| REVIEW ARTICLE |

Hormonal Control of Reproduction in Birds

https://doi.org/10.46419/cvj.58.1.1

Received: 10 April 2026
Accepted: 11 June 2026
Online publication: 30 November 2026

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Abstract

The development and function of the reproductive system of birds is influenced by hormones. The reproductive cycle is controlled by the action of the hypothalamic-pituitary-gonadal axis, which regulates the ovulatory-oviposition cycle. This highly coordinated sequence of endocrine and physiological events consists of follicle recruitment and development, ovulation, egg production and oviposition. The hypothalamus secretes gonadotropin-releasing hormones, while the pituitary gonadotropins are luteinizing hormone (LH) and follicle-stimulating hormone (FSH). The key roles of LH are stimulation of progesterone synthesis and induction of ovulation. In males, LH stimulates Leydig cells to differentiate and subsequently produce testosterone. In females, FSH affects follicle growth and development of the dominant preovulatory follicle. In male birds, the main role of FSH is to stimulate spermatogenesis. Prolactin influences incubation and nesting behaviour, including building and marking of the nest, and the subsequent incubation of eggs. The main ovarian hormones are oestrogen and progesterone. Oestrogen, mostly produced in theca cells, are responsible for the development and maintenance of female genital organs and secondary sexual characteristics, and they stimulate lipid mobilisation for yolk synthesis and mobilisation of calcium for the eggshell. Progesterone, produced in the granulosa cells of larger follicles, stimulates the growth of the genital organs and gonadal function, preventing the development of additional preovulatory follicles. The most important androgenic hormone is testosterone, which stimulates sperm production, the development of male sexual characteristics, bone and muscle growth, and influences reproductive behaviour in male birds. Understanding the avian photoperiodic response and nutrient requirements plays an important role in optimising reproductive cycle and egg production in controlled poultry production systems.

Keywords: *reproductive system; hormonal regulation; hypothalamic-pituitary-gonadal axis; ovulation; oviposition; egg incubation*.

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Introduction

Throughout their lifespan, birds employ various strategies that enable reproduction, ensuring species survival under diverse environmental conditions. The avian reproductive system is unique; females produce eggs, which in hens are formed within a 24-hour period (Roberts, 2004). All bird species are oviparous, and none exhibit viviparity (Bellairs, 2014).

The ovary and oviduct are the principal organs involved in egg production in birds. The primary function of the ovary is the development of the oocyte until ovulation. The oviduct is responsible for the transport of the oocyte in the form of yolk and for the complete formation of the egg. The oviduct also serves as the site of sperm storage and transport, fertilisation, and early embryonic development. In addition to the female reproductive organs, the male reproductive organs should be considered, as they are responsible for the production of spermatozoa and seminal plasma. Furthermore, the reproductive organs produce hormones that regulate reproductive processes.

The term *hormone* refers to a group of chemical signalling substances synthesised and secreted in small quantities by endocrine glands. These molecules are subsequently released into the bloodstream and transported to distant target organs, exhibiting tissue specificity, through which biochemical processes in the organism are regulated. Hormones, as chemical messengers, play a fundamental role in egg production and reproductive processes.

Hormonal regulation is controlled through the integrated action of the hypothalamus, pituitary gland, gonads, and parathyroid glands, liver and kidneys essential for the activation of vitamin D. Hormones act directly on the reproductive systems of both female and male birds. The aim of this paper is to provide an overview of the hormonal regulation of reproductive organ development, explore the regulation of follicular growth and selection, differentiation, ovulation, and regression, and examine the basic mechanisms involved in the synthesis of egg components and egg production.

Literature Search

A literature search was conducted in PubMed, Scopus, and Web of Science between October 2025 and March 2026 to identify publications on the hormonal control of reproduction in birds. The search included the keywords “reproductive system”, “hormonal regulation”, “hypothalamic-pituitary-gonadal axis”, “ovulation”, “oviposition”, and “egg incubation”, together with related terms such as “GnRH”, “LH”, “FSH”, “prolactin”, “oestrogen”, “progesterone”, and “testosterone”. Boolean operators AND and OR were used to combine search terms. Peer-reviewed original research and review articles published in English were considered, with particular emphasis on studies addressing endocrine regulation of avian reproduction. Relevant additional studies were identified by screening reference lists of selected publications. Both recent studies and earlier publications describing important discoveries and fundamental mechanisms of avian reproductive endocrinology were included.

Development of the reproductive system in birds

Domestic laying hens represent a widely used model for the study of the reproductive system and the mechanisms underlying egg production (Smith et al., 2007; Rahman, 2013). The reproductive system in birds develops in two phases. Development begins within the fertilised egg during embryonic development of the chick, during which undifferentiated reproductive organs develop concurrently with other organs of the body (Hamburger and Hamilton, 1992). The second phase takes place post-hatch, during sexual maturation, when the reproductive organs grow and become fully functional under the regulation of the hypothalamic-pituitary-gonadal axis (HPG axis).

The embryonic reproductive system originates from the intermediate mesoderm, from which the paired urogenital ridge forms by the third day of development (Bellairs and Osmond, 2014). Early gonadal development occurs in an indifferent stage, after which differentiation is strongly influenced by hormones. Hormonal manipulation can reverse sexual development, such as feminisation of male gonads by oestradiol (Faucounau et al., 1995; Rosati et al., 2021) or testicular development in females when aromatase activity is inhibited (Nakabayashi et al., 1998).

Circulating primordial germ cells (PGCs) reach the germinal crescent in two-day-old chick embryos and remain there until vascularisation, after which they enter the bloodstream. Peak numbers of circulating PGCs occur at stage 14 (50 h of embryonic development) (Tajima et al., 1999). They exit circulation and colonise the gonads, most likely via chemotactic mechanisms (Kuwana et al., 1986) rather than passive entrapment (Kuwana and Rogulska, 1999), and then give rise to gametes (Campanale et al., 2019).

During later development, an asymmetric accumulation of PGCs is observed, with higher numbers present in the left gonad (Zaccanti et al., 1990). Enhanced apoptosis occurs in the right gonad, leading to atrophy of the right ovary prior to hatching (Ukeshima and Fujimoto, 1991).

The indifferent gonad contains rete cords and primary sex cords. Rete cords appear on day 5 as epithelial structures in the mesenchyme. In males, they later canalise and connect the primary

Table 1. Overview of hormones influencing avian reproduction.

Hormone	Secretion site	Target cells / tissues	Effect
GnRH (*Gonadotropin-Releasing Hormone*)	Hypothalamus	Anterior pituitary gland	Stimulates the pituitary gland to synthesise and secrete LH and FSH
LH (*Luteinizing Hormone*)	Pituitary gland	**Male**: Leydig cells **Female**: Granulosa cells (F1 follicles) and theca cells	**Male**: Stimulates Leydig cell differentiation and testosterone production. **Female**: Stimulates progesterone synthesis in mature granulosa cells (inducing ovulation) and androgen synthesis in theca cells.
FSH (*Follicle-Stimulating Hormone*)	Pituitary gland	**Male**: Sertoli cells **Female**: Granulosa cells (of small, pre-hierarchal follicles)	**Male**: Stimulates spermatogenesis by supporting and nourishing developing sperm cells. **Female**: Promotes growth, differentiation, and selection of prehierarchal follicles; prevents follicular atresia.
Prolactin	Pituitary gland	Central nervous system (CNS) / Brain	Influences parental behaviour, including nest building and marking, and subsequent incubation (brooding) of eggs.
Oestrogen	Ovarian theca cells	Female genital organs, liver, and secondary sexual characteristics	Stimulate development and maintenance of reproductive organs, secondary sexual characteristics, and lipid mobilisation for yolk synthesis; mobilisation of calcium for eggshell.
Progesterone	Ovarian granulosa cells (of larger follicles)	Hypothalamic-pituitary axis and genital organs	Stimulates reproductive organ growth, regulates the ovulatory LH surge and blocks the maturation of excess preovulatory follicles.
Testosterone	Leydig cells (testes)	Musculoskeletal system, testes (Sertoli cells), and brain	Stimulates muscle, bone growth, maintains male secondary sexual characteristics, stimulate sperm production, influences courtship and reproductive behaviour.

sex cords with the Wolffian tubules, forming the rete testis. This connection does not form in females. Primary sex cords arise at the end of day 5 and differentiate into seminiferous tubules in males and medullary cords in females. Proliferation of both cord systems leads to gonadal enlargement and bulging of the genital ridge into the coelomic cavity (Bellairs and Osmond, 2014).

During the first 5–7 days of incubation, gonads are bipotential, with an inner medulla producing androgens and an outer cortex producing oestrogen (Méndez et al., 2003). Sex differentiation begins around day 6.5, with oestrogen directing ovarian development and androgens directing testicular development (Squires, 2003). After gonadal differentiation begins, aromatase expression, essential for the synthesis of oestrogen, becomes female-specific and higher in the left ovary than in the right (Villalpando et al., 2000). Normal male development involves anti-Müllerian hormone production (Oreal et al., 1998; Smith et al.; 2007) and Sox9 expression in the genital ridges (da Silva et al., 1996).

In male development, the sex cords proliferate by day 7, confining the rete cords to the hilum, while primary sex cords continue branching and only canalise around day 20. PGCs begin dividing into spermatogonia around day 13 (Bellairs, 2014). Sertoli and steroidogenic cells originate from mesonephric mesoderm (Sekido and Lovell-Badge, 2007).

Ovarian differentiation becomes evident on days 7–8 with expansion of the primary sex cords to form the medulla, while secondary sex cords derived from the epithelium form the cortex. PGCs localise to the secondary sex cords and differentiate into oogonia by day 7 (Bellairs and Osmond, 2014). The left ovary becomes fully functional, with a stromal medulla and a cortical region containing meiotic oocytes surrounded by granulosa and steroidogenic cells (DeFalco and Capel, 2009). In both sexes the left gonad is larger than the right and contains more PGCs (Birkhead et al., 1998; Villalpando et al., 2000).

Embryos initially possess both Wolffian and Müllerian ducts, reflecting the bipotential nature of the reproductive system. By day 8 of incubation, females exhibit a higher density of progesterone receptor-positive cells in the urogenital sinus epithelium (Gasc, 1991). The Wolffian duct functions early in mesonephric excretion and later forms the male genital duct, while regressing in females. Müllerian ducts develop later alongside Wolffian ducts and appear to depend on them for induction and guidance. In males, Müllerian ducts degenerate from day 8, likely under the influence of testicular hormones, and disappear by day 12 (Wolff, 1953).

Recent evidence shows that the Müllerian duct originates as a placode-like epithelial thickening closely associated with the Wolffian duct (Jacob et al., 1999). The Mulerian duct extends posteriorly through proliferative cell migration along its basal lamina (Guioli et al., 2007). In females, the ducts fuse with the cloaca by day 11, and the left duct later differentiates into oviductal regions.

External genitalia arise around the cloaca on approximately day 6 of incubation, forming a genital tubercle in both sexes. Their development shows marked interspecific variation and is influenced by embryonic hormones, with oestradiol promoting female phenotypes (Coco et al., 1992; Rosati et al., 2021). Morphogenesis of the phallus from the genital tubercle and lateral phallic bodies occurs between days 5 and 8. In males the genital tubercle forms the penis, which varies considerably among species (Bakst, 1986; Perriton et al., 2002).

Overview of hormones regulating reproduction in birds

Hormonal regulation of reproduction in birds is controlled by the integrated action of the hypothalamus, pituitary gland, and gonads (hypothalamus-pituitary gland-gonad axis, HPG axis). The hypothalamus and pituitary gland are located in the brain and form part of the central nervous system. The gonads, ovaries in females and testes in males, are integral parts of the reproductive system, synthesising hormones that directly or indirectly influence changes within the avian reproductive system (Table 1).

The principal endocrine factors regulating egg formation include gonadotropin-releasing hormones, follicle-stimulating hormone (FSH), luteinizing hormone (LH), and prolactin (PRL). Through their actions, these hormones directly stimulate the gonads to produce sex steroids.

Hypothalamic hormones

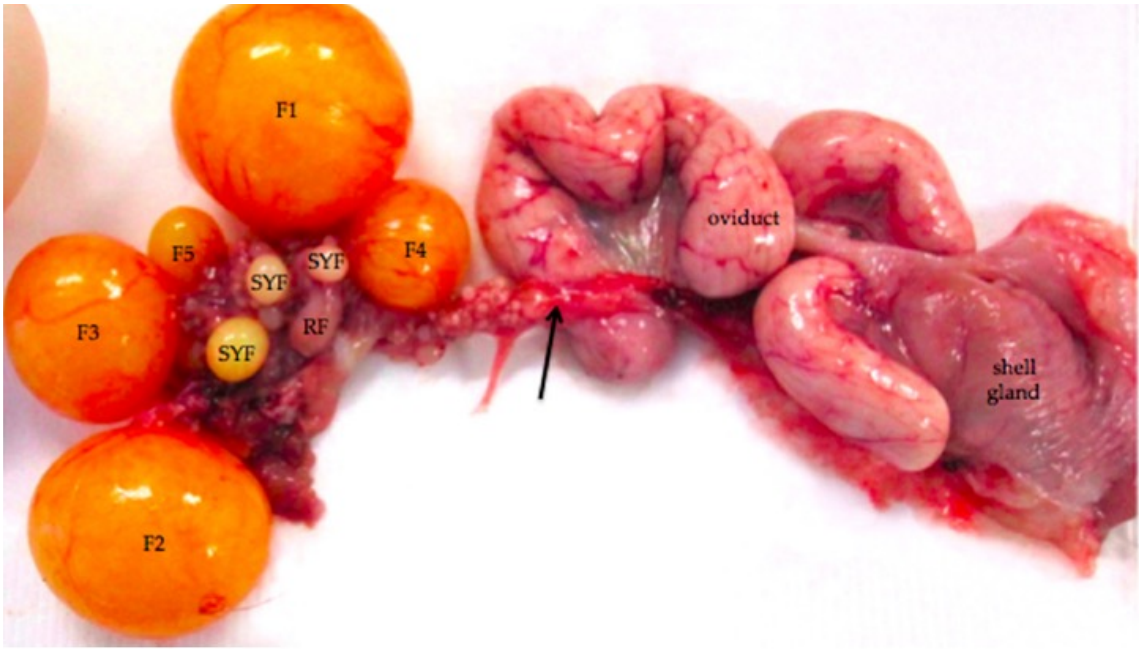
The hypothalamus integrates environmental, gonadal, and somatic signals to coordinate reproductive system development and maturation by regulating pituitary gonadotropin release, which stimulates gonadal growth and function. Proper functioning of the HPG axis is essential for controlling ovulation, semen production, incubation behaviour, and photorefractoriness. It also supports the success of poultry breeding and genetic selection for reproductive traits (Dunn et al., 2009).

The chicken gonadotrophin-releasing hormone (cGnRH) neurons integrate internal and external signals to regulate reproduction via the HPG axis, generating a pulsatile output that determines sexual activity. Chickens possess three GnRH isoforms: cGnRH-I and cGnRH-II and cGnRH-III (Miyamoto et al., 1982, 1984). cGnRH-I is the predominant form and is essential for stimulating anterior pituitary hormone synthesis and release, whereas cGnRH-II is primarily associated with mating and courtship behaviour (Maney et al., 1997). cGnRH-III neurons are located in multiple areas with a higher density around the third ventricle (Bédécarrats et al., 2006). Immunisation against cGnRH-I, but not cGnRH-II, inhibits ovulation. In hens, GnRH release from the hypothalamic-portal system is stimulated by photostimulation and increasing progesterone concentrations. It is modulated by catecholamines, vasotocin, vasoactive intestinal peptide, neuropeptide Y, and opioid peptides (Ottinger and Bakst, 1995). Although GnRH receptors have been identified in the oviduct of laying hens, their functional role in egg formation remains unclear (Mishra et al., 2020).

cGnRH-I mRNA expression, a marker of neuronal activity, is influenced by increased photoperiod (Kang et al., 2006), nest presence or removal (Dunn et al., 1996), and food availability (Mishra et al., 2020). Both cGnRH-I peptide and mRNA levels are negatively regulated by gonadal steroids. At puberty, cGnRH-I neurons show increased sensitivity to stimulatory inputs, likely reflecting steroid-induced hypothalamic reorganisation.

Sexual maturation in chickens is accelerated by longer photoperiods, perceived at the hypothalamic level (Perera and Follett, 1992). Long-day exposure increases cGnRH-I mRNA within 7 days in hens and cockerels (Dunn and Sharp, 1999) and within 3 days in turkeys (Kang et al., 2006). Food restriction decreases cGnRH-I mRNA levels compared with hens fed *ad libitum*, while hypothalamic neuropeptide Y is increased after food restriction and may be involved in the reduction of cGnRH-I gene expression in food-restricted hens (Ciccone et al., 2007). Tsutsui et al. (2000) discovered a hypothalamic peptide that directly inhibits gonadotropin release in quail and named it gonadotropin-inhibitory hormone (GnIH). GnIH and its receptor (GnIH-R) were identified in the avian hypothalamus, gonads and accessory reproductive organs (ovary, testis, oviduct, epididymis, vas deferens). Localisation in granulosa, thecal, interstitial, germ, and epithelial cells indicates that the avian reproductive system can synthesise and respond to GnIH. These findings support a role for GnIH in local autocrine/paracrine regulation of steroidogenesis and germ cell development (Bentley et al., 2008). GnIH acts on the pituitary and GnRH neurons to suppress gonadotropin synthesis and release, thereby inhibiting gonadal function. It is stimulated by melatonin and is evolutionarily conserved in birds and mammals. GnIH operates at multiple levels of the HPG axis and is recognised as a key regulator of vertebrate reproduction (Tsutsui et al., 2010).

Figure 1. Reproductive tract from an 18-month-old laying hen. Five pre-ovulatory follicles are present (F1–F5). Prehierarchal follicles (PHF), small yellow follicles (SYF) and post-ovulatory follicle (RF) are visible. The arrow marks nerves and blood vessels surrounded by mesothelium that enter the ovary at the ovarian hilus. The oviduct and shell gland are labelled (from Apperson et al., 2017).



Pituitary gland hormones

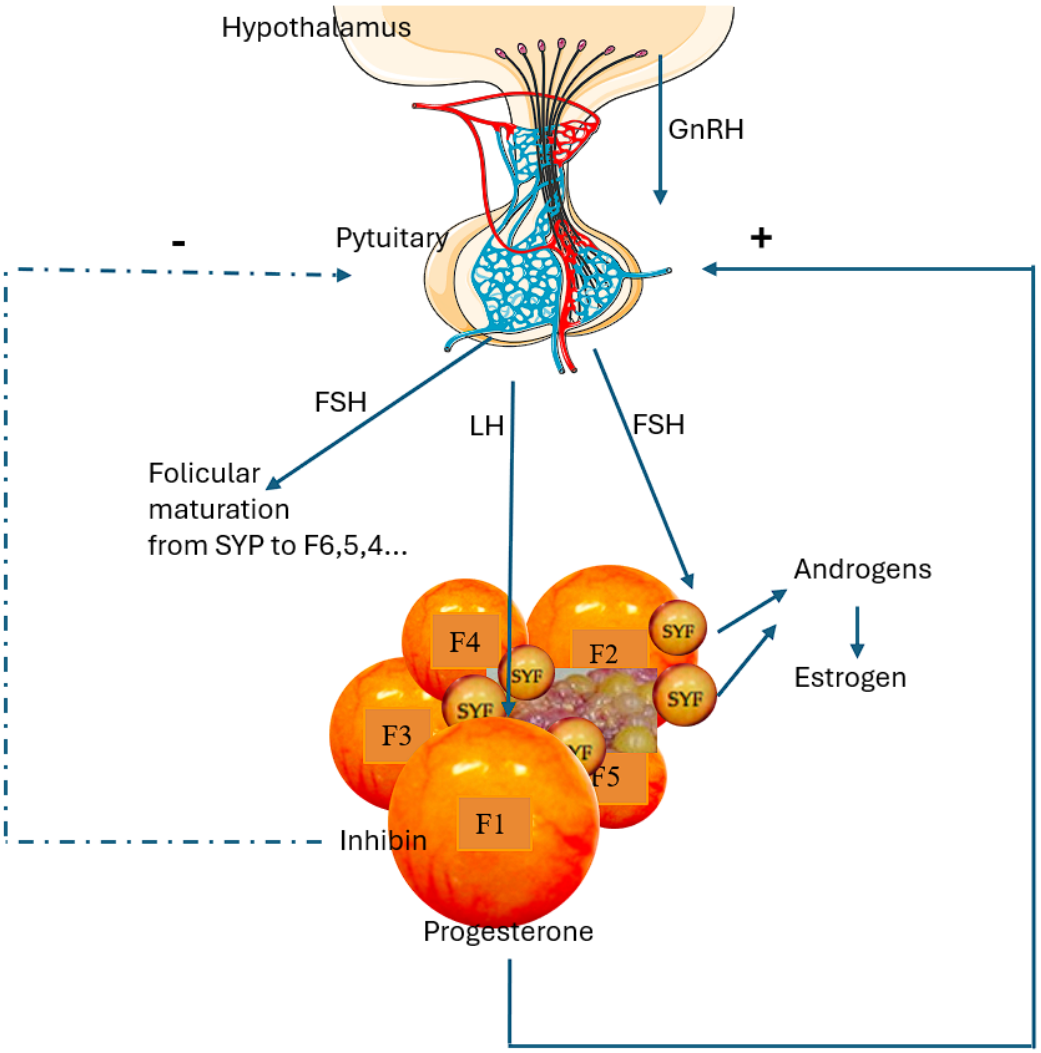
The principal hormones secreted by the pituitary gland are the gonadotropins, namely LH and FSH. In avian species gonadotropins are glycoproteins with an average molecular weight of approximately 30 kDa (Burke et al., 1979).

Follicular development is regulated by FSH maintaining follicular size hierarchy and regulating follicular atresia (Calvo and Bahr, 1983; Hernandez and Bahr, 2003). During the reproductive season, follicles of various sizes can be found in the avian ovary, developing under the influence of FSH and LH (Figure 1). Prior to selection, small follicles produce dehydroepiandrosterone (DHEA), androstenedione, and oestrogen (Etches and Duke, 1984). Follicles reaching ~10 mm are recruited into the yellow yolk-accumulating hierarchy, where four to eight follicles are maintained in a size-based maturation sequence (Johnson, 2015a). As shown in Fig. 2, FSH in the hen regulates selection and granulosa cell development of small follicles, acting primarily on the granulosa layer of small yellow follicles and F6-F3 follicles, where it also stimulates progesterone production (Mishra et al., 2020). After recruitment, yolk-filled follicles predominantly secrete progesterone, with reduced oestrogen production. As maturation proceeds, androgen and oestrogen synthesis declines, and the largest follicle produces high levels of progesterone (Zhang et al., 1997; Johnson, 2015a). The largest follicle (F1) ovulates on the following day, followed by F2, and so forth, at intervals of 24-26 h.

In poultry, the mechanisms controlling FSH synthesis and release remain incompletely understood. Evidence suggests that cGnRH-I modulates FSHβ expression, while oestrogen suppresses it. The potential involvement of the activin-inhibin system and other regulatory factors in controlling FSHβ synthesis and FSH secretion requires further investigation (Dunn et al., 2009). FSH secretion is suppressed by inhibin, produced mainly by the four largest preovulatory follicles (Khalil et al., 2009), particularly F1. Inhibin is a gonadal glycoprotein comprised of two subunits, α and β. Inhibin selectively inhibits FSH release from the anterior pituitary without affecting LH production (Chen and Johanson, 1996; Johnson, 2015a). Together with follistatin, inhibins locally antagonise activin signalling, and the balance between these hormones shifts during follicular development (Knight et al., 2012). Activin is a related protein comprised of two β-subunits. In contrast, activins regulate several intraovarian processes, including follicle growth, granulosa cell proliferation, and oocyte competence (Knight et al., 2012).

In birds, testicular function is regulated by the HPG axis, in which FSH plays a central role in the control of spermatogenesis and LH in steroidogenesis, primarily by acting on Sertoli cells within the seminiferous tubules, stimulating spermatogonial proliferation, supporting germ cell differentiation, and promoting the production of proteins and growth factors necessary for spermatogenesis (Vizcarra et al., 2015).

Figure 2. Hormonal regulation of follicular growth and maturation.



The anterior part of pituitary gland contains target cells for cGnRH-I and cGnRH-II. Responsiveness to both hormones is sexually differentiated in the domestic hen, with greater LH release in both sexes after intravenous injection of cGnRH-II (Proudman et al., 2006). No GnRH peptide provided specific or potent stimulus to FSH secretion, although a high dose of cGnRH-II modestly enhanced FSH levels in the adult male (Proudman et al., 2006).

A preovulatory progesterone surge induces LH release via positive feedback, further enhancing progesterone production and culminating in ovulation (Dunn et al., 2009; Scanes, 2022). The largest LH stimulation of granulosa cells of F1 was observed between 18 and 12 h before ovulation. F2 granulosa cells showed similar patterns, but with lower relative LH stimulation whereas F3 granulosa cells were not stimulated (Calvo et al., 1981). LH stimulated steroidogenesis in all follicles (Chalana and Guraya, 1978; Squires, 2003).

Ovulation is triggered by the LH surge and regulated by circadian rhythms entrained by the light-dark cycle. In the absence of photoperiodic cues, oviposition becomes arrhythmic, although minimal darkness (~1.25 h) can entrain rhythmicity. Ovulation typically occurs 12–18 h after the onset of darkness (Squires, 2003). Prolonged LH surge intervals are linked to lower egg production in turkey hens (Liu et al., 2001). Additionally, LH promotes androstenedione production in the theca cells of the next largest follicle (F2) (Tilly and Johnson, 1989) and enhances the synthesis of progesterone, DHEA, androsterone, and oestradiol in small follicles (Tilly et al., 1991).

After hatching, LH levels slowly increase, while progesterone levels remain low. Hens stop showing broody behaviour between 4 and 10 weeks after the chicks hatch. This corresponds to the time when the LH concentration increases to values found in laying hens (Sharp et al., 1979).

In male birds, LH stimulates the Leydig cells from the interstitial tissue of the testes to synthesis

and secrete testosterone. Testosterone is essential for the progression of spermatogenesis, development of secondary sexual characteristics, and regulation of reproductive behaviour in male birds (Vizcarra et al., 2015). The interaction between LH-induced testosterone production and FSH-mediated Sertoli cell activity ensures proper coordination of spermatogenesis within the seminiferous tubules. Seasonal variations in gonadotropin secretion, often influenced by photoperiod, can therefore significantly affect testicular growth, spermatogenic activity, and reproductive capacity in many avian species (Vizcarra et al., 2015).

In birds, PRL is implicated in the switch from breeding to brooding behaviour (nesting behaviour, nest protection, incubation, cessation of egg laying, and caring for the young). The defeathering, vascularisation, and epidermal hyperplasia of the brood patch is regulated by PRL and oestrogen, and other steroids may also be involved. Contact with eggs further stimulates PRL secretion through a positive feedback mechanism, thereby reinforcing the expression of broody behaviour (Ohkubo et al., 1998; Wang et al., 2020). Circulating levels of PRL are highest during the brooding and parental care of chicks. PRL acts as an adaptive hormone by preventing dehydration through the reduction of urine flow and increased food and water intake (Paster, 1991). Secretion of PRL in broody hens is facilitated by the presence of chicks, and increased concentrations of plasma PRL maintain incubation behaviour (Sharp et al., 1988). PRL secretion increases at the onset of incubation and support the view that the hormone is not secreted at an increased rate while hens are caring for their young (Sharp et al., 1979). The onset of incubation is accompanied by reduced circulating LH, oestrogen, and progesterone. The decline in LH often precedes the cessation of lay, thereby maintaining preovulatory follicles while inhibiting further follicular recruitment (Harvey et al., 1987). Plasma PRL increase parental responses and crop growth without affecting courtship, copulation, or pair maintenance. In males, it increases testes size and gonadotropin receptor expression, while in females it reduces oviduct size and oestrogen receptor expression, and PRL can promote parental care without suppressing reproductive behaviour or HPG axis activity (Farrar et al., 2022). In both the male and female, PRL concentrations gradually decrease as incubation progresses. Individuals with higher PRL concentrations spent more time incubating, and higher PRL in either sex was associated with greater nest survival (Wang et al., 2020).

Elevated gonadal steroids may stimulate PRL secretion and suppress LH via dopaminergic mechanisms. PRL exerts antigonadal effects by reducing LH secretion (likely through inhibition of GnRH), impairing LH-induced steroidogenesis, and potentially interfering with ovarian LH receptor function. Nocturnal PRL surges precede nesting behaviour, suggesting suppression of the HPG axis. Sustained PRL supports brood patch development and maintenance, while visual and tactile stimuli from the nest further reinforce PRL secretion through reflex mechanisms (Harvey et al., 1987).

Regulation of PRL secretion in birds is primarily controlled at the hypothalamic level and involves complex neuroendocrine interactions within the HPG axis. In avian species, PRL release from the anterior pituitary is predominantly under inhibitory control by hypothalamic dopamine. Dopamine acts via D2 receptors on lactotrophs to suppress PRL secretion, and therefore, reduced dopaminergic tone results in increased circulating PRL concentrations (Stewart and Marshall, 2022).

Vasoactive intestinal peptide (VIP) is considered the principal prolactin-releasing factor in birds. VIP is produced in the hypothalamus and stimulates PRL synthesis and secretion by acting directly on pituitary lactotrophs. Changes in VIP expression are closely associated with the onset of incubation and broodiness (Bhatt et al., 2003).

Gonadal steroids, particularly oestrogen, can enhance PRL synthesis, whereas interactions between PRL and gonadotropins (LH and FSH) contribute to the transition from laying to incubation (Harvey et al., 1987).

Gonadal Hormones

Pituitary hormones act directly on the gonads, stimulating sex steroid hormone production. Gonadotrophin receptors are in the gonads, specifically the granulosa and theca cells in the ovary and the Sertoli cells in the testes (Johnson, 2015a). The expression of FSH receptors in the domestic hen is correlated with the development of ovarian follicular responsiveness to FSH, and is highest in the granulosa cells of small yellow follicles (Redshaw and Follett, 1976; Zhang et al., 1997; Johnson, 2015a). Expression of FSH receptors in the theca remains relatively constant in all follicles (Tilly et al., 1991; Mishra et al., 2020). In birds, steroidogenesis in the ovaries begins with cholesterol, with granulosa cells producing progesterone and theca cells synthesising androgens and oestrogen (Marrone and Hertelendy, 1983; Paster, 1991). Androgens are converted to oestrogen by aromatase, which is essential for reproductive system development and the reproductive cycle (Paster, 1991; Rosati et al., 2021).

Oestrogen are mainly produced by the theca cells of the small follicles (Figures 2 and 3). The highest plasma concentration of oestradiol occurs 4–6 h before ovulation, while it is lowest 20 h before ovulation (Etches and Duke, 1984). Oestrogen

plays a key role in egg yolk formation by stimulating hepatic synthesis of vitellogenin and very low density lipoprotein, the principal sources of yolk protein and lipid, respectively (Redshaw and Follett, 1976). Oestradiol also sensitises the hypothalamus to the positive feedback effect of progesterone. This hormone is essential for the growth and development of the oviduct. It also regulates secondary sex characteristics, such as the colour and shape of plumage. Oestrogen controls sexual behaviour and the sexual differentiation of the female brain (Johnson, 2015), in addition to affecting the synthesis of ovalbumin, conalbumin, ovomucoid, and lysozyme, thereby playing a key role in egg white formation (Moran, 1987). Oestrogen with androgens stimulate formation of the medullary bone (a labile source of calcium) (Deng et al., 2010). Based on different experimental models, *in vitro* studies and clinical data, it can be concluded that oestrogen plays an essential role in male reproduction, specifically in the development of spermatozoa (Carreau et al., 2011; Rosati et al., 2021).

Progesterone is mainly produced by the granulosa cells of the larger follicles (F1–F3; Marrone and Hertelendy, 1983). Plasma LH and progesterone peak 4–6 h before ovulation (Redshaw and Follett, 1976; Calvo et al., 1981). During the preovulatory LH surge, only the largest follicle secretes progesterone, stimulating GnRH release and further LH secretion, leading to ovulation. Progesterone receptors in the hypothalamus, pituitary, and oviduct indicate its role in avidin production, myometrial contraction, and eggshell formation (Yoshimura and Bahr, 1991).

Androgens are produced in the theca and granulosa cells of both small and large follicles. Peak preovulatory concentration of testosterone occurs 6–10 h prior to ovulation, whereas the highest concentration of the 5α-dihydrotestosterone occurs 6 h before ovulation (Johnson, 2015). Androgens regulate ovomucoid and ovalbumin gene expression independently of oestrogen (Compere et al., 1981). Androgens also facilitate the development of the secondary sexual characters in hens, such as growth and colouring of the comb and wattle.

The most important androgen hormone is testosterone, produced from cholesterol by the Leydig cells. Synthesis is stimulated by LH from hypophysis. Testosterone inhibits GnRH secretion and acts on the anterior pituitary, reducing its response to GnRH stimulation. As a result, it decreases the secretion of LH and FSH from the anterior pituitary.

Testosterone regulates reproductive and aggressive behaviour, changes in testosterone levels predict mating systems and breeding strategies. Testosterone is involved in the development of several secondary sex characters. These include the vas deferens, cloacal protuberance and associated glands, combs, wattles, modified plumes, and, in some species, development of brightly coloured nuptial plumage (Wingfield et al., 1990). Polygynous males are less responsive to social cues than monogamous males. These patterns suggest flexible hormonal and neural mechanisms linking social interactions to endocrine responses (Wingfield et al., 1990; Ball and Balthazart, 2008). Circulating androgen levels depend on the seasonal androgen response, and androgen responsiveness to male-male competition, to receptive females, and to non-social environmental cues. They also depend on the physiological capacity to produce and secrete androgens (Goymann et al., 2007). Aromatase and oestrogen receptors are localised in the spermatids and testis/epididymal spermatozoa during the reproductive period. This localisation suggests a prevalent role of oestrogen in spermiogenesis and spermatozoa maturation (Rosati et al., 2021).

Hormonal regulation of the ovulatory-oviposition cycle and egg formation in the avian oviduct

The ovulatory-oviposition cycle in birds is a highly coordinated sequence of endocrine and physiological events that regulate follicle recruitment and development, ovulation, egg production and oviposition. In the domestic hen, the cycle lasts approximately 24–25 hours and is controlled by the HPG axis (Johnson, 2015). As described in the previous section, the coordinated actions of GnRH, FSH, and LH regulate follicular development and ovulation. After ovulation, the oocyte enters the oviduct, where the egg undergoes sequential formation of its structural components. Blood flow in oviductal segments around the egg increases three- to four-fold during its passage, likely due to enhanced metabolism of oviductal muscle cells. Shell-gland blood flow peaks five-fold about 5 h after egg entry, paralleling with eggshell calcification. Changes in blood flow to the ovarian follicles and other oviduct regions are minimal (Wolfenson et al., 1982; Wang et al., 2021).

The avian oviduct consists of several specialised regions, including the infundibulum, magnum, isthmus, shell gland, and vagina, each responsible for distinct stages of egg formation (Rahman, 2013; Sah and Mishra, 1918). Fertilisation, if it occurs, takes place in the infundibulum shortly after ovulation. In the magnum, the longest region of the oviduct, tubular gland cells secrete most of the egg white (albumen). The isthmus is responsible for the formation of the inner and outer shell membranes, while the shell gland mediates deposition of calcium carbonate to form the eggshell (Bakst, 2011; Sah and Mishra, 1918). The shell is produced through the precipitation of calcium carbonate

(Ca2+ + HCO3-) in the form of calcite on the outer shell membrane (Hincke et al., 2012). Progesterone or 1,25-(OH)2D3 may affect the ultrastructure of the mammillary layer by regulating the expression of shell gland genes (Zhang et al., 2019). The shell gland expresses several ion transporters for transepithelial transport of calcium and bicarbonate during eggshell formation (Jonchère et al., 2012).

Oviposition is the final stage of the avian ovulatory cycle, during which the fully formed egg is expelled from the shell gland through the vagina and cloaca into the external environment. This process is initiated by coordinated contractions of the shell gland musculature accompanied by relaxation of the uterovaginal sphincter and vaginal wall, allowing the egg to pass through the oviduct. Expulsion of the egg is further facilitated by increased abdominal pressure generated by contractions of the abdominal muscles (Harvey et al., 1987).

In the domestic hen, oviposition occurs approximately 26 h after ovulation. It occurs about 30 min before the ovulation of the next follicle in the laying sequence, reflecting a tightly regulated reproductive rhythm (Harvey et al., 1987). Although the endocrine mechanisms controlling oviposition are not fully understood, posterior pituitary hormones play an important role. In particular, arginine vasotocin and mesotocin, together with shell gland prostaglandins (PGE_1, PGE_2 and $PGF_2\alpha$), are involved in the regulation of oviposition (Shimada and Asai, 1979; Harvey et al., 1987).

Prostaglandins stimulate shell gland smooth muscle contractions and promote relaxation of the uterovaginal junction, thereby facilitating egg passage (Shimada and Asai, 1979). Evidence suggests that prostaglandins act as mediators of arginine vasotocin activity, as vasotocin stimulates prostaglandin synthesis and release from the shell gland (Rząsa, 1984). In addition, ovarian steroids such as oestrogen and progesterone modulate oviductal contractility and influence shell gland prostaglandin production (Harvey et al., 1987). Prostaglandin concentrations also increase in the largest preovulatory follicle approximately 6-4 h before ovulation, further indicating their involvement in coordinating ovulation and oviposition (Johnson, 2015).

Reproductive management practices in poultry

The principal environmental method for controlling reproduction in poultry is photoperiod manipulation. In birds, light signal is perceived not only via the retina but also through deep brain photoreceptors (Sharp, 1993; Banerjee et al., 2017). Increased photoperiod stimulates secretion of GnRHs, which in turn promotes the pituitary release of LH and FSH. These gonadotropins induce the development of functioning gonads (Banerjee et al., 2017). Long photoperiods and reproductive activity are associated with gradual increases in PRL (Hall et al., 1986). The minimum and maximum day lengths required to stimulate reproductive function in short-day hens are about 10 and 13 h, respectively, depending on genotype (Sharp, 1993). Commercially, pullets are brought into lay by increasing both the photoperiod and the light intensity (Scanes et al., 2020). Egg production, egg mass, and average daily feed intake increased with increasing photoperiod length. Higher levels of oestradiol, progesterone, FSH and the increased expressions of oestrogen, LH and progesterone receptors were observed in 16 h photoperiods (Cui et al., 2021).

Lewis and Gous (2006) concluded that extending the photoperiod to 16 h provides no benefit to egg production in comparison with constant light. This was particularly evident in broiler breeders kept in light-proof housing with access to illuminated nest boxes. Higher egg production, adequate egg quality and energy savings, can be obtained with Japanese quail using compact fluorescent lamps or LEDs and a photoperiod of 15 h per day (Molino et al., 2015). Geng et al. (2014) suggested that the photoperiod 12L:2D:4L:6D is optimal for bird performance to give the lowest broodiness rate and the highest egg-laying rate in native laying hens during the whole laying period. It was also observed that photoperiod significantly affected average feed intake (Geng et al, 2018).

Light colour, or wavelength, significantly affects physiological and production responses in poultry. Lighting emitting wavelengths within the ultraviolet, yellow, and red ranges appears to be more favourable for laying hens than conventional lighting (de Souza Granja Barros et al., 2024). Hassan et al. (2013) found that higher egg production was found under monochromatic red and combination red to green light treatments. Also, heavier eggs were laid under blue and green compared to fluorescent white light. Light intensity also plays an important role in poultry productivity and welfare (Molino et al., 2015).

Better understanding of the avian photoperiodic response helps optimise egg production in controlled poultry houses. Knowledge of the photoperiodic response curve for gonadotropin release allows producers to synchronise the onset of laying using appropriate photoperiods. After hens are photostimulated, day length should be increased gradually to balance the development of photorefractoriness and to maintain egg production (Sharp, 1993).

In poultry, nutrition is integrally linked to the HPG axis (Scanes et al., 2020). Food deprivation prevents egg laying and decreases plasma LH, oestradiol, and progesterone concentrations (Tanabe et al., 1981). Protein deficiency reduces

plasma LH levels through an effect on the hypothalamus and decreases gonadal weight (Buonomo et al., 1982). Food restriction after peak egg production is widely practised in commercial flocks to match nutritional, limit excessive weight gain and reduce food costs (Hocking et al., 2002). Definition of a nutrient requirement has changed from first being a requirement, as a percent of a diet, to preventing a nutrient deficiency, to now being a requirement to optimise growth or egg production response (Applegate and Angel, 2014). The 9th edition of *Nutrient Requirements of Poultry* was published by the National Academies (NASEM) in 1994, and its 10th edition is expected in 2025, with updated research, identified research gaps, and mathematical models for the prediction of nutrient requirements (Klasing et al., 2025).

Conclusion

The avian reproductive system develops during embryonic life and continues after hatching. The development and function of the reproductive system of birds is influenced by hormones, while the reproductive cycle is controlled by GnRH and pituitary hormones LH, FSH and PRL that stimulate ovarian follicle maturation and ovulation. Ovulation, the release of a mature ovum from the dominant follicle, is directly regulated by LH and enables egg production. Eggshell calcification depends on precise calcium metabolism regulated by vitamin D and oestrogen, allowing efficient calcium deposition in the shell gland and mineralisation of the shell matrix. Sex hormones such as oestrogen and androgens in females and testosterone in males support the development of secondary sexual characteristics and reproductive behaviour. Oviposition represents the last step of the egg-laying cycle and requires coordinated oviduct contractions and hormonal signals that regulate the timing and frequency of egg laying. Understanding the avian photoperiodic response and nutrient requirements plays an important role in optimising egg production in controlled poultry production systems.

Data availability statement

No new datasets were generated or analysed and the manuscript is based on the previously published literature.

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> Hormonska regulacija reprodukcije u ptica

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Ključne riječi: *reprodukcijski sustav; hormonska regulacija; os hipotalamus-hipofiza-spolne žlijezde; ovulacija; ovipozicija; inkubacija jaja*.