91 ± 3.76[a]	78.78 ± 4.56[ab]	
	E72W	298.91 ± 11.83	302.65 ± 14.23	314.21 ± 15.37	
	Egg weight (g)	70.25 ± 5.73	69.79 ± 5.24	68.98 ± 4.56	

Values within a row with no common superscript differ ($P < 0.05$); n: the number of genotypes in the duck population; AFE: age at first egg; E300D: egg number at 300 days; E (33,34,59,72)W: egg number at 33, 34, 59, and 72 weeks.

3.1. Polymorphisms of the prolactin gene and its association with egg-laying traits

Prolactin (PRL), which is produced in the anterior pituitary of animals, is a single-chain polypeptide hormone that belongs to the GH gene family (Power, 2005; Jiang et al., 2009). In mammals, PRL controls various biological functions, which include promoting mammary gland development, lactation inducement, pregnancy maintenance and embryo development (Bonomo et al., 2007; Lü et al., 2010). Additionally, in poultry, PRL regulates follicle development and egg production and induces brooding behaviour (Reddy et al., 2002; Wang et al., 2011; Yadav et al., 2018). A primary function of PRL is to decrease the quantity of Graafian follicles in the avian ovary, which leads to less egg production (Bhattacharya et al., 2011). After cloning and sequencing the chicken PRL gene in 1989, several studies concentrated on identifying polymorphisms of this gene related to egg-laying performance in ducks and hens (Wang et al., 2011; Bagheri Sarvestani et al., 2013; Kulibaba, 2015; Tempfli et al., 2015; Zhang et al., 2015; Mohamed et al., 2017; Yadav et al., 2018; Bai et al., 2019).

In a recent study, there was investigation of the polymorphisms in the PRL gene in the Jinding and Youxian egg-laying duck breeds and the association with egg production. With use of PCR-SSCP analyses, there was identification of one polymorphism (A-412 G) with three genotypes (GG, AG, and AA) in Intron 1 of the gene. Results from association analyses indicated that egg weight and egg production was greater in ducks with the GG genotype compared with those with the AA and AG genotype (Table 2) (Bai et al., 2019). In Khaki Campbell ducks, the C-359A polymorphism was identified as being associated with egg production at 300 days, with ducks with the GT genotype having a larger number of eggs than those with the TT and GG genotype (Chuekwon and Boonlum, 2017). It was concluded after results were obtained from association analyses of the F2 duck resource population (White Liancheng and White Kaiya) that the C-5961 T PRL polymorphism was related to the number of eggs produced and egg weight in ducks with the CC genotype and this polymorphism had a much greater effect on these traits than in the ducks with a CT and TT genotype (Wang

et al., 2011). These findings indicate PRL might be a candidate gene that affects egg-laying performance and reproduction in ducks.

3.2. Polymorphisms of the growth hormone (GH) gene and its association with egg-laying traits

Life processes, growth, development and physiological functions of organs and the organism as a whole cannot occur in the absence of growth hormone. There is synthesis of the single polypeptide chain protein of GH in the anterior pituitary as a result of functions in HPG and GH/IGF axes. There is secretion of GH into the bloodstream and there is binding of GH in various tissues where it functions to induce several differentiation processes that are important in growth and development (Martínez-Moreno et al., 2011). Another action of GH is to regulate reproductive function during the period of tissue differentiation and growth in females and gametogenesis and steroidogenesis in males (Komisarek et al., 2011; Hull and Harvey, 2014). The mRNA for GH has been detected in the spermatids, spermatocytes, and spermatogonia (Martínez-Moreno et al., 2011). Primary actions of GH are cellular proliferation, steroidogenesis, and apoptosis during sexual maturation in regulation of growth, maturation, and hormonal actions at the ovarian follicles (Hrabia et al., 2011; Ahumada-Solórzano et al., 2012). Results from a study with GH genotypes indicated there was a marked association with the hen-day rate of egg production (HDR) and age at first egg (AFE) laying in White Leghorn chickens (Feng et al., 1997). To ascertain the relationship between the GH gene and egg-laying traits in ducks, a study was conducted using Muscovy ducks to identify GH polymorphisms and gene expression profiles (Wu et al., 2014). Using the PCR-SSCP method, one SNP (g.3270 A > G) with GG, AG, and AA genotypes was identified in Intron 3. Results from use of this analysis indicated the ducks with the AA genotype produced the largest number of eggs by the time these ducks were 300 days (E300D) of age, and had the highest peak clutch and average clutch in days (56.56 ± 17.54 and 27.26 ± 7.85 respectively) than ducks with the AG and GG genotypes (Table 2). There, however, was no difference for AFE laying among the three duck genotypes (Wu et al., 2014). These outcomes indicate that GH might be a candidate gene that affects egg production in ducks.

3.3. Polymorphisms of the ovoinhibitor (OIH) gene and its association with egg production traits

In the albumen, ovoinhibitor is the main proteinase inhibitor produced in the hollow gland cells of the oviduct, which is controlled by progesterone and estrogen (Liu et al., 1971; Kinoshita et al., 2004). The OIH inhibits the activity of other proteinases such as trypsin, elastase, and chymotrypsin in the egg white and blood plasma in chickens (Shechter et al., 1977; Vered et al., 1981; Laskowski and Kato, 2003). The OIH protein functions to stabilize the constituent milieu in the epididymis and ductus deferens for enhancing sperm survival and has a function in egg yolk protein degradation and is associated with the reproductive performance of poultry (Słowińska et al., 2014; Gao et al., 2017). The OIH gene is also expressed from the greatest to the least extent in the liver, magnum, and uterine tissues as well as in the egg yolk, and eggshell precursor substances of chickens (Bourin et al., 2011). During sexual maturation, OIH gene expression is relatively greater in the liver as compared with later in the maturation period (Bourin et al., 2011). Research on OIH functions in ducks, however, is rare.

There has been an evaluation of the expression profile of the OIH gene in the ovary and there was detection of SNPs associated with egg-laying traits of two duck breeds (Wu et al., 2018). These SNPs in Introns 7 and 9 and Exons 3–5, 5–6, and 14–16 of the OIH gene were identified using DNA pool sequencing and PCR-RFLP methods. There was only one variation (389 G > A) in Exon 5–6 that was associated with egg-laying traits. Evaluation of the genotypes, specifically GG, AG, and AA, indicated that ducks with AG genotypes were considerably younger at the time of AFE, laying and had the greatest quantity of eggs produced at 72 weeks of age. Furthermore, ducks with the AG genotype had a greater weight at the AFE laying but a lesser egg weight and body weight at the time of hatching than ducks with the AA and GG genotypes (Table 2) (Wu et al., 2018).

3.4. Polymorphisms of the melatonin (MTNR) gene and its association with egg-laying traits

Melatonin, otherwise known as N-acetyl-5-methoxytryptamina, is an essential hormone in regulation of biorhythms produced in the pineal gland. In poultry, MTNR affects several physiological processes such as reproduction and circadian rhythm via its unique receptors (Kumar Kharwar and Haldar, 2011; Yadav and Haldar, 2013; Trivedi and Kumar, 2014). In poultry, three melatonin receptors (MTNR1A, MTNR1B, and MTNR1C) have been replicated in the G-protein-coupled receptor superfamily (Reppert, 1997; Li et al., 2013). The genes for the MTNR subtypes were expressed in chicken ovaries indicating melatonin may have a direct effect on ovarian function, and in geese, the three MTNR subtype proteins increased initially and decreased later during follicular development indicating that the MTNR may activate small yellow and white follicles to mature into larger follicles (Wang et al., 2008; Sundaresan et al., 2009; He et al., 2014). In other avian species, melatonin regulates the maturation of the gonads by inhibiting the secretion of luteinizing hormone (LH) and activating the secretion of the gonadotropin-inhibitory hormone (GnIH) (Rozenboim et al., 2002; Ubuka et al., 2005; El Halawani et al., 2009; Chowdhury et al., 2010; Surbhi Kumari et al., 2015). The MTNR1C mRNA is co-localized with GnIH neurons indicating there is melatonin binding to its receptors in these neurons to induce GnIH expression. Several researchers have analyzed the association between MTNR subtypes and egg-laying traits in chicken and geese but not ducks (Li et al., 2013; Alsiddig et al., 2017).

There has been identification of the SNPs of MTNR genes and analysis of the association with egg-laying traits in Shaoxing ducks (Feng et al., 2018). The results after qRT/PCR analysis indicated seven novel polymorphisms were identified in all three MTNR genes. Results from association analyses indicated the SNP (g268C > T) of MTNR1A was associated ($P < 0.05$) with AFE laying, whereas the SNP (g108C > T) of MTNR1C was associated with the total quantity of eggs produced by 34 weeks of age (E34W). Ducks with the CT polymorphism, MTNR1C (g108C > T), produced a larger number of eggs than ducks with the CC genotype by 34 weeks of age,

whereas those with the TT genotype had an earlier AFE laying than those with the CC genotypes. Ducks with the CT genotype, MTNR1A (g268C > T), had had a later AFE laying than those with the TT genotype (Table 2) (Feng et al., 2018). These outcomes indicate the SNPs identified in ducks, MTNR1A and MTNR1C, may affect the AFE laying in ducks and can be used as novel molecular markers to ascertain early maturation traits in duck selection and genetic improvement for egg production.

3.5. Polymorphisms of the follicle stimulating hormone receptor (FSHR) gene and its association with egg production traits

The FSH and FSH receptor proteins are important for ovarian follicular growth and regulation of spermatogenesis and steroidogenesis in the testis and ovary, respectively. In avian species, FSH has primarily reproductive functions. There is regulation by FSH of the development of ovarian follicles by stimulating the production of the steroid hormone and physiological and behavioural maturation processes (Grzegorzewska et al., 2009; Li et al., 2011; Johnson, 2014). Stimulation of reproductive functions as a result of FSH binding to its receptor occurs in the testis and ovary, implying that FSH activates FSHR (You et al., 2005; George et al., 2010). The FSHR has been detected in large amounts in the ovary and when this receptor is activated there is expression of the LH receptor (Woods and Johnson, 2005; You et al., 2005). There has also been identification of an association between SNPs of the FSHR gene and egg-laying performance in chickens (Li et al., 2011; Kang et al., 2012).

Because little has been reported about the FSHR gene and egg-laying performance in ducks, there was a study conducted in which there was characterization of the FSHR gene expression profile and its SNPs that were associated with egg-laying traits in Muscovy ducks (Xu et al., 2017). The results indicated that there were 16 SNPs in total of which four were in the gene-coding region, four in the 5′ flanking region and eight in the intronic regions. Results from the association analysis indicated the SNPs, C320 T and A227 G, were associated with number of eggs produced by 59 weeks of age (E59W) and AFE laying, respectively (Xu et al., 2017). The results of the analysis also indicate that the ducks with the CC genotype that have the C320 T SNP had a lesser E59W than the ducks with the CT genotype, whereas ducks with the AG genotype, A227 G SNP, had lesser AFE values than ducks with the AA genotype (Table 2) (Xu et al., 2017). This finding indicates the SNPs, C320 T and A227 G, may be utilized for marker-assisted selection programs to increase egg production in ducks.

3.6. Polymorphisms of the insulin growth factor (IGF-2) gene and its association with egg-laying traits

Insulin-like growth factor-2 (IGF-2) is essential for body growth and development, tissue differentiation and tissue proliferation in the animal growth process, and reproduction as a result of actions on ovarian follicular development through an enhanced responsiveness to FSH (Mao et al., 2004; Kaneda et al., 2007; Baumgarten et al., 2015). Several studies of IGF-2 have centred on body growth analysis and its polymorphism effects on growth-related traits.

A study was conducted with Muscovy ducks to analyze the association profile of IGF-2 polymorphisms with egg-laying traits (Ye et al., 2017). There were five SNPs detected in the 5′ flanking region of the IGF-2 gene. Results from mixed pool sequencing analysis led to selection of two of the SNPs, C-1704 G and A − 1864 G, because these were probably correlated with egg-laying traits. Association analysis confirmed that the two SNPs of IGF-2 were both associated with relatively greater egg numbers at 59 weeks of age. Additionally, ducks with the AG genotype layer more eggs than ducks with the GG genotype, −1864 G ($P < 0.01$), whereas ducks with the GG genotype layer more eggs than the those with the CC genotype, C-1704G (Ye et al., 2017).

4. Conclusion

The reproductive performance of ducks has improved as a result of the traditional method of selection, but further improvement using this approach has been slow. Identifying polymorphisms of candidate genes has enhanced the selection of ducks with greater reproductive performance resulting in an increase of egg production in ducks. The expression of the GH, PRL, OIH, FSHR, and IGF-2 genes has been studied in the ovary, and the polymorphisms have been found to affect egg-laying traits. The SNPs of these genes can serve as novel genetic markers to select genotypically superior ducks to increase the production of eggs with high-quality nutritional constituents.

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Declaration of Competing Interest

No conflict of interest exists in the submission of this review, and the review is approved by all authors for publication. I would like to declare on behalf of my co-authors that the work described is original research that has not been published previously and is not under consideration for publication elsewhere, in whole or in part.

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