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Early Phenotype Programming in Birds by Temperature and Nutrition: A Mini-Review

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Early development is a critical period during which environmental influences can have a significant impact on the health, welfare, robustness and performance of livestock. In oviparous vertebrates, such as birds, embryonic development takes place entirely in the egg. This allows the effects of environmental cues to be studied directly on the developing embryo. Interestingly, beneficial effects have been identified in several studies, leading to innovative procedures to improve the phenotype of the animals in the long term. In this review, we discuss the effects of early temperature and dietary programming strategies that both show promising results, as well as their potential transgenerational effects. The timing, duration and intensity of these procedures are critical to ensure that they produce beneficial effects without affecting animal survival or final product quality. For example, cyclic increases in egg incubation temperature have been shown to improve temperature tolerance and promote muscular growth in chickens or fatty liver production in mule ducks. *In ovo* feeding has also been successfully used to enhance digestive tract maturation, optimize chick development and growth, and thus obtain higher quality chicks. In addition, changes in the nutritional availability of methyl donors, for example, was shown to influence offspring phenotype. The molecular mechanisms behind early phenotype programming are still under investigation and are probably epigenetic in nature as shown by recent work in chickens.

Keywords: programming, bird, temperature, nutrition, *in ovo*, embryo

INTRODUCTION

Early development is a critical period during which the environment influences the health, welfare, robustness and performance of livestock (Ho et al., 2011; Reed and Clark, 2011). Long-term effects of the early environment, i.e., during embryogenesis or the first days of life, have been demonstrated in cattle (Reynolds and Vonnahme, 2017), sheep (Reynolds et al., 2010), pigs (Feeney et al., 2014), fish (Panserat et al., 2019), and birds (Feeney et al., 2014; Loyau et al., 2015) among others. The oviparous vertebrate model differs from the others due to an embryonic development outside of the dam. Therefore, the embryo can be easily manipulated, opening up new opportunities for phenotypic programming to improve poultry production.

Embryonic incubation conditions have been studied since the mid-20th century to find optimal incubation parameters for poultry production. The concept of programming has emerged more recently with the demonstration of beneficial effects of different stimuli such as temperature (Loyau et al., 2015), nutrition (Uni et al., 2005; Cherian, 2011) or changes in maternal diet (Hynd et al., 2016; Baéza et al., 2017). The purpose of this review is to provide a concise description of the advancement of this concept in four poultry species (broiler chickens, quails, ducks and turkeys) with a particular interest on two main embryonic programming strategies, nutrition and temperature.

NUTRITIONAL PROGRAMMING STRATEGIES

The Maternal Nutrition as a Lever to Program the Progeny's Phenotype

Several maternal nutritional strategies have been developed to modulate egg nutrient content to obtain higher quality chicks in terms of robustness, growth and body composition. The links between hen nutrition and management, egg composition and subsequent animal behavior, performance, and disease susceptibility are well-established (Aigueperse et al., 2013). The breeder hen's diet can modulate the levels of other essential nutrients, which in turn can impact the fitness of hatched chicks and their phenotype later in life (for reviews, see Rühl, 2007; Morisson et al., 2017).

Fatty acids are essential for embryonic development, bird growth, the development of the central nervous system and the immune system (Noble et al., 1984; Ding and Lilburn, 1996; Wang et al., 2004; Cherian, 2015; Koppenol et al., 2015; Thanabalan and Kiarie, 2021). The balance of fatty acids (FA) can be modulated via the hen's diet. Ducklings from ducks fed with a FA ω3-enriched diet have a higher live weight at hatch (D0), D28 and D56 and a lower feed conversion ratio for the growing period (Baéza et al., 2017). Reduced hyperactivity and stress responsiveness in ducklings were also observed. Supplementation with FA ω3 LC also reduced the frequency and severity of pecking in ducklings.

In low protein feeding programs, not only are egg-laying rate and egg weight altered, but also the amount of leptin in the yolk sac and the expression of a number of genes in the yolk sac, hypothalamus, or muscle of the offspring (Rao et al., 2009). The chicks have lower hatch weight but faster post-hatch growth. More recently, it has been shown that feeding broiler breeders reduced protein diets has a negative impact on reproductive performance but improved offspring performance (Lesuisse et al., 2017), even in subsequent generations (Lesuisse et al., 2017, 2018). Studies testing different levels of digestible lysine (Ciacciariello and Tyler, 2013) or arginine (Fernandes et al., 2014) in hen diets have shown positive effects on offspring such as performance improvement, carcass yield, abdominal fat content, and bone quality for arginine supplementation.

Mineral and vitamin supplementations have often been studied to solve defects of mineralization of the skeleton and legs problems. Vitamins can be enriched in the egg through the hen's diet. Vitamin A is produced by the hen from the carotenoids in the feed. They have antioxidant properties, which are essential for the embryo. Indeed, in the last stage of incubation, fatty acid oxidation increases, as does the production of free radicals and oxidative stress. These processes mainly cause damage to the embryos (Surai et al., 2016). Vitamin D3 regulates the flow of calcium through the chorioallantoic membrane. A vitamin D-deficient diet leads to decreased Ca^{++} transport across the chorioallantoic membrane and decreased Ca^{++} accumulation in the embryo, as well as increased late embryonic mortality (malposition, beak unable to break through the shell). Minerals such as iodine, selenium, magnesium, zinc, copper, iron or manganese can also be enriched in eggs (Jiakui and Xiaolong, 2004; Chinrasri et al., 2013; Favero et al., 2013; Saunders-Blades and Korver, 2015; Torres and Korver, 2018; Xie et al., 2019).

Overall, maternal feeding approaches optimize the hen's diet through supplementation or restriction of a wide variety of nutrients. However, it is often difficult to assess whether the effects of maternal diet on offspring are direct or not.

In ovo Nutrition Programming Strategies

In ovo feeding is a more direct way to influence offspring phenotype. Several studies have reported the use of *in ovo* nutrient supplementation to reduce the hatch window and improve health, post-hatch immune status, hatchability, hatched chick weight, growth performance, and meat quality (Uni and Ferket, 2004; Wei et al., 2011; Kadam et al., 2013; Roto et al., 2016; Gao et al., 2017; Peebles, 2018; Taha-Abdelaziz et al., 2018; Jha et al., 2019; Kalantar et al., 2019; Ayansola et al., 2021). New *in ovo* strategies also aim to address new challenges such as finding alternatives to antibiotic use through probiotic injections (Oladokun and Adewole, 2020). Therefore, *in ovo* stimulation of chicken microflora offers a better approach in establishing intestinal microflora (Alagawany et al., 2021).

At hatching, chicks switch from a yolk FA-based diet to a complete diet. Injection of carbohydrates and amino acids (AA) during embryonic development allows chicks to adapt to their post-hatch diet. Carbohydrates are widely studied because their concentration within the egg is less than one percent of total nutrients (Campos et al., 2011). To limit the utilization of FA and proteolysis of muscle proteins for energy purposes, injections of carbohydrates alone or combined with other nutrients of interest have been performed *in ovo* to increase glycogen storage and modulate energy status of chicks (Retes et al., 2017). Results depended on the type of sugar injected, injection site, embryo developmental stage, and genetics. Smirnov et al. (2006) showed an effect of carbohydrate injection on intestinal epithelium development with a 27% increase in villus area at hatching.

Amino acid administration improves hatching weight (Ohta et al., 2001) which persists up to 56 days of age in some studies (Al-Murrani, 1982). *In ovo* injection of AA such as arginine, considered an essential amino acid in birds, has been used to improve post-hatch growth performance via regulation of protein synthesis through the mTOR pathway (Yu et al., 2018). Arginine also stimulated myogenin gene expression in cultured chicken tissues (Li et al., 2016b). Moreover, *in ovo* injection of sulfur AA (methionine plus cysteine) resulted in improved embryonic development, IGF-I and TLR4 gene expression, antioxidant status and jejunum histomorphometry of newly hatched broiler chicks exposed to heat stress during incubation (Elnesr et al., 2019; Elwan et al., 2019).

In ovo injection of AA, FA, vitamins, and trace elements on early post-hatch growth may also impact the development of lymphoid organs (thymus, bursa, and spleen) and immune parameters in broilers (Bakyaraj et al., 2012). *In ovo* vitamin and mineral administration significantly augmented the hatchability percentage and body weight of chicks post hatching (Alagawany et al., 2020; Hassan et al., 2021). The efficacy of vitamins C, E, D3, and folic acid on embryonic health and development has been reported in the literature (Peebles, 2018). The use of the yolk by the embryo for energy purposes results in oxidative processes, leading to the degradation of polyunsaturated fatty acids in cell membranes. Vitamins, such as vitamin E or C, protect the embryo by limiting the negative effects of free radicals (Surai et al., 2016; Araújo et al., 2018; Peebles, 2018). Results may depend on doses, ages, and injection sites.

Determining the mechanisms by which egg nutrients regulate cellular metabolism, signaling, gene expression and function is critical to improving nutrient utilization, poultry production efficiency and animal robustness. In birds, most studies only report phenotypic results of *in ovo* injections. Only a few recent studies are beginning to decipher the mechanisms involved in these phenotypic changes. Epigenetic changes may be involved, especially when methyl group donors, such as methionine, are injected (Anderson et al., 2012; Donohoe and Bultman, 2012; Veron et al., 2018). Thus, manipulation of sulfur AA content can induce changes in cellular function that may have implications for the development, long-term growth, and health of the animal. The early utilization of nutrients like AA can influence disease resistance and embryo survival (Saeed et al., 2019). Folate supplementation improved growth performance, immune function, and folate metabolism of broilers through epigenetic regulation of immune genes by altering chromatin conformation and epigenetic marks such as histone methylation (Li et al., 2016a). Injection of betaine (a component of the methionine cycle), also considered an effective antioxidant agent and methyl donor, affects hepatic cholesterol metabolism through epigenetic gene regulation in newly hatched chicks (Hu et al., 2015).

TEMPERATURE PROGRAMMING STRATEGIES

Temperature Increases During Egg Incubation

Thermal manipulation (TM) during embryogenesis has been studied for over three decades. TM involves altering egg incubation temperature to improve post-hatch physiological responses of birds (Iqbal et al., 1990). In particular, fine-tuning egg incubation temperature has been used to develop strategies to help chickens better withstand heat later in life (Loyau et al., 2015). TM has since been studied in several other avian species, including turkeys for thermoregulation and muscle growth (Maltby et al., 2004; Piestun et al., 2015), ducks for the lipid metabolism and liver (Wang et al., 2014; Massimino et al., 2019), and quail for growth, physiological and metabolic parameters (Vitorino Carvalho et al., 2020).

Cyclic increases in incubation temperature, mimicking naturally fluctuating conditions, have been found to improve thermal tolerance while minimizing hatching defects (Piestun et al., 2008; Loyau et al., 2015). Because of the interference between the thermoregulatory system and other body functions, TM has also been shown to alter a broader range of phenotypes. For instance, TM has been shown to affect growth in broiler chickens and quails (Loyau et al., 2013; Vitorino Carvalho et al., 2020), muscle development in broiler chickens (Collin et al., 2007; Piestun et al., 2009), skin vascularization in broiler chickens (Morita et al., 2016) and immunity in Pekin ducks (Shanmugasundaram et al., 2018). In Pekin ducks, TM positively impacted muscle fiber diameter and regulatory pathways of muscle development (Liu et al., 2015; Li et al., 2017). Interestingly, TM increased liver weight (Liu et al., 2015) and lipogenesis gene activity in Pekin ducks (Wang et al., 2014). Three different TM conditions were shown to result in increased fatty liver weight, lipid amount, and droplets size after the overfeeding period in mule ducks (Massimino et al., 2019).

Several factors must be considered when implementing a thermal incubation strategy, the most important being the timing and the cyclicality of the treatment and the level of temperature increase (Loyau et al., 2015). For example, early days of embryogenesis and continuous temperature increases should be avoided, as they are associated with hatching defects (Massimino et al., 2019; Vitorino Carvalho et al., 2020). Breeding age and genetics contribute to the effectiveness of TM (Yalçin et al., 2005). Increasing the relative humidity in the incubator is another important parameter to prevent dehydration during temperature elevation (Loyau et al., 2015). Therefore, incubation parameters must be finely tuned to tip the balance toward positive rather than negative effects. This may explain why this seemingly straightforward procedure is not yet widely used in hatcheries.

One way to refine practices is to understand the mechanisms underlying the effects of TM. With advances in next-generation sequencing, genome-wide gene expression and epigenetic data have shed the light on some central and peripheral molecular effects of TM. In 35-day-old chickens and quails, TM has been shown to have a limited effect on gene expression in muscle and hypothalamus under normal rearing conditions (Loyau et al., 2016; Vitorino Carvalho et al., 2021). However, when animals were subjected to heat exposure at the same age, a much stronger gene expression response was found in the TM group compared to the control group. This may be explained by the involvement of epigenetic marks that are imprinted during the embryonic heat exposure and may trigger a differential response when the animals are again exposed to heat. This hypothesis is supported by the identification of several hundred differential peaks of histone marks altered by TM in the hypothalamus of 35-day-old chickens (David et al., 2019). In ducks, TM has been shown to affect the gene expression level of methylation enzymes (Yan et al., 2015), suggesting that incubation temperature may influence DNA methylation in ducks during early development. In addition, several studies have shown the involvement of heat shock proteins (HSP) and factors (HSF) that protect cells from deleterious effects of stress such as misfolding and apoptosis (Costa et al., 2020). Interestingly, a recent study showed that TM altered the basal expression of HSP108, HSP90, HSF-1 and HSF-2 during late embryogenesis and the first week of life, but also the mRNA expression dynamics of these HSPs and HSFs during heat stress (Al-Zghoul and El-Bahr, 2019). HSPs were also identified as differentially expressed in genome-wide studies (Loyau et al., 2016; Vitorino Carvalho et al., 2021) but did not appear to be altered at the epigenetic level (David et al., 2019), suggesting that other mechanisms may be involved in TM lifelong memory.

Temperature Decreases During the Egg Incubation

Exposure of eggs to low incubation temperatures has several impacts on chick physiology, but also on long-term health and welfare traits. The young broiler chick is particularly sensitive to cold after hatching (Collin et al., 2003), and later in life, fast-growing broilers placed in a cold environment may develop an accumulation of fluid in the peritoneal cavity called ascites (Decuypere et al., 2000). While continuous incubation of eggs at low temperatures below 36°C results in degraded hatchability and increased pre-hatch incubation time (Kühn et al., 1982; Black and Burggren, 2004a,b), fine decreases in incubation temperatures have been proposed to stimulate subsequent cold tolerance in birds (Nichelmann and Tzschentke, 2002; Shinder et al., 2009; Akşit et al., 2013). Exposure to cold at the end of incubation did not alter hatchability but resulted in an increase in internal temperature at 3 days of age compared to control broilers chicks. This improved performance with a 5–10% increase in body weight at 14 and 35 days of age in standard temperature rearing (Shinder et al., 2011) and a 4% increase in female weight at 40 days of age, whereas no such change was observed in males (Nyuiadzi et al., 2020). The authors demonstrated beneficial effects of embryonic thermal programming on broiler health, with 19 and 26% reductions in mortality and incidence of ascites, respectively, compared to control chickens under ascites-inducing conditions. Less intense but cyclic cold embryonic thermal programming decreased mortality and ascites incidence during growth of chicks from old breeders (Shinder et al., 2011). Such treatment induced an increase in body weight but a degradation in feed efficiency and a better cold tolerance of broilers when subsequently subjected to cold (Akşit et al., 2013). Loyau et al. (2014) reported that at hatching, the same embryonic cold exposure conditions resulted in a 9-fold increase in catalase activity in the liver of treated chicks compared to controls. This suggests that cyclic embryonic cold exposure stimulated antioxidant defenses in chicks, presumably in response to a transient increase in cold-induced tissue oxidation risk during incubation (Mujahid and Furuse, 2009).

These medium- to long-term effects of short cold exposures during incubation have been shown to trigger heat production through modifications in thermoregulatory mechanisms via a change in neuronal receptors sensitivity in the hypothalamus (Nichelmann and Tzschentke, 2002), and an increase in plasma triiodothyronine T3 concentration (Kamanli et al., 2015). Finally, the impacts of cold exposure during incubation on subsequent chick behavior were reported by Bertin et al. (2018). The authors analyzed the effect of acute decreases in temperature during days 12–19 of incubation on the expression of fear-related behaviors in broilers. At hatching, this treatment affected neurodevelopmental plasticity in the brain with higher expression of corticotropin-releasing factor in nuclei of the amygdala, altering the chicks' social behavior, novelty perception, and increasing their fear behavior. However, cold exposures during incubation under these conditions impaired the health and welfare of chickens reared in postnatal cold (Nyuiadzi et al., 2020).

TRANSGENERATIONAL PROGRAMMING

A growing number of studies have suggested that environmental exposures may be transmitted beyond exposed generations via "transgenerational epigenetic inheritance" (Jablonka and Raz, 2009). Non-genetic transgenerational inheritance has recently been shown to occur in birds (Brun et al., 2015; Leroux et al., 2017). For instance, Brun et al. (2015) showed that the Muscovy duck diet is capable of affecting traits related to growth and lipid metabolism in the grand-offspring, via the sire. In quail, *in ovo* injection of genistein, a phytoestrogen, impacted reproductive and behavioral traits after 3 generations without further injection (Leroux et al., 2017). In a 3-generation study in broilers, a reduced balanced protein diet induced transgenerational effects, including feather condition, polydipsia and frustration-related behavior (Buyse et al., 2020).

While these examples illustrate the existence of non-genetic inheritance of embryonic exposure in birds, the magnitude of these effects remains to be assessed in most cases. Although "epigenetic heritability" has been estimated at very low values for several egg quality traits in meat-type quails (Paiva et al., 2018b), an epigenetic heritability of 0.10 for the weight at 7 days of age has been reported (Paiva et al., 2018a). Concurrently, very little is known about the molecular mechanisms involved, especially in poultry (Guerrero-Bosagna et al., 2018). These may include alterations in sperm miRNAs and lncRNAs (Wu et al., 2019), or putative RNA modifications, DNA methylation, and retained histones (Matsushima et al., 2019).

CONCLUSIONS AND PERSPECTIVES

To face future challenges, including fluctuations due to climate change and changing farming systems, breeders are under pressure to increase performance and productivity, but also to ensure resilience and reduce resource use and environmental impact. In this context, epigenetic programming is an underestimated lever, as maternal or embryonic nutritional and thermal programming offers promising prospects to improve poultry performance and welfare. Programming the environment of animals (e.g., optimizing the way they are housed and fed) can indeed promote non-genetic factors that may be passed on the subsequent generations. This aspect is particularly important in the poultry industry where, generally, production farms are located all over the world, including in warm climate regions, while breeding farms are concentrated in a few temperate locations. Identifying environmental changes in ancestors that affect offspring traits through the transmission of epigenetic marks would therefore allow breeders to produce commercial animals better adapted to local production environments. In order to implement such fine-tuned practices in the field, additional research is needed in this challenging area to account for the potential variability of breeders and the response of their offspring.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this review cites approved studies.

AUTHOR CONTRIBUTIONS

All authors contributed to the writing of the review.

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