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Review Article

Prospective Regulators of Domestic Goose Ovarian Follicles Development and Survival: Review

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ABSTRACT

Geese are seasonally breeding animals, and their egg yield depends on various genetical, endocrine, and biophysiological interactions primarily occurring in ovarian organs. The major constraint hindering the extensive goose production is a lengthy brooding cycle of which the research focus now is on shortening the brooding period through investigating the folliculogenesis dynamics. Follicle development/growth starts with the recruitment of small undifferentiated primordial follicles to a well-defined structure of large fertile follicles known as pre ovulatory follicles. This progression can be determined by the differentiation of protective follicular membranes, namely the theca and granulosa cells surrounding the oocyte. The interaction of external and locally produced growth factors effectively targets these cells and their secreted hormones as the key elements participating in follicle development and survival. This review provides an overview of anti-müllerian hormone (AMH), bone morphogenic protein 4 (BMP4), heat shock protein 27 (HSP27), Small mothers against decapentaplegic homolog 9 (SMAD9), inhibins, and melatonin contribution at different developmental stages of geese ovarian follicles. This review summarizes the available information on the selected biological regulators associated with goose egg production. This information will be useful in genetic marker assisted breeding aiming at raising highly prolific generation of geese in future.

INTRODUCTION

Enhancing food security through livestock husbandry is of highest priority worldwide. Lately, there is an increasing demand for goose meat for human consumption (Ni *et al*., 2022). Goose meat is highly preferred as it is rich in niacin, fat, vitamin A, protein, sugar, and vitamin B and considered healthy since it has less cholesterol and low fat but precious in protein (Ibtisham *et al*., 2017). In garments industry, goose feathers are important inputs to final product for clothing and bedding (Liu *et al*., 2020).

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The most reared domestic goose breeds are the well-known species of *Anser anser* and *Anser cygnoides* descending from ancestral family Anatidae. *Anser anser domesticus* is largely raised in Western Asia, Northern Africa, and Europe instigated from the Greylag goose (Kozák, 2019). *Anser cygnoides domesticus* is mainly bred in eastern Asia, known as indigenous Chinese goose evolving from the Swan goose (Gyuranecz *et al*., 2020).

Statistically, China is the leading country in goose farming as it produces roughly 95.2% of goose meat, thus 2.4 million tons of 2.5 million tons worldwide annual meat production (Yu *et al*., 2020). Based on universal percentage proportionality, goose industrialization is still tracking from behind and this is linked to poor egg laying performance. The poor egg laying performance of geese is affiliated with environmental adaptability, nutrition, diseases outbreak, strong broodiness traits, and chiefly prolonged follicle recruitment cycles (Sun *et al*., 2019; Wang *et al*., 2021).

Folliculogenesis commences with one follicle being selected from a resting pool of primordial follicles entering

prehierarchical, hierarchical, and ovulatory phase while other competitive follicles undergo cell degeneration (Sello *et al*., 2020). Avian follicle developmental stages are classified according to size, color, and the thickness of follicular membranes (theca and granulosa cells) (Lei *et al*., 2020). Development and selection of dominant follicle to attain maturity and its readiness to ovulate rely on endocrine signals from pituitary gland and paracrine signals from ovarian follicles and other growth factors (Songsasen and Nagashima, 2020). These orchestrated mechanisms of follicular development are also not functioning in isolation from molecular driven signaling cascades. The nonhierarchical stage of ovarian follicles is the critical phase of the successive fundamental processes to choose one healthy dominant follicle for ovulation per cycle (Liu *et al*., 2015). Therefore, this stage of folliculogenesis requires extra effort to unravel the growth factors involved, gene profiling, and unique signaling pathways. Currently, the next generation sequencing (NGS) technique is leading in various fields of studies including those interested in goose egg production, offering useful techniques in analyzing gene expression patterns at each stage ovary development (Ouyang *et al*., 2020; Qin *et al*., 2021). To our knowledge, there are no studies conducted to summarize the discoveries on the contributary effects and role associated with biological growth factors (Anti müllerian hormone (AMH), bone morphogenic protein 4 (BMP4), small mothers against decapentaplegic homolog 9 (SMAD9), inhibins, melatonin hormone, and heat shock protein 27 (HSP27) during goose ovarian follicular development. This literature review will focus on developmental stages of goose ovarian follicles along with somatic follicular membranes and the phenotypic differences between the two goose species as well as genes and transforming growth factor β (TGF-β) family members associated with follicular developmental stages.

The information used in this review was obtained from scientific research articles published in three databases PubMed, Google Scholar, and ScienceDirect. The general keywords used in search for relevant articles included “goose ovarian follicles”, “gene expression”, “egg production”, “poultry”, “prehierarchical follicles”, “hierarchical follicles”, “AMH”, “BMP4”, “SMAD9”, “inhibin”, “melatonin hormone”, and “HSP27”. The findings of each study were compared to the citations in the discussion sections for comprehensive inclusion of such information to the current review article. These data used in this review were extracted from English written research articles and review articles, however, review articles were mainly used to trace back to the original research articles. The findings about the candidate gene from the kingdom animalia were considered to support the relevance of particular gene in reproduction in comparison to goose. The data provided in this review was not limited to years of publication. In total, this review is comprised of 139 references that provide a comprehensive analysis of the selected topic.

EGG YIELD OF DIFFERENT BREEDS

A number of factors affect goose egg yield such as breed, environment, and age. Table I summarizes the annual performance for individual laying breed. The annual egg production per bird ranges from 25 to 100 eggs.

Table I. Estimated egg yield per annum for different breeds of goose.

Breeds	Species	Distribution by provinces	Annual egg production per bird	Reference
Zi goose	*A. cygnoides*	Jilin and Heilongjiang Province	80-100 eggs	(Ji *et al*., 2020; Zhang *et al*., 2013)
Zhedong goose	*A. cygnoides*	Zhejiang province	30–40 eggs	(Zhao *et al*., 2013)
Huoyan goose	*A. cygnoides*	Liaoning province	70 to 100 eggs	(Wang *et al*., 2011)
Mangang goose	*A. cygnoides*	Guangdong Province	30 to 50 eggs	(Qin *et al*., 2013b)
Sichuan white goose	*A. cygnoides*	Sichuan province	80 to 100 eggs	(Kang *et al*., 2014)
Xupu goose	*A. cygnoides*	Hunan Province	30 eggs	(Qin *et al*., 2021)
Taihu goose	*A. cygnoides*	Taihu Lake drainage in eastern China	75 eggs	(Liu *et al*., 2021)
Shitou goose	*A. cygnoides*	Raoping County, Guangdong Province	25 eggs	(Liu *et al*., 2021)
Wanxi white goose	*A. cygnoides*	Anhui province	25 eggs	(Chen *et al*., 2012b)
Wanjiang white goose	*A. anser*	Anhui province	More than 90 eggs	(Chen *et al*., 2011)

DOMESTIC GOOSE SPECIES

Swan goose (Anser cygnoides)

Anser cygnoides goose species evolved from wild swan goose (Fig. 1A) mainly in Central Asia, Mongolia, South Eastern and Northern China, Southern Russia and wintering in North/South Korea and Eastern and Central China (Wang *et al*., 2016). Loss of habitat due to unwarranted hunting of swan goose caused a falloff in their distribution and eventually is regarded as endangered large goose species (Randler, 2003). Wild swan goose is recognized by its eloquent plumage with grey stripes, long black bill, and orange legs whereas the domesticated swan goose species all have white plumage with orange legs and bill (Ren *et al*., 2021). Mostly, *A. cygnoides domesticus* farmed in Africa (African goose) and China (Chinese goose) is distinguishable by a pronounced protrusion on the frontal area of the skull although obscure in *A. cygnoides* wild species (Mead, 2013). This protrusion is commonly referred to as a "knob". The knob size varies relatively within and among the breeds of *A. cygnoides* congruent to age and sex (Deng *et al*., 2021). The knob is slightly larger in male than in females and bigger in grownups than adolescents (Ji *et al*., 2021).

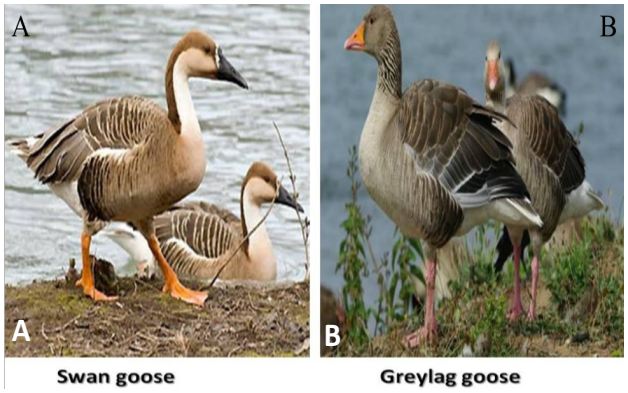

Fig. 1. Ancestral species of largely domesticated goose breeds (Makram, 2018).

Greylag goose (Anser anser)

The greylag goose (Fig. 1B) belongs to phylum Chordata in the class Aves (Basyouny *et al*., 2014). *Anser anser domesticus* goose descended from an ancestor wild goose called greylag (Honka *et al*., 2018). *A. anser* is widely distributed in European countries mainly in Ukraine, Hungary, and Poland (Cilavdaroğlu *et al*., 2020). *A. anser* goose is characterized by varying color of plumage distributed from cranial to the caudal regions and mostly appears to be brown, grey white or cream/buff with pink or orange legs (Yang *et al*., 2022). *A. anser* have either chunky, duck-like or orange long beak and thick neck. *A. anser* goose on average weighs 2.9-3.7 kg contingent on sex, season, and age, body length ranges between 76-89 cm and wingspan stretching between 147-180 cm (Fox and Kahlert, 2005; Mirzaeinia *et al*., 2020). This species is large, heavy and show limited flying capabilities (Islam *et al*., 2016).

BROODING IN GOOSE

Brooding is the caring behaviour displayed by domestic female fowls resulting in temporary termination of oviposition (Jiang *et al*., 2010). Brooding fowls are overprotective by obstinately sitting on the nest to incubate clutch of eggs, leave the nest for short stretch of time, reduced food and water intake, and the elevated body temperature (Romanov *et al*., 2002). The cessation of laying is orchestrated by fallopian and ovarian atrophy (He *et al*., 2022). At this period, the white pre-hierarchical follicles (WPF) are prominent while the yellow pre-hierarchical follicles (YPF) diminish limiting the successive transition of follicle growth/development to ovulation (Liu *et al*., 2018). The brooding comportment of goose is identical to that of chicken; however, goose has strong brooding characteristics based on the clutch size and total number of eggs laid per mature female per annum (Chen *et al*., 2014). In birds, folliculogenesis is regulated by number of factors including the external stimulus (light) actuating the endocrine activity triggered by hypothalamic-pituitary-gonadal (HPG) axis (Wang *et al*., 2019). For instance, light stimulates the hypothalamus to secrete gonadotrophin-releasing hormones (GnRH) to the pituitary gland which synthesize and release follicle stimulating hormone (FSH), prolactin hormone (PRL) and luteinizing hormone (LH) (Fattah *et al*., 2021). The FSH, PRL, and LH affect the gonads to functionally initiate sex steroid hormone release "estrogens, gestagens, and androgens" and gametogenesis "oogenesis and spermatogenesis" (Luan *et al*., 2014). The FSH, PRL, and LH have been shown to significantly contribute to folliculogenesis and therefore suggesting their potential role during folliculogenesis.

FUNDAMENTAL UNITS OF OVARIAN FOLLICLE AND SUBSTANTIAL DEVELOPMENT REGULATORS IN GOOSE

Follicular development and ovulation are facilitated by biological crosstalk between the granulosa cells, theca cells, and oocyte through autocrine, endocrine, and paracrine signaling controlled by HPG axis (Li *et al*., 2021). The anatomy and physiology of mammalian ovaries have been comprehensively studied. However, in

the geese, the knowledge about the inter and extracellular factors modulating the follicle viability is inadequate. The corresponding signaling pathways during follicle development trigger heat shock proteins (HSPs), small mothers against decapentaplegic (SMAD) related genes, members of transforming growth factor family inclusive of AMH, bone morphogenic proteins (BMPs), inhibins, as well as the glands secretion products such as melatonin in a stage and time dependent manner reaffirming their indispensable roles in follicle maturation.

Oocyte

The release of a mature healthy oocyte for fertilization is the center for female reproduction process. Oocyte maturation is initiated as soon as the follicle enters the pool of growing follicles and is almost completed upon the antral follicle (Sen and Caiazza, 2013). Before fertilization, multiple intercellular communications controlled by various signaling pathways at different stages of development are essential for gaining the developmental competence of the oocyte. These cellular intercommunications are of crucial importance to maintain the oocyte arrested in the diplotene stage of prophase 1 of meiosis during prenatal life or immediately prior to birth (Fabritius *et al*., 2011). During follicle development, the ovulatory gonadotropins known as FSH and LH surge stimulate the resumption of meiosis which progress by orchestrated disassembly germinal vesicle (nuclear envelope) termed germinal vesicle breakdown (GVBD) and eventually the oocyte enters the metaphase II (MII) stage until fertilization (Zeleznik, 2004).

Granulosa cells

Follicular growth and development begin with the formation of several layers from the somatic cells, oocyte enlargement and a fluid filled antrum. During the early antral follicle recruitment stage, follicular growth relies dependently on the pituitary gonadotrophins such as FSH (Tiwari *et al*., 2015). At this stage, the antrum divides the granulosa cells into two separate cell layer parts: the outer layer (mural granulosa cells) and inner layer (cumulus cells) which encircle the oocyte. The mural granulosa cells (MGCs) possess endocrine function and support follicle growth whereas the cumulus granulosa cells (CGC) have a high rate of proliferation, low steroidogenic capacity, low LH receptor (LHR) expression and high levels of insulin growth factor I (IGF-1) (Mehlmann, 2005). Decreased granulosa cell-oocyte crosstalk impedes the transmission of nitric oxide (NO), guanosine 3′,5′-cyclic monophosphate (cGMP), adenosine 3′,5′-cyclic monophosphate (cAMP) levels to the follicular oocyte (Jahromi *et al*., 2015). Granulosa cells provide nutrients for oocyte maturation through cell-to-cell gap junction intercommunications (Chaube *et al*., 2005) and their intactness protects oocytes from oxidative stress damage by reactive oxygen species (ROS) (Tiwari *et al*., 2017). Granulosa cells generally produce sex steroids, and numerous growth factors that interact with the oocyte during its development. The sex steroid production consists of FSH that stimulates granulosa cells to convert androgens produced by thecal cells to estradiol by aromatase during the follicular phase of the reproduction cycle (Magoffin, 2005).

Theca cells

The theca cells are divided into two layers, the theca interna and the theca externa. The theca interna produces androstenedione, and indirectly produces 17β estradiol (E2), thus providing the neighboring granulosa cells with androstenedione, which can be converted into estradiol by enzyme aromatase (Wu *et al*., 2015). Estradiol has multiple functions on granulosa cells including cell apoptosis inhibition, increasing gonadotrophin expression, promote folliculogenesis, and promotes LH receptors formation on the granulosa cells, which also possesses FSH receptors (Manna *et al*., 2009). Additionally, the theca interna possesses luteinizing hormone receptors and greatly vascular with no FSH. Theca cells are also a source of keratinocyte growth factor (KGF), a factor that has been shown to suppress apoptosis in cultured preantral follicles. Moreover, theca cells are much differentiated with structural characteristic features of steroid-secreting cells including agranular endoplasmic reticulum containing enzymes necessary to produce androgen; lipid vesicles which store the cholesterol esters (precursors for steroid hormone synthesis) which are transported into the mitochondria by steroidogenic acute regulatory protein; and abundant mitochondria with vesicular cristae which contain the first enzyme in the steroidogenic pathway (cholesterol sidechain cleavage cytochrome P450 (CYP11A)) (Ginther *et al*., 2003).

Anti-mullerian hormone (AMH)

Anti-Mullerian hormone (AHM), formerly known as Mullerian-inhibiting substance (MIS), belongs to the transformation growth factor beta (TGF-b) superfamily produced by the sertoli cells in male's testis and granulosa cells in females during ovarian follicular development and growth (Zhao *et al*., 2018). It is however undisputable that more investigations about AMH focused on mammalian ovary development as it possessed paramount regulatory function during the transition of primordial follicles from the resting pool of follicles to mature ovary ready for ovulation (Nilsson *et al*., 2011). AMH have been shown to restrict the pre-hierarchical follicles maturation

in laying hens (Huang *et al*., 2021b), inhibit initiation primordial follicles in mouse (Durlinger *et al*., 2002), bovine (Yang *et al*., 2017), and human (Carlsson *et al*., 2006) by deactivating the granulosa cell sensitivity to FSH (Carlsson *et al*., 2006). In goose, the abundance of *AMH* was inversely proportional to the thickness of the ovarian granulosa cells as the follicles progress towards maturity (Yang *et al*., 2019), and less detected in laying goose than brooding goose in time specific manner (Wang *et al*., 2021). The *AMH* mRNA levels increased significantly in a stage dependent manner during follicles development and gradually drop to optimum levels over time (Hu *et al*., 2021). Immunized goose against AMH showed improvement in follicles development rate with an increase in number of eggs per cycle and established the short brooding period (Chen *et al*., 2020a; Zhang *et al*., 2021a).

Heat stress and heat shock protein 27 (HSP27)

Internal (physiological) and external (environmental) stress weaken the follicular walls, thereby hindering normal ovarian activities related to growth and development (Abdelnour *et al*., 2020). Heat stress has lethal effects on the female reproduction performance of animals as it causes the gonadal hormones imbalances and consequently affects oocyte development and quality, thus reducing fertility (Bei *et al*., 2020; Tu *et al*., 2016). HSP27 is a member of the p38 MAPK signaling pathway classified as class II type of small heat shock proteins (15-40 kDa) widely distributed in various tissues induced by various intra or extracellular stress stimuli including heat shock, ROS, and death receptor ligation (Bei *et al*., 2020). HSP27 proteins are involved in multiple cellular functions such as signal transduction and development, cytoskeletal integrity maintenance, protein degradation and folding, cell cycle, cell death differentiation, and stress tolerance (Santana *et al*., 2020). Previous studies indicated that HSP27 acts an anti-apoptotic chaperon that inhibits the activation of cell death ligands (caspase 9) by obstructing the mitochondrial cytochrome C collaboration with apoptotic protease activating factor (APAF) from arbitrating programmed cell death signaling cascades (Shan *et al*., 2021). Follicular atresia is referred to as automated follicular cells degeneration mainly the granulosa and theca cells exposing the oocytes to detrimental apoptotic effects initiated by TNF-and Fas death receptor proteins (Sugimoto *et al*., 2010). HSP27 transcripts or proteins were detectable in normal human oocyte and the polycystic ovarian syndrome (PCOS) and can be associated with oocyte maturation and fitness to reach ovulatory stage (Cai *et al*., 2013). The mRNA expression patterns of *HSP27* in bovine granulosa and theca cells varied with the condition of the follicles and maturity stage (Velazquez *et al*., 2010). In mice ovaries, the distribution of *HSP27* transcripts showed a downward regulation expression over time with the highest level at initial stage of heat shock treatment indicating that *HSP27* genes play a protective role from heat stress induced damage (Bei *et al*., 2020). Although HSP27 has been identified as anti-apoptotic protein, its downregulation in mouse enhanced the oocyte development and maturation and yet improved oocyte apoptosis at early stage by activating extrinsic, caspase 8-aided cascade (Liu *et al*., 2010). We have for the first time revealed that goose pre-hierarchical follicles convey *HSP27* gene during normal ovarian growth/development with predominance in both theca cells and granulosa cells of the middle white follicle suggesting its potential contributary effects during folliculogenesis (Sello *et al*., 2020). The functional role of HSP27 during the morphological changes related to follicular development/growth and degeneration needs to be explored to understand molecular mechanisms underlying goose folliculogenesis.

Bone morphogenetic protein 4 (BMP4)

Bone morphogenetic proteins (BMPs) are the greatest growth factors, members of TGF-b superfamily functioning in cell differentiation, proliferation, growth, and degeneration (Halloran *et al*., 2020; Shimasaki *et al*., 2004). These groups of proteins were first discovered during bone formation (Urist, 1965). The inquisitiveness on BMPs existence further discovered their involvement in autocrine/ paracrine regulation of mammalian ovary development and their abundance vary with cell types and developmental stages (Shimasaki *et al*., 1999; Shimizu *et al*., 2004). According to Lankford and Weber (2010), downwards expression of *BMP4* was inversely proportional to the stage of ovarian developmental stage in rainbow trout. Furthermore, *BMP4* higher abundance was detected in ovarian somatic cell layers than oocytes in Zebrafish ovary (Li and Ge, 2011). Likewise, the *BMP4* expression levels varied in chicken granulosa and theca cells preovulatory follicles with exceptional abundance in the granulosa cells of largest follicles (F1) suggesting its possible functional contribution in proximity to ovulation (Onagbesan *et al*., 2003). BMP4 was reported to enhance prehierarchical follicles resistance to apoptosis and promoted follicles development in chicken granulosa cells exposed to physiological endoplasmic reticulum stress (Yao *et al*., 2020). Besides the ovary cell types, BMP4 immunoreactions were detected in other reproductive tract organs such as oviduct and uterus throughout estrus stages/ cycle in mice (Tanwar and McFarlane, 2011). Contrary to chicken, in goose, fewer amounts of BMP4 transcripts

were detected in F1, but predominant in prehierarchical follicles and repressed granulosa cells caspase-mediated cell death through PI3K/AKT/Caspases signaling pathway (Yuan *et al*., 2019). In some studies, BMP4 inhibited the secretion of progesterone by granulosa cells (Pierre *et al*., 2004; Spicer *et al*., 2021) and FSH and FSHb mRNA expression from pituitary cells in ovine (Faure *et al*., 2005). Detection of BMP4 and its receptor molecules in female reproduction organs provides evidence about their contributive effects in maintaining follicular viability.

Small mothers against decapentaplegic homolog 9 (SMAD9)

The development/growth follicles rely mainly on complex interaction of cell-signaling pathways producing either positive or negative feedback information (de Figueiredo *et al*., 2018). The SMAD polypeptides are important signal transducers of TGF-b comprising of different types of BMPs, inhibins, activins, and nodal (Coda *et al*., 2022). The SMAD signaling pathway interaction with BMPs signaling cascades regulate follicular development through binding to distinct forms of receptors (Atwood and Meethal, 2016). According to Chen *et al*. (2012a) receptor-regulated Smads (R- Smads) downstream activities are phosphorylated by BMP type 1 receptor kinases through ligand binding. In mammals, BMP/Smads signaling cascade played functional roles during the dominant follicle selection, follicular atresia, and development (Costello *et al*., 2009; Haugen and Johnson, 2010). Smad9 is a member of R- Smads that acts synergistically or antagonistically with BMP signaling pathways depending on its expression levels (Tsukamoto *et al*., 2014). Interestingly, Smad9 can also be associated with male prolificacy traits as it has been found in reproduction tissues in rams (Chen *et al*., 2020b). According to Zhang *et al*. (2018a) mouse ovarian granulosa cells and estradiol hormone rejuvenation including the LHR transcription were interlinked with *Smad9* expression while its upregulation unveiled negative feedback on FSH secretion and granulosa cells proliferation. Another study by Diaz *et al*. (2011) in *Gallus domesticus* ovarian follicles revealed the up-regulation pattern of *Smad9* mRNA transcripts in an ascending order based on size, which was approximately 10-20-fold expression difference compared to other selected candidate genes of the study. In reference to Yu *et al*. (2019), *Smad9* gene and protein clampdown noticeably increased the annual laying performance in Chinese Wanxi white geese. This was correlated with an increased amounts of LHR expression and Estradiol biosynthesis which are the key hormones in follicle viability for ovulation while no evident shifts observed in expression levels of FSH and progesterone (P4). It was also demonstrated that the variations in Smad9 gene structure can be related to egg laying performance in Wanjiang white geese and hence reaffirmed its potential to be used as genetic marker in selective breeding of prolific geese (Xu *et al*., 2015).

Inhibins

Inhibins belong to the transforming growth factor-β (TGF-β) superfamily, reproductive hormones secreted mainly by testes and ovaries acting as negative modulators of FSH and characterized by their antagonistic interaction with activins (Looyenga *et al*., 2010). Inhibins comprise of α (INHA) and β (INHBA) subunits linked by disulfide bonds actively forming inhibin A (α-βA) and B (α-βB) respectively (Meunier *et al*., 1988). Inhibins have been implicated in female reproduction physiology such as oocyte and follicle maturation, and embryogenesis (Sirotkin, 2011). Previous studies revealed that INHA expression is associated with regulatory functions during folliculogenesis by controlling cell proliferation, sex hormones levels and programmed cell death in the chicken (Cui *et al*., 2019, 2020, 2021). The study of function has also shown that the shutdown of inhibin α subunits increased the granulosa cell death via numerous apoptotic signaling pathways and altered the hormonal production in the mice (Kadariya *et al*., 2015). In the bovine the *in vitro* supplementation of granulosa cells (GC) with inhibin A downregulated the automated cell death induced proteins and hence increasing GC viability in a dose dependent manner (Xu *et al*., 2020). Further study elucidated the presence of inhibin α transcripts and proteins were abundant in sterile allotriploid crucian carp ovaries and testes as compared to diploid red crucian carp (Huang *et al*., 2021a). According to Chen *et al*. (2007), inhibin α gene was dominantly expressed in healthy F1 follicle GC than in GC of follicles undergoing atresia and suppressing this gene under laboratory conditions elevated the granulosa cell death with reduced estradiol levels in Yangzhou geese. Effective immunization against inhibin improved the egg laying performance in Magang and Landaise goose breeds (Huang *et al*., 2007). According to Qin *et al*. (2013a), *INHA* and *INHBA* were highly expressed in GC of mature follicles suggesting their potential in endocrine activities associated with follicular recruitment towards dominant follicles selection and oviposition. It was further reported that Zhedong geese showed reduced brooding period intervals associated with an increasing amount of luteinizing hormone when immunized against INHA anticipating an increase on egg laying trait (Zhang *et al*., 2021b).

Melatonin

Melatonin (N-aceyl-5-methoxytryptamine) is a

chief hormone secreted by pineal gland involved in number biophysiological activities including cytoskeletal organization, biological rhythms, antioxidative associated stress, digestion, neurons, and reproduction in animals (Ezzati *et al*., 2021). The production of melatonin is dependent on the day and night longevity cycle activating necessary biological processes in seasonally breeding organisms (Tabecka-Lonczynska *et al*., 2017). Detection of melatonin membrane receptors (MT1 and MT2) and enzymes associated with melatonin synthesis arylalkylamine N-acetyltransferase (AANAT) and hydroxyindole-O-methyltransferase (HIOMT) in corpus luteum in sheep (Xiao *et al*., 2018) and sows (Zhang *et al*., 2018b) indicating that melatonin may influence reproduction cycle. Melatonin action through its receptors improved the primordial follicle stimulation which involved the regulation of developmental mechanisms of follicular membranes including the sex steroids in *in vitro* in bovine (Feng *et al*., 2018b; Wang *et al*., 2012, 2017, 2018) and mare (Pedreros *et al*., 2011). *In vitro* studies have confirmed that melatonin can enhance the survival and approve meiotic capability of oocytes, upsurges the mitochondrial action supported by decline in ROS production nonetheless of administered dosage in sheep ovarian follicles (Barros *et al*., 2020a, b). Single nucleotide polymorphisms (SNPs) of high-affinity melatonin receptor subtype genes (*MTR1A*, *MTNR1B* , and *MTNR1C*) were quantifiable between closely related species and different organisms linked with the fecundity and seasonal breeding indicating their functional contribution in regulating reproduction traits (Feng *et al*., 2018a; He *et al*., 2019; Naby and Basha, 2016). In accordance with the previous study by Tamura *et al*. (2017), melatonin downregulated number of genes associated with ovarian aging in mice and also reported to accelerate puberty on set in mice by promoting FSH synthesis (Yang *et al*., 2021). These outcomes underline the importance of melatonin in increasing oocyte viability. In chicken, exogenous melatonin triggers mTOR signaling cascade through its receptors, a signaling pathway that promotes folliculogenesis with elevating sex hormones, antioxidant enzymes and controlling granulosa cells propagation and death (Hao *et al*., 2020a, b). In mares, melatonin deferred the embryonic development persuaded by the reduced levels of prolactin and inverse increase in levels of FSH and luteinizing hormone (Wang *et al*., 2014). According to He *et al*. (2014) MTNR1A, MTNR1B, and MTNR1C were predominantly expressed in preovulatory follicles with cumulative tendency from early developmental stage and declined significantly in postovulatory follicles in Sichuan white goose. Another study on identification of SNPs in the goose *MTNR1A* gene revealed the notable variation within the genotypes that could be associated with egg production (Alsiddig *et al*., 2017).

CONCLUSION

In conclusion, avian egg production is a complex interaction between intra- and inter- ovarian signaling pathways orchestrated by hypothalamic pituitary gonadal axis intertwining with multiple growth factors and genetic regulators influencing ovarian follicle maturation. Pertaining to shortening of seasonal brooding in geese, several technical research focused on investigating potential molecular regulators involved in folliculogenesis such as heat shock proteins, and melatonin receptor genes together with some growth factors such as AMH, inhibins, BMP4, and Smad TGF families. The findings of these studies provided insightful information towards increasing egg yield in different goose species. This review summarized the available information on the selected biological regulators intended to improve goose egg production. More studies need to be carried out in order to reveal how these biological processes affect goose laying performance in a species dependent manner and their significance in molecular breeding.

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