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Major regulatory factors for reproductive performances of female chickens

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ABSTRACT

The reproductive performance of female chickens is critical for determining the efficiency of production and productivity and thus profitability. Studies have shown that the reproductive performance of female chickens is mainly regulated by the feed, hormones, genes, and light conditions. Herein, we review the major factors regulating female chicken reproductive performance and assess the reproductive organs and their functions. In the current review, we highlight how the interconnections of hormones, candidate genes, and photo-stimulation regulate female chicken reproductive hormones and thus regulate the reproductive organ performance. In this regard, the roles of main hormones [gonadotropin-releasing hormone (GnRH) and genes (GnRH- I)] in regulating sexual maturation and ovarian development and maintenance by influencing the survival and function of follicular granulosa cells were also reviewed. In addition, the current review also highlights how feeding female chickens with diets and artificial light-emitting diodes (LEDs) support the effective functioning of their reproductive capacity through the stimulation of sexual maturity at an appropriate age and regeneration of aged reproductive organs.

KEYWORDS: Chicken reproduction; Gonadotropins; *GnRH-I* gene; Light emitting diodes

1. Introduction

The contribution of chickens to global food security is substantial in both rural and urban areas[1]. The current scenarios of an increasing urban population[2] and growing demand for animal protein-sourced food[3,4] have resulted in increased competition for animal proteins[5], which are believed to be obtained from the poultry sector in a large proportion[6]. However, the efficiency of production and productivity and thus profitability of farms are dependent on the reproductive performance of breeding hens[7]. Studies have

shown that the reproductive performances of female chickens are regulated by numerous factors, ranging from nutrition[8–11], to light conditions[12,13], genetics[7,14–16], and hormones[17–19].

Dietary sources of energy, minerals, and Omega-3 fatty acids govern reproductive capabilities by regulating the secretion of reproductive hormones, promoting follicular development, protecting ovarian cells against apoptotic cell death, expression of reproduction-related genes in the hypothalamic-pituitary-gonadal (HPG) axis, and initiating the earlier onset of sexual maturity[11,20–22]. Vitamins A, E, selenium, quercetin, and minerals are known to moderate reproductive organ impairments like oxidative stress[23,24], and intestinal morphology[25–28].

Hormones found within the hypothalamic-pituitary-gonad axis, such as follicle stimulating (FSH) and luteinizing hormones (LH), estrogen, and prolactin, are known to mainly govern chicken reproductive organ development and functioning by regulating the levels of reproductive hormones released by the hypothalamus, pituitary gland, and ovary[29,30]. These hormones regulate the reproduction processes of female chickens by initiating ovarian development, gametogenesis, steroidogenesis, follicular growth, ovulation, and development of female secondary sexual characteristics[31–37].

Light and lighting conditions influence the reproductive capabilities of chickens by influencing various physiological processes and the reproductive axis, which are regulated by

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photosensitive hormones[38]. Therefore, the presence of artificial light with recommended sources, wavelength, color intensity, and duration at night has been associated with the advancement of the reproductive system and expedited maturation of poultry reproductive organs[13,39,40]. This effect is achieved by triggering plasma LH, FSH, and gonadal hormones and by enhancing the expression of LH and FSH mRNA in the HPG axis[41].

The differential expression of reproduction-related genes [*GnRH-I*, Forkhead Box L2 (*FOXL2*), *SLC5A5*, and *HEP2I*] in different parts of chicken reproductive organs and the interrelationship between these genes and hormones influence the reproductive efficiency of female chickens[17,42].

To date, several studies have predominantly focused on the specific reproductive organ(s) and regulatory factor(s) that influence the reproductive performance of female chickens. However, to provide basic and immediate knowledge and implement effective management strategies, it is imperative to conduct comprehensive studies that integrate the latest information. Therefore, this review aims to investigate the effects of major regulatory factors such as diet, light conditions, genetics, and hormones on the reproductive performance of female chickens.

2. Reproductive physiology in female chickens

2.1. Ovary

The ovary and associated oviduct are important reproductive organs of female chickens, and their development is regulated by various genes, hormones, and feed[43]. The reproductive system of chickens is characterized by exclusive growth of the left ovary and left Müllerian duct. Subsequently, the Müllerian duct transforms into the oviduct, a process favored by the presence of estrogen and the absence of an anti-Müllerian factor[44]. In chickens, the gonads of individuals with the ZW genotype develop asymmetrically into ovaries, while the gonads of individuals with the ZZ genotype undergo symmetrical differentiation into testes. These developmental processes are controlled by a combination of genetic and hormonal factors[45]. Before day 4.5 of the embryonic period, the gonads can develop into ovaries or testes. After it is confirmed that the gonads regress into ovaries, the regression of the right ovary progresses through apoptosis and anti-Müllerian hormone activity[46]. In addition to its role in egg production, the ovary plays a crucial role in ovulation by regulating hormone production and secretion, which affects reproductive capacity[31]. The ovaries of domestic hens are characterized by a collection of numerous follicles consisting of many primordial primary, pre-hierarchical, and pre-ovulatory follicles[47].

The ovarian follicles of chickens contain three types of cells: oocytes, granulosa cells and theca cells. Granulosa cells, which

envelop the oocyte, serve as the primary regulators of follicular development[48]. Both granulosa cells and theca cells are integral components of the follicle, and their functional relationships are pivotal in the processes of steroidogenesis and follicular development[49,50].

2.2. Oviduct

The oviduct is a biological pipeline[51] and an important reproductive organ that determines egg quality[52]. In the laying hen, the oviduct plays a crucial role as the site of ovum fertilization by facilitating the movement of the ovum from the ovary, facilitating the formation of egg membranes and eggshells, and transporting eggs via peristaltic movements to the cloaca for oviposition[53]. In chickens, the oviduct develops from the left Müllerian duct, and its differentiation into different regions becomes apparent after embryonic day 12, whereas the right duct starts to regress from about day 11 and then matures to sexual maturity about seven weeks earlier[54]. The oviduct contains five regions: the infundibulum, magnum, isthmus, uterus, and vagina, each of which is suited to different functions in transforming the ova into a hard-shelled egg[55].

2.2.1. Infundibulum

The infundibulum is located in the anterior part of the oviduct, where fertilization occurs. It is wide and funnel-shaped and receives and engulfs the ovulated ovum (yolk) from the ovary. The ovum spends around 15–30 min and is fertilized, with the semen from male chickens being deposited there. The first layer of egg white is secreted in this region, and the first stage of egg formation also starts in this region. The mucosal folds of this region are relatively thin, and the surface epithelium contains ciliated cells, which, together with muscle contractions, facilitate the movement of yolk in the oviduct[56].

2.2.2. Magnum

Among the oviduct regions in chickens, the magnum is the longest (about 33 cm) and the region of albumen formation, as the ovum spends 2–3 h in this region[52]. Within the magnum is a tubular structure, whose walls are characterized by robust development, and the epithelial surface is covered with glandular cells that secrete albumin. Chalazae, which hold the yolk in the center of the egg, are also formed in this region[56].

2.2.3. Isthmus

The isthmus is the shortest region of the oviduct (approximately 8 cm), and its wall is thicker than that of the magnum[56]. In the isthmus, inner and outer shell membranes are secreted, initiation of eggshell calcification takes place, and the oval shape of the egg is maintained within a stay period of approximately 74 min[52].

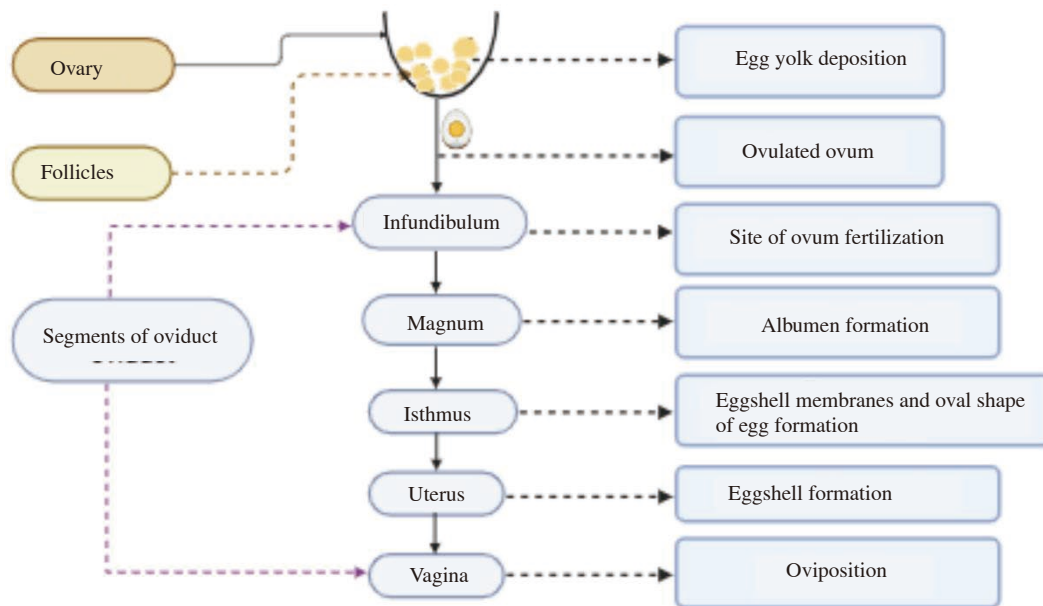


Figure 1. Schematic diagram outlining female chicken's reproductive organs and their specific functions.

2.2.4. Uterus

The uterus is a muscular sac-like structure. Based on its length and structure, it is subcategorized into tubular (approximately 2 cm) and sac-like (approximately 7 cm). Most eggshell constituents are produced by tubular glands. An eggshell is produced in the uterus within 18–24 h of the longest stay period in the egg production process and, thus, the so-called shell gland. In the uterus, pigmentation is also added to eggshells at the end of formation to determine egg color. The uterus also secretes a thin protective cuticle over the eggshell[52]. During this time, albumin takes up fluid via a process known as “plumping”[56].

2.2.5. Vagina

The vagina is the final part of the oviduct in chickens, and its length is approximately 10 cm. It is separated from the uterus by the uterovaginal sphincter muscle. It connects to the cloaca and is primarily composed of muscle tissues. It does not have any known functions in the egg formation process, but with the coordination of the uterus, it regulates egg output aide with muscular contractions[57]. In the vagina, the immune system is well developed, thus preventing the invasion of pathogens from the cloaca[56].

Schematic diagram outlining female chicken's reproductive organs and their specific functions is shown in Figure 1.

3. Nutritional effects on female chickens' reproductive performances

The nutritional status of chickens at all developmental stages influences reproductive performance. Maternal nutritional status determines the amount of nutrients transferred to the embryo and

offspring[58], especially vitamins A and E, micronutrients, zinc, copper, and selenium, which enhance the reproductive performance of broiler breeders[59]. Parameters such as fertility and hatchability of the egg, which are used to evaluate the reproductive performance of breeder hens, are influenced by the level and type of maternal nutrition, among other factors[60].

Dietary energy levels govern reproductive capabilities by altering the expression of reproduction-related genes along the HPG axis. The relatively high energy level (3122 kcal/kg) may also initiate the earlier onset of sexual maturity in chickens[11]. Similarly, amino acid levels affect reproductive performance and feather quality[21], as feather cover also has an indirect effect on fertility and hatchability[61]. Supplementation with soya saponin[40], standard calcium, and available phosphorus also plays a significant role in the secretion and regulation of reproductive hormones, thereby governing the reproductive activities of chickens[22].

Senescence primarily affects the reproductive organs[24] and intestinal morphology[26]. Such impairment is prominent because oxidative stress is linked to age and negatively affects the feed conversion ratio[23]. In such cases, supplements of vitamins A, E, quercetin, and minerals provide important solutions[25,27,28]. In addition, vitamin E and selenium also alleviate the effects of heat stress and maintain the reproductive capabilities of chickens[62]. Similarly, certain supplementary products, such as homemade selenium-enriched yeast, can also be used[63]. In the same way, treating aged Lohman Brown laying hens with royal jelly (200 mg royal jelly kg⁻¹ subcutaneously) improves follicular growth and the oviduct, as it is rich in dietary components[64]. Similarly, the antioxidant ability of aged laying hens can be boosted by dietary supplementation with astaxanthin to prevent ovarian aging and promote reproductive hormone production[65]. Dietary

supplementation with mulberry and moringa leaves has also been reported to improve the reproductive performance of aged Chinese local-strain hens by initiating the expression of steroid hormone synthesis-related genes[9]. Omega-3 fatty acids and vitamin E have been shown to protect ovarian cells against apoptotic cell death. Furthermore, omega-3 sources may promote follicular development and increase the ovulation rate in aged laying hens by increasing fatty acid levels[20].

In addition, in search of an alternative solution for the risks of excessive fat accumulation in the reproductive organs of broiler breeders[66], treatment of broiler breeders with supplementary grape seeds could provide relief through reduced plasma and tissue oxidative stress and improved offspring viability[67]. Therefore, the nutritional status of chickens directly or indirectly affects their reproductive performance.

4. Hormonal effects on female chicken's reproductive performance

Hormones are essential for reproductive development and function in chickens, and their reproductive performance depends heavily on gonadal development and maturation. Studies have shown that the reproductive activities of avian species are affected by reproductive hormones found within the hypothalamic-pituitary-gonad axis[30]. The hypothalamic-pituitary-ovarian axis (HPO) controls the ovulation cycle and egg production by regulating the levels of reproductive hormones released by the hypothalamus, pituitary gland, and ovary[29].

4.1. Gonadotropin-inhibitory hormone (GnIH)

GnIH is secreted by the hypothalamus and suppresses the release of the hypothalamic gonadotropin-releasing hormone FSH and LH[68]. GnIH is mediated by its receptor (GnIHR) in the chicken ovary, which regulates follicle maturation. *GnIHR* mRNA expression is significantly elevated in the ovaries of immature hens compared with mature hens, leading to the suppression of follicle development. This differential expression of GnIHR is intricately regulated by steroid hormones, highlighting the complex interplay between hormonal regulation and ovarian function in chicken reproductive physiology[69].

4.2. FSH and LH

GnRH is a crucial factor in the secretion of gonadotropins (FSH and LH) from the anterior pituitary gland and is recognized as the key hormone controlling reproductive functions[70]. Both FSH and LH are responsible for gametogenesis, steroidogenesis, follicular

growth, and maturation by interacting with their respective receptors (FSH and LH hormone receptors) located in the granulosa and theca cells of ovarian follicles[35]. Additionally, LH induces ovulation in avian species[36]. Therefore, the combined effect of FSH and LH determines egg production success[71]. Furthermore, FSH is required for ovarian development and promotes primordial follicle formation in chickens[32]. FSH secretion also prevents chicken ovarian aging by recovering cellular damage, mitigating mitochondrial impairment, and rectifying disorders of energy metabolism[18].

4.3. Progesterone

Progesterone receptors are found in the HPO axis throughout all stages of a chicken's life, indicating their role as a reproductive hormone in chickens[72], participating in the development of reproductive organs, ovulation, albumen synthesis, eggshell formation, oviposition, and regulation of sexual and nesting behaviors[73]. However, its main role is related to ovulation, and it is known to have a positive correlation with egg production and the regulation of LH concentration[37].

4.4. Estrogens

Two forms of estrogen receptors regulate the effects of estrogen: alpha ($ER\alpha$) and beta ($ER\beta$). Estrogen regulates steroidogenesis in mature ovaries. In chickens, estrogen mediated by $ER\alpha$ plays a significant role in sex differentiation of the gonads and ovarian cortex development in the left gonad, as estrogen receptor mRNA is more abundant in the left female gonad than in the right. Moreover, estrogens are involved in the development of secondary sexual characteristics in females and the neuroendocrine system[34].

4.5. Growth hormone

Growth hormones can also be synthesized in the ovaries of chickens and influence ovarian function. Growth hormone receptors are present in the ovaries of chickens, and growth hormone mRNA mainly occurs in the granulosa layer[74]. In chickens, the main role of ovarian growth hormones is to modulate the action of LH and folliculogenesis[75].

4.6. Prolactin

Prolactin hormone is also expressed in the HPG axis of chickens and mainly functions in the regulation of bird incubation behavior; its elevated concentration causes ovarian regression and a reduction in ovarian steroidogenesis[31]. In chickens, the direct site of prolactin action is the ovary, and its receptor is located in the granulosa and theca layers; thus, its action is related to ovarian steroid synthesis[76].

In addition to the aforementioned hormones, hormones such as androgens act on ovarian tissues, and their receptors are found in granulosa cells and theca cells, regulating follicle development and maintaining full secretory activity[77]. Testosterone also plays a major role in ovulatory follicles even in the absence of LH[78]. Thyroid hormone is another hormone used to regulate the seasonal reproductive cycle and the manifestation of incubation behavior[79]. In egg-laying chickens, thyroid hormones negatively affect the LH, thereby affecting ovarian steroidogenesis[80].

5. Light effects on female chicken's reproductive performance

Light is an important environmental factor that influences the reproductive capabilities of chickens[38], because it regulates various physiological processes in chickens[38,80]. In other words, light exposure and lighting conditions have a significant impact on the reproductive status[81], behavioral patterns[30], and production traits of chickens[41].

The presence of light, especially artificial light at night, has been associated with the advancement of the reproductive system and expedited maturation of poultry reproductive organs[13,39,40]. This effect is achieved by triggering plasma LH, FSH, and gonadal hormones and by enhancing the expression levels of LH and FSH mRNA in the HPG axis[41]. Various studies have verified that photostimulation has the potential to accelerate the sexual maturation process of pullets when implemented at the appropriate age, which is typically around 20 weeks for native chickens[82] and 18 weeks for exotic chickens[13]. This suggests that light indirectly influences the reproductive axis regulated by photosensitive hormones through its effects on the hormonal system.

The management of light for chickens encompasses various factors, such as the source of light and its intensity, duration, and wavelength[83]. The interaction between light pattern and photoperiod also has a significant effect on the reproductive performance of chickens[84]. In addition, different colors work differently in the regulation of chicken reproduction. Blue light-emitting diodes (LED) improves the reproductive performance of chickens through the upregulation of the mRNA expression of the reproduction-related genes GnRH-1 and FSH β , and thus increases the release of FSH[85]. The combination of red and green light also improves the reproductive performance of chickens by regulating the development of reproductive organs and the secretion of reproductive hormones[30]. Wavelength determines the color of light[86], and red LED improves egg production in laying hens by stimulating and increasing the concentration of FSH and LH[87]. Red light has a long wavelength and thus contains high energy that easily penetrates the skin and skull of a chicken to excite the hypothalamus and

stimulate the secretion of reproductive hormones, whereas blue and green lights have short wavelengths and thus are required at higher intensities due to their low energy levels[12]. This indicates that light and lighting conditions are important factors in the regulation of ovarian growth as well as the number of ovarian follicles.

In chickens, the primary photoreceptors are retina of the eye, the pineal gland, and deep brain (hypothalamus)[30]. The retina of the eye and pineal gland tend to produce melatonin during a short photoperiod. As melatonin production levels increase, GnIH production also increases, which in turn negatively affects GnRH release. Consequently, melatonin exerts an inhibitory feedback effect on the HPG axis. However, as the photoperiod increases, melatonin production decreases, leading to an increase in GnRH production with a positive feedback effect on the HPG axis[88]. Therefore, for reproductive purposes, birds should be photo-stimulated mainly via the hypothalamus and pituitary glands[30]. The hypothalamic region of the brain receives light either through the optic nerve or directly through the translucent skull and tissues. Light exposure plays a crucial role in regulating GnRH secretion. GnRH stimulates the pituitary gland to release LH and FSH[83], thereby influencing the rates of sexual maturation and ovulation[35].

Schematic diagram outlining the effect of light stimulation (photo-stimulation) of photoreceptors on female chicken's reproductive performance is presented in Figure 2.

6. Genetic effects on female chicken's reproductive performances

Starting from the initial stage of chicken follicular development, many genes participate in cell signaling and transcription factors[30]. Genes are differentially expressed in different parts of chicken reproductive organs and regulate the physiological systems of animals. For example, *GnRH-I* is a decisive gene in the hypothalamus and ovaries of chickens and is involved in the processes of follicle development and sexual maturation, which are regulated by the concentration of LH[17]. Forkhead box L2 (*FOX L2*) is mainly expressed in the ovary, and regulates ovarian development and maintenance[89], participates in ovarian granulosa cell differentiation[42], and its mutation causes granulosa cell tumors[90]. Likewise, *SLC5A5* is known to potentially regulate chicken follicle development by influencing the survival and function of granulosa cells[91]. Puberty, the transitional phase during which animals attain sexual maturity, is controlled by multiple genes and pathways[92]. One such gene, *HEP21*, plays a crucial role in the regulation of the growth and maturation of reproductive organs[93]. During this phase, there is an increase in both growth and metabolic rates, the emergence of secondary sexual characteristics, rapid development of gonads leading to gamete production, and the onset of fertility in

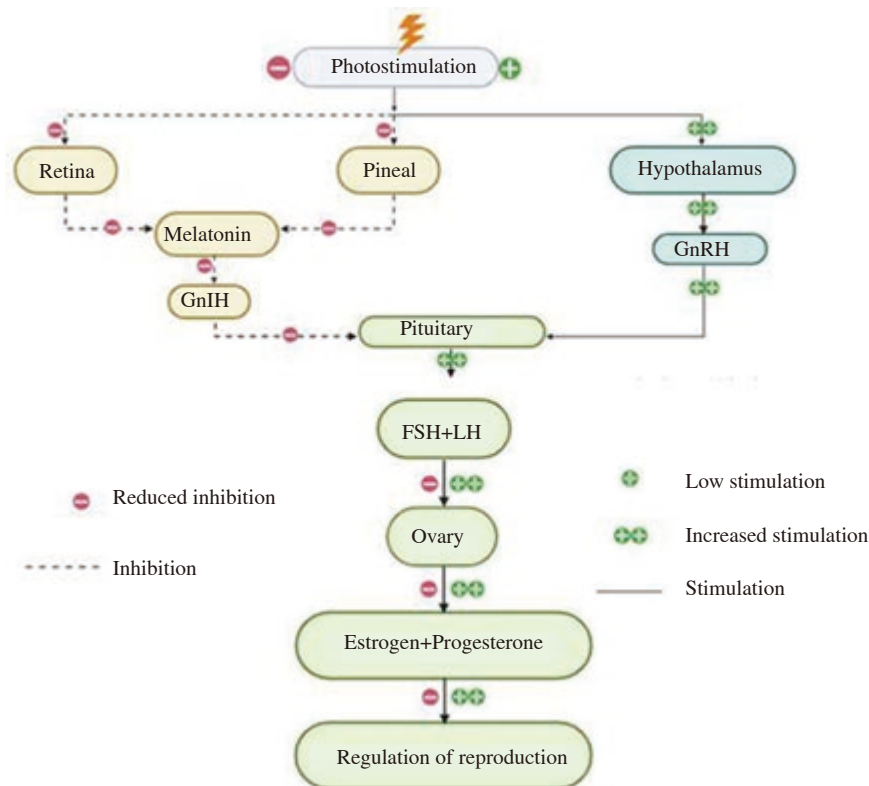


Figure 2. Schematic diagram outlining the effect of light stimulation (photo-stimulation) of photoreceptors on the production of reproductive hormones responsible for regulating reproduction.

animals[94]. The HPG axis is involved in the transition from puberty to sexual maturity, and involves various of reproductive hormones with distinct effects on this process[30]. Activation of the HPG axis during prepuberty is primarily attributed to upregulation of GnRH. GnRH stimulates the secretion of LH and FSH, thereby initiating the onset of puberty. In vertebrates, *KISS-1* governs the HPG axis by regulating the levels of estradiol-17 β (E_2) and testosterone in the brain and gonads, thereby regulating their reproductive processes[95]. Thus, the interrelationships between hormones and genes significantly influence the reproductive processes of animals. As revealed by the genome-wide association, many more genes, such as *CKAP2*, *CCKAR*, *NCAPG*, *IGFBP3*, and *GORAB*, also regulate oviduct developmental characteristics by regulating cell survival, appetite, and growth[96]. Furthermore, *C2H9orf152* is highly expressed in the liver and oviduct, especially in the uterine tissue, thereby regulating calcium metabolism in the reproductive system and is responsible for reproductive organ maturity[97]. This indicates that genes directly or indirectly influence the reproductive success of chickens.

7. Conclusions and future prospects

As discussed, the reproductive performance of female chickens is mainly influenced by the diet, light and lighting conditions, reproductive hormones, and genetics. The interrelationship

between these factors also plays a significant role in regulating the reproductive efficiency of chickens. Dietary sources of energy, minerals, omega-3 fatty acids, and vitamins A and E enhance reproductive efficiency. Reproduction-related hormones (FSH, LH, estrogen, and prolactin) and genes [*GnRH-I*, Forkhead Box L2 (*FOXL2*), *SLC5A5*, and *HEP2I*] mainly influence the functioning of reproductive organs. Color, wavelength, intensity, pattern of light, and photoperiod have a great influence on the excitement of the hypothalamus to stimulate reproductive hormones and genes, thereby regulating reproductive performance. Blue light LED upregulates mRNA levels of GnRH-1 and FSH β and then increases the release of FSH. Red light has a longer wavelength and higher energy than blue and green lights and is thus required at lower intensities to excite the hypothalamus to stimulate the secretion of reproductive hormones. Under a short photoperiod, the production of melatonin and GnIH increases, negatively affecting the release of GnRH and exerting an inhibitory feedback effect on the HPG axis to influence the reproduction process. However, the reverse is true for increasing the photoperiod. It is also imperative to recognize that these factors may not be exhaustive, and that more factors may regulate the reproductive success of chickens. Therefore, further information is needed to uncover more details regarding the molecular mechanisms through which these regulatory factors interact and regulate the reproductive performance of female chickens.

Conflict of interest statement

The authors declare no conflict of interest.

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Authors' contributions

Debela Bayu Derese conceived the study, conducted the literature search, and drafted the figures. Fangxiong Shi reviewed and edited the concept and design of the study. Lizhi Lu reviewed the concept and design of the study. All authors have read and approved the final version of the manuscript.

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