



The Effect of Maternal Hormones on the Avian Offspring: A Review

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Author's contribution

The sole author designed, analyzed, interpreted and prepared the manuscript.

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Review Article

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ABSTRACT

Maternal hormones have a significant impact on the development of avian embryos, controlling vital physiological functions such as immune system development, metabolism control, and productive traits. This review will examine the different types of maternal hormones, synthesis, regulation, and effects on avian physiology and productivity, as well as the implications for embryonic development. Additionally, it appears that how they might affect hatchability and chick quality. Studies have shown that maternal hormones transfer to eggs and subsequently affect the offspring's development, greatly influencing the behavior and phenotype of avian offspring overall. Understanding these mechanisms can help improve our knowledge of developmental biology, parental investment, and evolutionary processes that influence avian traits. Different species of birds may experience different effects when exposed to maternal hormones. For example injecting testosterone into bird eggs can increase the rate at which certain species hatch, such as quail, other species may see a decrease in hatchling weight. This emphasizes the complexity of hormonal influences on bird development and the necessity of more research. In particular, it is still unclear how yolk steroids affect birds' immune systems; early research indicates that they may chickens' ability to produce antibodies. Undertaking further research is necessary to completely understand the implications of avian immunity to fill in these gaps in knowledge across species and developmental stages.

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1. INTRODUCTION

The complex procedure of avian reproduction includes the interaction of several hormone signals between the mother and the developing offspring. Bird offspring's behavior and phenotype are greatly influenced by maternal hormones, which also have an impact on the offspring's long-term fitness [1]. In avian species, maternal deposition of their hormones to the eggs [2].

The mother can transfer maternal hormones, including steroids and other physiologically active substances, to the developing eggs either directly into the follicle or through the circulation [1,3]. According to studies, the deposition of androgens by the mother can impact the growth, metabolism, and behavior of offspring [4]. According to Verboven et al. [5], there are a few species where elevated levels of maternal androgens do without altering offspring performance.

The direct effects are the immediate physiological or behavioral changes that the hormones cause in developing embryos [6]. On the contrary, indirect effects include modifying the way parents behave or allocate resources, which can then affect the environment in which their offspring develop [7]. Research has shown, for example, that avian ectoparasites can alter the way parents devote their resources to the eggs, thereby altering the hormone levels and developmental results of the offspring [8].

Knowing the factors that contribute to phenotypic variation and adaptive strategies in birds, as well as the mechanisms underlying avian development, requires an understanding of the effects of maternal hormones on avian offspring [1,9]. Furthermore, because they shed light on how parental investment and the transmission of genetic and non-genetic factors can influence the development and fitness of offspring, these studies have wider implications for evolutionary biology [1,10]. To clarify the processes and ecological significance of maternal hormone transmission in avian species, a thorough analysis of the literature will be conducted in to investigate the impact of maternal hormones on the development, behavior, and fitness of avian offspring.

2. FACTORS AFFECTING THE DEPOSITION OF EGG YOLK HORMONES

Several variables can affect the hormones that are deposited in egg yolks. Some crucial factors to consider are the levels of maternal hormones, dietary factors, and environmental factors: The laying hen's bloodstream contains hormones that can be passed on to the eggs. Research suggests that elevated hen levels of particular hormones, such as estradiol and progesterone, may result in higher hormone concentrations in the eggs [11]. **Dietary Factors:** The hormone content of eggs can be influenced by the hen's diet. For example, using lipids supplements during avian feeding may have an effect on the hormone levels in eggs [12]. **Environmental Factors:** Stressors, temperature changes, and other environmental elements may have an impact on a bird's hormonal balance, which in turn may have an impact on the hormone levels in eggs [13]. The hen's age has also an impact on the hormones that are deposited in her eggs. In comparison to older hens, younger hens may produce eggs with distinct hormone profiles [14]. **Breed and Genetic Factors:** The hormonal responses and hormone content of eggs can differ amongst chicken breeds [15]. **Health:** Hormone levels in eggs can be influenced by the health status of birds, including illnesses or infections [16]. **Laying Cycle:** Hormone concentrations can be influenced by the stage of egg development and the time of day the egg is laid [17]. **Analytical Techniques:** The approach taken to determine the hormone levels in eggs can have an impact on the outcomes. Measurements obtained using various analytical methods may differ [18].

3. MECHANISMS OF YOLK HORMONES DEPOSITION

The process of yolk hormone deposition in avian reproduction is controlled by a complex interplay between the female endocrine system and ovarian follicular development. Important female hormones like progesterone and estrogen promote the production of yolk proteins, which are then transferred to the developing oocyte [19]. The process of vitellogenesis, which involves the incorporation of yolk proteins and lipids into the oocyte, is critical in creating an environment rich in nutrients that are necessary for the development of the embryo [20].

Moreover, thyroid hormones play an important role in regulating the energy balance of developing embryos [21]. The intricacy of these regulatory mechanisms is highlighted by the fact that environmental factors, such as photoperiod, can affect yolk hormone deposition [22]. Hormones are transported from the bloodstream to the oocyte through particular receptors and signaling pathways, which precisely regulate the deposition of yolks [19]. Overall, improving our comprehension of hormone-mediated trait integration and the trade-offs and limitations related to maternal hormone transfer will require a greater understanding of the mechanisms underlying the pleiotropic effects hormones have on diverse bodily traits and functions. According to Groothuis et al. [10], no study has quantified the costs of maternal plasticity in hormone transfer in response to environmental variation, and very few have quantified the fitness implications of maternal hormone transfer for the mother.

4. TYPES OF MATERNAL YOLK HORMONES

Hegyí et al. [23], hypothesized that androstenedione, not testosterone, might be the yolk androgen with a long-term function and adaptive deposition pattern in some species as collared flycatcher, particularly those with significantly higher levels of androstenedione than testosterone. The yolk concentrations of testosterone, estradiol, androstenedione, progesterone, and dihydrotestosterone were noted by Aslam et al. [24]. According to Jenni-Eiermann et al. [25], the season had an impact on the intra-individual increases in progesterone and testosterone levels in the yolk, but not the amount of time that had passed since the first egg a measure of laying order. According to Hsu et al. [26], precocial birds deposited more total thyroid hormones (T3 and T4) in their yolks than in altricial species. According to Della Costa et al. [13], the development of chicks with a reduced stress was linked to higher yolk corticosterone and lower yolk progesterone levels.

5. EFFECT OF MATERNAL HORMONES ON OFFSPRING PERFORMANCE

5.1 Effect of Maternal Hormones on Hatchability

Among other glucocorticoid hormones, corticosterone is essential for controlling some of physiological functions in birds. Higher

corticosterone levels in avian eggs were linked to lower hatchability and a delayed hatching, according to Monaghan et al. [27], who indicated the corticosterone hormone can impact embryo development through regulating energy allocation, metabolic processes, and stress responses. Bowers et al. [28], showed a negative correlation between a reduction in nestling pre-fledging mass and higher levels of corticosterone in eggs. The detrimental effect on hatchability can be ascribed to the effects of corticosterone on embryonic development, specifically modifications in metabolic processes and modifications to the integrity of the eggshell. In a study on Japanese quails (*Coturnix japonica*), Groothuis et al. [1], discovered that lower hatchability rates resulted from females with higher circulating corticosterone levels depositing more corticosterone in their eggs. This indicates that maternal stress, which raises corticosterone secretion, may harm developing embryos and hatchability. These results demonstrate the complex interactions that occur in avian species between hormone transfer, parental physiology, and reproductive success. Moderate levels of corticosterone may improve hatchability, according to some studies. Breuner et al. [29], discovered that intermediate levels of corticosterone in eggs were associated with higher hatching success than both low and high levels. This "inverted U-shaped" response suggests that hatchability may be positively influenced by a range of corticosterone levels that promote specific physiological processes while avoiding negative effects. One of the main hormones controlling the physiology and behavior of avian reproduction is testosterone. Its effects on male birds, particularly those related to courtship, aggression, and territory establishment, are its main known effects. Although it hasn't been thoroughly studied, the relationship between testosterone and hatchability can be deduced from its effect on parental investment [19]. Studies indicated that higher testosterone levels in males may result in heightened territorial defense and decreased parental care expenditure, which could indirectly impact hatchability [30]. Although testosterone primarily affects male behavior, a few studies have examined how it might affect females and hatchability. Ryder et al. [31], examined how different levels of testosterone affected environmental, social, and reproductive dynamics in a tropical lekking bird (*Pipra filicauda*), they discovered that testosterone plays an important role in the establishment of male dominance hierarchies. These data suggest

that testosterone may have an indirect effect on hatchability by influencing maternal investment and incubation behaviors, even though a direct relationship to hatchability was not specifically investigated. There are species-specific consequences to the more intricate phenomenon of maternal testosterone's effect on hatchability. Schwabl [3], discovered that the transfer of testosterone to the eggs in some bird species caused changes in the growth patterns of developing embryos. Nevertheless, there is still much to learn about the precise relationship between hatchability and maternal testosterone levels. Thyroxine (T4) and triiodothyronine (T3) are two thyroid hormones that are essential for controlling several physiological functions in birds. Although there hasn't been much research on the direct effects of thyroid hormones on hatchability, their involvement in metabolic processes and embryonic development raises the possibility of indirect effects. The neurological and cardiovascular systems, which are critical to the developing embryo's overall viability [26]. Hatchability may be indirectly impacted by thyroid hormones, which have been linked to the regulation of avian metabolic rates and thermoregulation. Because of the high-energy requirements of avian embryonic development and incubation, changes in thyroid hormone levels may affect the parents' capacity to supply enough heat and energy for incubation, which may then affect hatchability. The study conducted by Darras [21], demonstrated that perturbations in the levels of thyroid hormone in avian eggs may lead to aberrant development and decreased hatchability.

5.2 Effect of Yolk Androgen on Avian Offspring Development

According to Andersson et al. [32], the variation in androgen levels in the yolk of Chinese quail eggs has no effect on the growth and development of the embryos 20 days after hatching. When House Finch eggs were injected with 200 ng of testosterone, their weight was unaffected at hatching [33]. Bertin et al. [34], indicated that injecting 15.6 ng of testosterone into Northern Bobwhite quail eggs did not significantly alter the weights of the hatched birds.

The growth of European starling chicks was significantly better than that of chicks hatched from low-androgen eggs, even though other studies showed a significant increase in growth rates when treated with androgen [35]. When

compared to chicks hatched from uninjected eggs, the growth of canary chicks hatched from eggs injected with testosterone showed a significant improvement [36]. When testosterone was injected into eggs before hatching, domesticated canaries [37], European Starlings [38], and Bluebirds [39], all showed higher growth rates following hatching. Many vertebrate embryos, including red winged black birds [40], and other bird species [41], benefit from the positive influence of yolk androgens during their early development.

Tschirren et al. [42], found that increasing the amount of testosterone in the yolk increased the Great Tit's growth rate after hatching, a finding that was further supported by studies conducted by Groothuis et al. [1], Müller et al. [43], Hegyi and Schwabl [44]. However, Okuliarova et al. [45], found that injecting 25 ng of testosterone into quail eggs causes a significant decrease in the weights of the hatched birds when compared to the control group birds. According to Navara & Mendonca [46], the widespread effects of yolk androgens on body weight gain, muscle growth, and skeletal growth may be due to androgens directly affecting fat, muscle, and skeletal tissue, or indirectly through androgen-mediated effects on the hypothalamic-pituitary-adrenal (HPA), thyroid, and growth hormone axis, or through androgen-mediated motivational effects on food intake and begging behavior. Many of these effects may combine to produce the phenotypic endpoint. Fig. 1 explains the effect of yolk androgens on the growth and development of avian offspring.

5.3 Effect of Yolk Androgen on Avian Offspring Immunity

It is currently unknown how yolk steroids affect immunological function. The first few weeks of a chick's life are essential for the development of the avian immune system because this is when the bursa of Fabricius undergoes gene conversion, which diversifies the antibody repertoire [47]. Research has demonstrated that early in embryonic development, high doses of testosterone administered in ovo resulted in regression of the bursa in chickens, which decreased the production of IgG [48]. Studies of bird species have reported immunosuppression due to exposure to elevated yolk steroid levels; however, most of these studies have employed a single immunological test, namely the test for (unspecific) cell-mediated immunity by injection with PHA. [49,33,32]. A study by Müller et al.

[50], on black-headed gulls is one of the few that has evaluated the impact of yolk androgens on avian immunity using an integrative approach. However, this study only looked at the first week of life, when the chicks' endogenous immune system is still developing and is still in the early stages of the chick phase. Prior to the injection on day six, there was a difference in antibody titers against lipopolysaccharide (LPS) between chicks from androgen-treated eggs and control chicks. According to Janeway et al. [51], antigens

in LPS cause a non-specific antibody response at high concentrations as well as a B-cell response that is independent of T cells. In addition to their known suppressive effects, androgens can also influence on function of immune tissues such as the spleen, thymus, and bursa glands through their interactions with the thyroid, growth hormone, hypothalamic-pituitary-adrenal (HPA), and hypothalamic-pituitary-gonadal (HPG) axes [46]. Fig. 2 shows the effect of yolk androgens on avian offspring immunity.

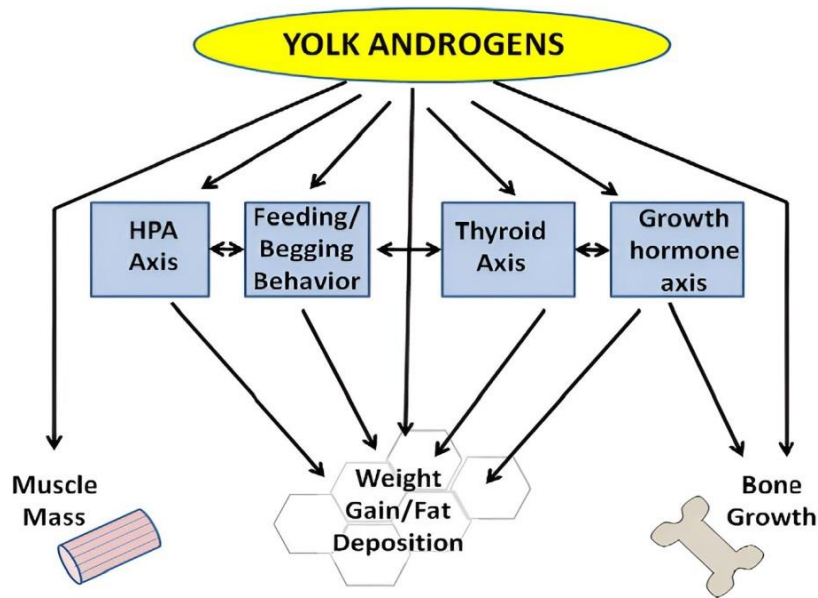


Fig. 1. The effect of yolk androgens on the growth and development of avian offspring (Source: Navara & Mendonca, [46])

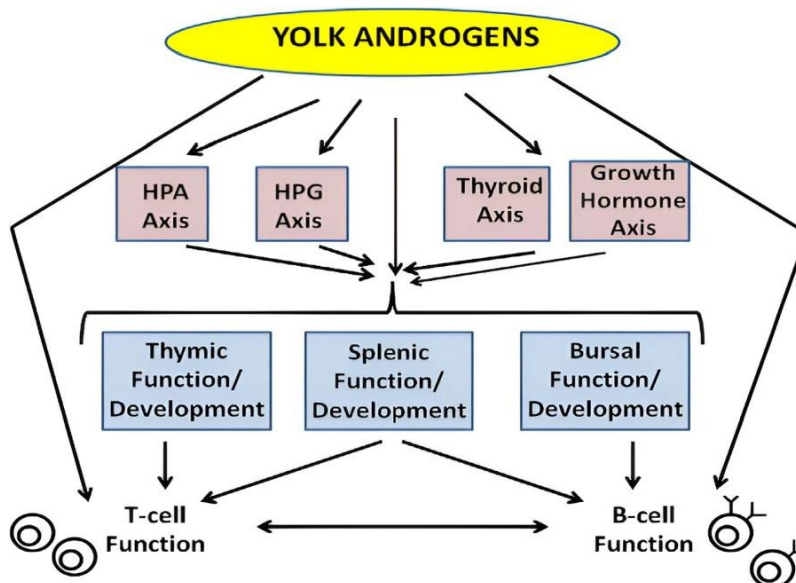


Fig. 2. Effect of yolk androgens on avian offspring immunity (Source: Navara & Mendonca, [46])

6. CONCLUSION

In conclusion, the behavior and phenotype of avian offspring are significantly influenced by maternal hormones. Several studies examined how these hormones get to the eggs and explained how they affect the development of the embryos both immediately and later. Understanding the mechanisms and effects of maternal hormone transfer in bird species advances our knowledge of developmental biology, parental investment, and the evolutionary processes influencing the traits of avian offspring. Studies indicate that the infusion of testosterone into avian eggs may impact the growth rates of the offspring. A testosterone injection improved the growth of some bird chicks, and studies on a variety of bird species confirmed this trend. Effects can differ, though, as demonstrated by quail, where testosterone injection resulted in lower hatchling weights. All things considered, these results demonstrate the various effects of hormone modification on avian development, highlighting the necessity of more research into the underlying mechanisms. It is unclear how yolk steroids affect the immunological system in birds. Although preliminary studies indicate that high testosterone administered in ovo may prevent chickens from producing antibodies, a thorough understanding across species and developmental stages is lacking. To fully understand these effects and their wider implications for avian immunity, more research is required.

COMPETING INTERESTS

Author has declared that no competing interests exist.

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