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Role of Hormones in the Fecundity of Silkworm: A Review

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Abstract— *Fecundity is an important reproductive feature in sericulture since it controls how many eggs a female silkworm produces and affects the availability of silkworm seed for commercial rearing. Hormones have an important role in controlling ovarian growth, oocyte maturation, vitellogenesis, transformation, and reproductive behaviour in the silkworm. Juvenile hormone (JH), ecdysteroids, particularly 20-hydroxyecdysone (20E), and insulin-related peptides are important endocrine regulators that influence ovarian growth, nutrition allocation, and reproductive physiology. Ecdysteroids are especially critical during pupal development, when the ovaries rapidly expand and convert to vitellogenesis. Insulin-like growth factor-like peptides also stimulate ovarian development, emphasising the link between hormonal signalling and food availability. However, reproductive performance depends on the coordinated action of several physiological and environmental factors rather than on a single hormone. This review investigates the primary hormonal pathways regulating silkworm fecundity, their prospective uses in sericulture, and the research gaps that must be filled to optimise female reproductive performance and seed production.*

Keywords— **Bombyx mori*, *fecundity, juvenile hormone, ecdysteroids, 20-hydroxyecdysone, ovarian development, vitellogenesis.***

I. INTRODUCTION

Mulberry silk (*Bombyx mori*) comprises 90% of commercial supply, with non-mulberry types (eri and tasar) adding niche value. Sericulture employs 10–15 million people worldwide, primarily rural women in Asia, providing supplemental income and poverty alleviation through low-investment rearing. Fecundity in silkworms (*Bombyx mori*) refers to the total number of eggs laid per female moth, typically ranging from 300–500 eggs under standard conditions, directly impacting seed production for commercial rearing cycles [1]. Innovations such as hybrid strains and hormone applications for 20–50% higher fecundity address supply gaps and enhance farmer returns.

Fertility measures the percentage of eggs fertilized by sperm, producing viable embryos, with rates up to 88.77% under ideal conditions [2]. Hatchability is the proportion of eggs (often 95%+) that successfully hatch into larvae, typically after 10–12 days of incubation triggered by light exposure. Embryonic viability assesses development and survival post-treatments like permeabilization, with over 62% reaching second instar in optimized protocols [3]. The most significant variables affecting cocoon production on a commercial scale are moth fecundity, egg hatchability, and egg incubation time. Ecological parameters, relative humidity, egg and cocoon magnetization, and larval performance have all been studied in relation to silkworm performance. It has been observed that ecdysone affects *Bombyx mori*'s ability to procreate [4–18].

The regulation of insect reproduction is orchestrated through a complex endocrine system involving multiple hormones and signalling pathways. This review synthesizes current knowledge on the roles of key hormonal regulators in enhancing silkworm fecundity and examines strategies for their application in sericulture. The prothoracic glands produce ecdysteroids in response to stimulation by the prothoracicotropic hormone (PTTH) and subsequently release them into the hemolymph [19]. In contrast, juvenile hormones (JHs) are secreted by the corpora allata (CA), a pair of endocrine glands located posterior to the brain [20]. One of the main steroid hormones, ecdysteroids, is critical for controlling metamorphosis and larval molting [21], but it is also

essential for controlling insect reproductive physiology [22]. Through a series of hydroxylation and oxidation processes, insects transform cholesterol into ecdysone and 20E (active metabolite). Halloween genes encode cytochrome P450 enzymes, which are responsible for these reactions [23].

II. KEY HORMONES INVOLVED IN FECUNDITY

2.1 JH Hormones

The JHs are a family of acyclic sesquiterpenoid chemicals synthesized by the minute corpora allata (CA) gland, which is located in the head of the insect. It is one of the most versatile hormones in nature and has crucial roles in development and reproduction in insects.

2.1.1 Structures of Juvenile Hormone

There are four JH variations that are unique to Lepidoptera: JH0, iso JH0 (also known as 4-methyl JH I), JH I, and JH II [24], [25]. Corpora allata produce JH at different fractions in Lepidoptera, namely JH 0, JH I, JH II, JH III, and 4-methyl JH I [26]–[28]. The main difference between these JHs lies in the number and type of alkyl groups (ethyl and methyl) attached to their carbon atoms. JH 0 contains three ethyl groups and one ketone group; JH I contains two ethyl groups, one methyl group, and one ketone group; JH II contains one ethyl group, one methyl group, and one ketone group; and JH III contains three methyl groups and one ketone group (Fig. 1). These structural variations can influence their biological activity and role in insect physiology.

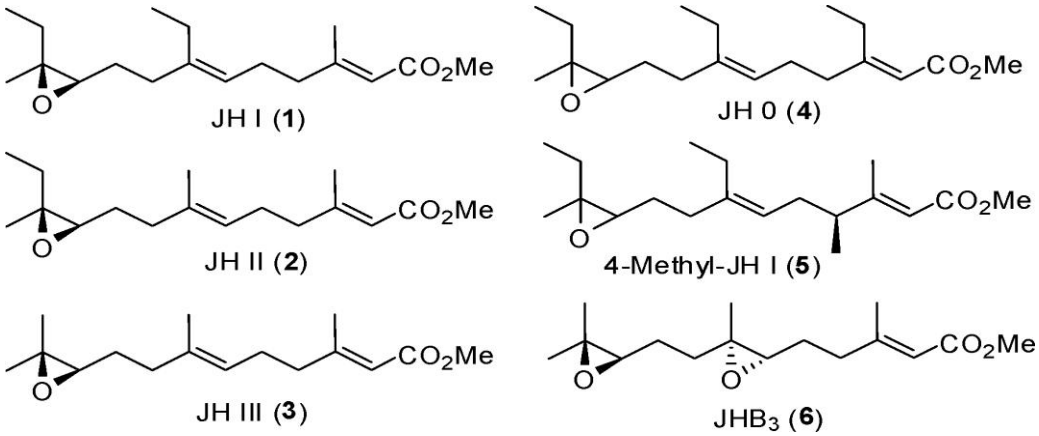


FIGURE 1: Structures of juvenile hormones (Kotaki et al., 2009) [29].

2.1.2 JH Biosynthesis

Juvenile hormone (JH) plays a major role in the growth and development of the silkworm, a commercially significant holometabolous insect. JH is a crucial chemical in the reproductive process of adult insects, which has been well investigated at the physiological and molecular levels [30], [31]. This process includes vitellogenesis, egg maturation, and reproductive behaviour. In insects, eight different forms of natural JHs have been identified. In insects, only JH III is present everywhere. The mevalonate (MVA) pathway and the isoprenoid branch comprise the synthesis of JH [32], [33]. The genes linked to the upstream seven steps of the MVA pathway of JH biosynthesis, which produces isopentenyl pyrophosphate (IPP) as a farnesyl diphosphate (FPP) precursor, were found by Cheng et al. [34] to exist as a single copy and to exhibit a strict orthologous relationship in a range of insects. There are two ways that farnesoic acid (FA) can be converted into JH [35]:

(1) Cytochrome oxidase catalyzes FA to produce juvenile hormone acid (JHa), which is then catalyzed by JH acid methyltransferase (JHAMT) to produce biologically active JH.

(2) Farnesoic acid O-methyltransferase (FAMeT) catalyzes FA to methyl farnesoate (MF), and cytochrome P450 (CYP15) catalyzes MF to produce JH.

2.1.3 Roles of JH in Reproduction

In insects, JH is responsible for the regulation of development and reproductive maturation [33]. In female reproduction, JH plays a significant role, although its effects vary across different species; it encourages endoreplication in fat body cells, which

is a critical requirement in oocyte development. It reduces the expression of some genes that block ovarian development, whereas in cockroaches, insulin-IGF signalling enhances JH biosynthesis to activate reproductive processes.

2.1.4 JH as a Gonadotropic Hormone

Juvenile hormone stands as one of the most significant regulators of reproduction in hemimetabolous insects such as cockroaches, bugs, and locusts [36]. In insects, JH functions as a principal gonadotropic hormone with a central role in vitellogenesis and oogenesis [31]. It stimulates the yolk protein precursor vitellogenin (Vg), mainly produced in the fat body, a critical egg-yolk protein essential for oocyte development and embryonic nutrition [28], [37], [38]. These Vg proteins are then transported through the intercellular spaces (patency) and taken up by developing oocytes via receptor-mediated endocytosis [38]. The synthesis of vitellogenin is a prerequisite for successful vitellogenesis, making JH central to reproductive success. Studies demonstrate that JH acts through its receptor, Methoprene-tolerant (Met), to activate transcriptional cascades controlling reproduction-related gene expression.

2.1.5 Vitellogenesis Regulation

The silkworm is a holometabolous insect belonging to Lepidoptera and has been a classical model organism for the biology of juvenile hormone. In this economically important insect, JH plays complex but distinct roles in reproduction. Unlike hemimetabolous insects, where JH acts as the principal gonadotropin, in silkworms and other lepidopterans, JH shares reproductive functions with 20-hydroxyecdysone (20E), which regulates the expression of Krüppel homolog 1 (Kr-h1), vitellogenesis, and ovarian development in different insect species [39]. Kr-h1 is a critical transcription factor for juvenile hormone (JH) signalling, known to play a key role in regulating metamorphosis and adult reproduction in insects. The induced expression of Kr-h1 by 20E exists in a variety of insects. BmKr-h1 was highly expressed in ovaries during the late pupal and adult stages, and the expression was induced by 20E. RNAi-mediated depletion of BmKr-h1 in female pupae during the late pupal stage repressed the transcription of vitellogenin receptor (VgR) and reduced Vg deposition in oocytes [40].

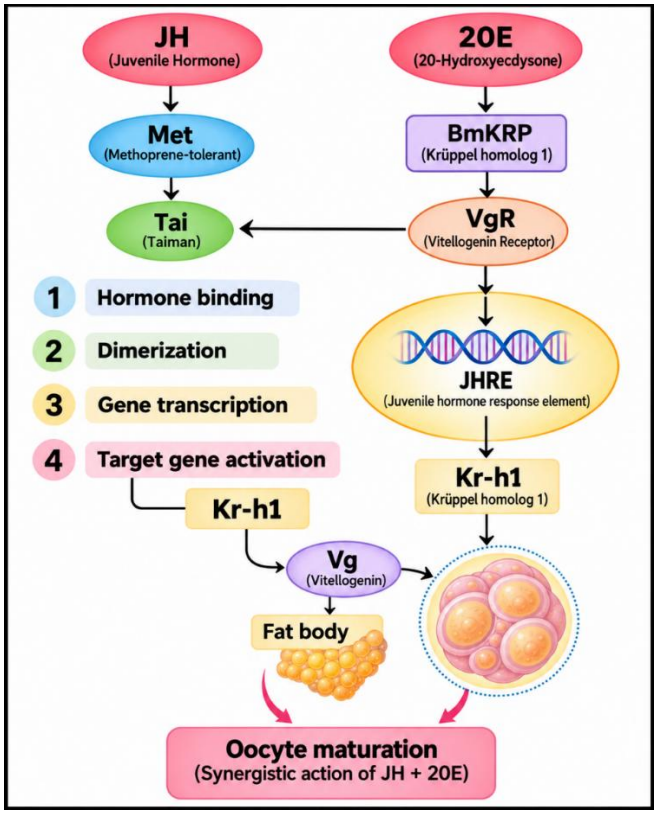


FIGURE 2: Hormone Binding: The juvenile hormone (JH) acts as a ligand and binds to its primary intracellular receptor, the Methoprene-tolerant (Met) protein. Dimerization: Upon JH binding, Met forms a heterodimer with another protein, Taiman (Tai) (also known as SRC in some insects). This Met-Tai complex is the active form of the JH receptor. Gene Transcription: The active Met-Tai complex then moves to the nucleus and binds directly to specific DNA sequences, known as JH response elements (JHREs) or E-box-like motifs, in the promoter region of target genes. Target Gene Activation: Binding of the complex to these motifs triggers the transcriptional activation of the Kr-h1 gene, making Kr-h1 an early and key downstream target gene of the JH signalling pathway.

2.2 Ecdysteroids (20-Hydroxyecdysone)

In insects, development is marked by phases of growth separated by molts, culminating in the transition from juvenile to adult stages [41], [42]. In holometabolous insects, development occurs from embryo to adult, involving larval, pre-pupal, and pupal stages. These stages are attained by a series of molts, which are mainly controlled by the juvenile hormone (JH) and 20-hydroxyecdysone (20E) [42], [44]. Likewise, JH and 20E are the most important hormones and primary regulators of silkworm development, controlling molting, metamorphosis, and silk production. 20E is the driving force for molting, and high levels of JH ensure larval-to-larval molts, while a decrease in JH levels allows 20E to induce metamorphosis.

TABLE 1
COMPARATIVE OVERVIEW OF ECDYSONE (E) AND 20-HYDROXYECDYSONE (20E) INCLUDING BIOSYNTHESIS, ACTIVITY, TRANSPORT, AND REGULATION

Aspect	Ecdysone (E)	20-Hydroxyecdysone (20E)
Site of Synthesis	Prothoracic glands (PGs)	Peripheral tissues (fat body, epidermis via Shade)
Activity Level	Low; precursor	High; active molting hormone
Transport	Hemolymph circulation	Systemic equilibration post-conversion
Regulation	PTTH/insulin pulses in PGs	Tissue-specific Shade timing

III. INSULIN-LIKE PEPTIDES AND NUTRITIONAL REGULATION

Insulin-like peptides and insulin-like growth factor-like peptides connect nutritional status with growth, metabolism, and organ development. Their role is especially relevant to fecundity because developing ovaries require energy, amino acids, lipids, and other nutrients for oocyte growth and yolk deposition.

Fujinaga et al. (2019) investigated the function of a *B. mori* insulin-like growth factor-like peptide (BIGFLP) using gene knockout and transplantation approaches [45]. The researchers found that knockout females had substantially lower ovarian weights and produced fewer eggs than wild-type females. The recovery of ovarian growth when mutant ovaries were transplanted into wild-type pupae further indicated that circulating hormonal signals promote ovarian development.

This study provides direct evidence that insulin-related signalling contributes to the reproductive capacity of the silkworm. It also demonstrates that fecundity is linked to the physiological processes supporting whole-body growth and organ development.

Nutritional signalling should therefore be considered alongside juvenile hormone and ecdysteroids. Inadequate larval nutrition can limit the resources available for adult ovarian development, whereas appropriate nutrition may support reproductive maturation. Nevertheless, the effects of nutrition depend on the silkworm strain, larval feeding conditions, and developmental stage. Further experiments are needed to determine how nutritional status interacts with specific hormones to influence eggs laid per female.

IV. INTERACTIONS AMONG HORMONES

The hormonal regulation of fecundity is not controlled by a single endocrine factor. Instead, reproductive development is determined by the interplay of juvenile hormone, ecdysteroids, insulin-related peptides, and nutritional signalling pathways.

Juvenile hormone may influence developmental timing and reproductive physiology, whereas ecdysteroids regulate important transitions during ovarian development. Insulin-related peptides contribute to organ growth and metabolic regulation. These signals work together to regulate ovarian maturation in coordination with nutrient availability and the silkworm's developmental stage [45], [28], [46].

The balance among these hormonal pathways is particularly important during the transition from the final larval instar to pupal and adult development. Alterations in the timing or magnitude of hormonal signals may disrupt normal development, even when individual hormones have beneficial effects under other conditions.

Consequently, increasing the concentration of a particular hormone does not necessarily increase fecundity. The outcome may depend on the dose, timing, method of administration, genetic background, and interaction with other hormones. This complexity should be considered when evaluating hormonal treatments for commercial sericulture.

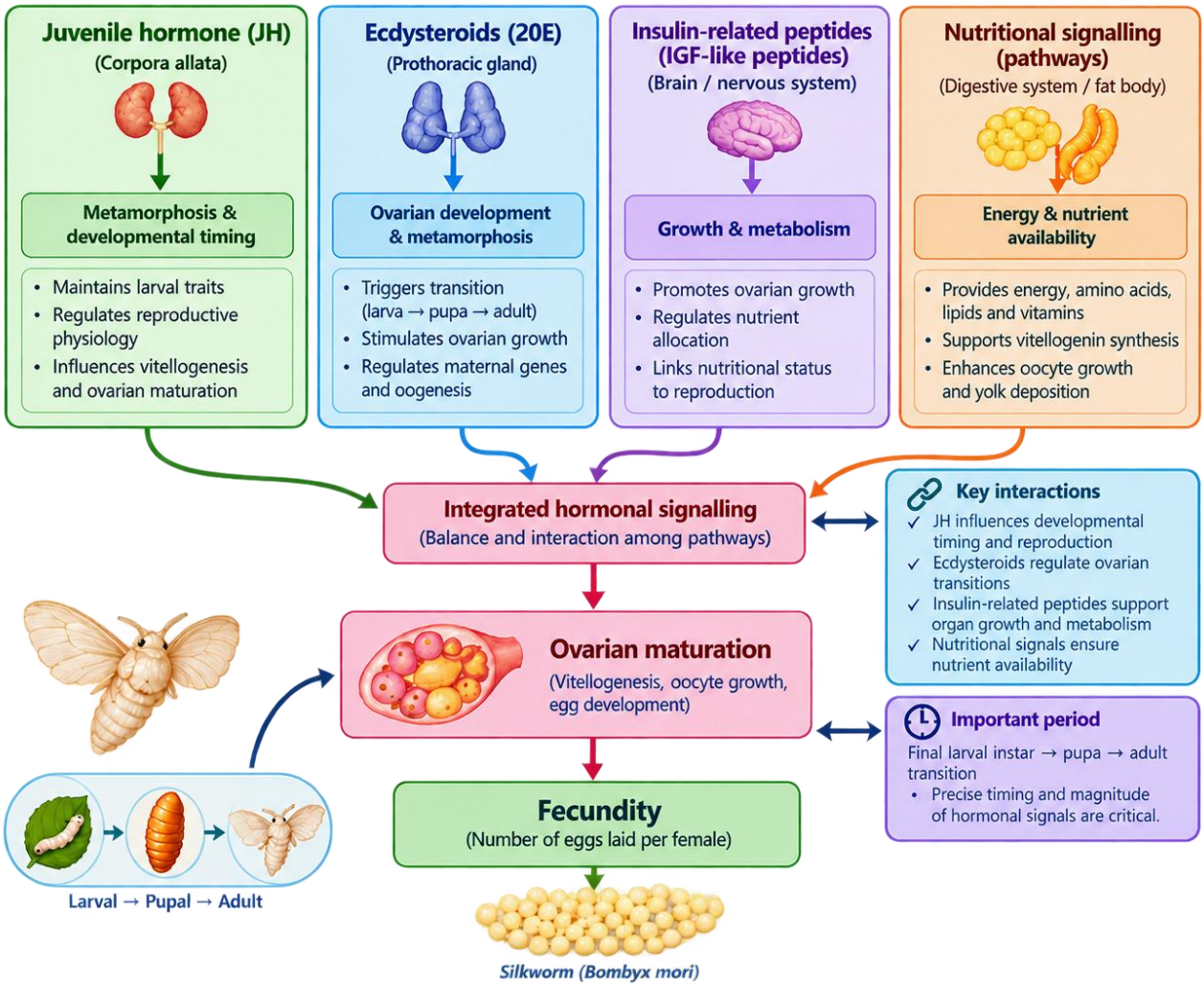


FIGURE 3: Schematic representation of hormonal regulation of fecundity in the silkworm. Juvenile hormone (JH), ecdysteroids (20E), insulin-related peptides, and dietary signalling pathways work together to control developmental timing, ovarian growth, vitellogenesis, oocyte maturation, and egg production.

V. APPLICATIONS OF HORMONAL RESEARCH IN SERICULTURE

Knowledge of hormonal regulation offers several opportunities for improving silkworm seed production and reproductive management.

1) **Improvement of reproductive performance:** Understanding the roles of juvenile hormone, ecdysteroids, and insulin-related peptides may help identify physiological factors associated with higher egg production.

2) **Developmental synchronisation:** Research on juvenile hormone analogues may help explain how endocrine manipulation affects developmental timing. However, the reproductive consequences must be evaluated independently of growth and cocoon traits [47].

3) **Improvement of seed quality:** Research on ecdysteroid accumulation and maternal gene expression may help identify biological indicators associated with egg viability and successful hatching [48].

4) **Molecular approaches to reproductive regulation:** Studies of insulin-like growth factor-like peptides and the molecular machinery involved in yolk uptake provide potential avenues for investigating the mechanisms underlying female fecundity [45], [49], [50].

5) **Integration with rearing management:** Hormonal regulation should be studied alongside larval nutrition, environmental conditions, genetic background, and female health. Integrated management is more appropriate than assuming that manipulation of a single hormone will consistently improve reproductive performance.

These applications remain research opportunities rather than universally validated commercial recommendations. Hormone-based interventions require controlled evaluation of efficacy, dosage, developmental timing, safety, and possible adverse effects before adoption in sericulture.

VI. RESEARCH GAPS AND FUTURE PROSPECTS

Despite progress in understanding the endocrine regulation of silkworms, several areas require further investigation, including *Bombyx mori*, muga (*Antheraea assamensis*), and eri (*Samia ricini*) silkworms.

First, additional experiments are required to establish the direct effects of juvenile hormone on female fecundity under controlled conditions. Second, the interactions between juvenile hormone, 20E, and insulin-related peptides should be examined across different developmental stages. Third, research should determine how hormonal variation relates to the number of mature oocytes, eggs laid, fertilization rate, hatchability, and larval survival.

Comparative studies involving different silkworm breeds and commercial hybrids would also help determine whether hormonal responses are genotype-dependent. Furthermore, molecular studies of hormone receptors, vitellogenin synthesis, nutrient mobilisation, and oocyte maturation may shed light on the mechanisms linking endocrine activity to reproductive performance.

Future research should include suitable control groups, replicated experiments, dose-response analyses, and well-defined reproductive endpoints. Such approaches would provide stronger evidence for the practical application of endocrine research in silkworm seed production.

VII. CONCLUSION

Hormones are important regulators of fecundity in the silkworm. Juvenile hormone helps regulate development and reproduction; ecdysteroids, mainly 20-hydroxyecdysone, have an important role in ovarian development and maternal gene expression; and insulin-related peptides promote ovarian growth and reproductive potential. These endocrine pathways interact with vitellogenesis, nutrient availability, and the molecular mechanisms involved in oocyte maturation.

Experimental investigations show that disrupting these systems might lower egg yield or impair egg developmental competence. Hormonal impacts, however, are determined by developmental stage, physiological condition, and endocrine pathway connections. Therefore, fecundity should be studied separately from fertility and hatchability.

Further research integrating endocrinology, molecular biology, nutrition, and silkworm breeding may help identify effective approaches to improve reproductive performance and seed quality. A better understanding of hormonal regulation could ultimately contribute to more reliable and productive sericulture systems.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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