Consequences of different growth rates in broiler breeder and layer hens on embryogenesis, metabolism and metabolic rate: A review

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ABSTRACT Intensive genetic selection of broiler breeders and layer hens for economically important production traits, which has been carried out for almost a century, resulted in considerable differences in the mechanisms of growth and development and, thus, in avian metabolism, both during embryogenesis and after hatching. Selection for meat production (broiler breeders) and eggs (layer hens) led to increased productivity but also brought about metabolic disorders. That intensive genetic selection of broiler breeders and layer hens is effective is seen, for example, in the differences in growth and development, metabolism of the yolk sac, hormones and lipids, gas exchange, and thermogenesis. Due to genetic proximity and different developmental mechanisms in broiler breeders and layer hens, avian embryos and chicks serve as excellent models for fundamental scientific research. This review paper discusses the consequences of different growth rates as a result of long-term genetic selection on embryonic development and metabolic rate of broilers and layers. The evidence presented herein indicates that it would be worth comparing these issues in a meta-analysis.

Key words: development, metabolism, genetic selection, broiler breeder, layer hen

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INTRODUCTION

The genetic selection that has been carried out for almost a century by poultry breeders has led to significant progress in improving productive traits in poultry (Joseph and Moran, 2005; Zheng et al., 2009; Buzała et al., 2014; Tavaniello et al., 2014). Modern molecular genetic techniques, coupled with classic qualitative genetic methods, have proved very successful in selecting broiler breeders and layer hens for egg and meat production (Emmerson, 1997). Genetic selection for different performance traits results in considerable differences in the mechanisms of growth and development and, thus, in avian metabolism (Sato et al., 2006a; Druyan, 2010). In broiler breeders and layer hens, the effectiveness of intensive genetic selection is already seen during the first 48 h of embryonic development and after hatching (Janke et al., 2004; Druyan, 2010; Ho et al., 2011). The improvement in layer hens in terms of intensive egg production and of broiler breeders in terms of high body weight and rapid rate of growth has led to considerable differences in their production efficiency (Havenstein et al., 2003a,b; Janke et al., 2004). Poultry productivity has increased almost 3-fold over the last 100 years (Hafez and Hauck, 2005). Today, layer hens produce more than 320 eggs during 52 weeks of egg production, while broiler breeders achieve 50- to 60-fold increases in body weight from hatch to marketing (Druyan, 2010). One of the consequences is that broiler breeders differ in their requirement for minerals, in particular calcium and phosphorus (Rao et al., 1999, 2003), and need half as many days to reach market weight. In 1956, a broiler breeder needed 84 d to reach 1.82 kg; 10 years later this period was shortened to 60 d as a result of intensive selection, and in 2000 it took a broiler 34 d to reach the same weight (Hafez and Hauck, 2005). Consequently, at 42 d of age a broiler breeder weighs 5 times as much as a layer hen (Zhao et al., 2004).

Intensive genetic selection for economically important production traits significantly shortened the time needed to achieve the desired traits but also significantly accelerated the occurrence of metabolic disorders, which are often detected at the embryo level (Emmerson, 1997). As a result of broiler breeder selection, bone and internal organ growth fails to keep pace with rapid muscle mass gain. Consequently, the birds have reduced cardiopulmonary capacity in relation to their muscle mass and cannot tolerate much physical exertion (Hafez and Hauck, 2005). Compared to layer hens, broiler breeders are more predisposed to developing pulmonary arterial hypertension, as a result of which the energy demands of muscle tissue exceed the capacity of the cardiovascular system to deliver adequate amounts of oxygen to the tissues. To compensate for muscle hypoxemia, the circulatory system of both

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juvenile and adult broiler breeders must perform at a higher capacity than that of layer hens to supply sufficient oxygen to relatively underperfused muscle tissue (Olkowski, 2007; Ho et al., 2011; Wideman et al., 2010, 2013). These metabolic disorders may also lead to congestive heart failure and ascites. Unlike in layer hens, a significant factor in predisposing broiler breeders to these conditions is the endothelin system, which has a vasoconstrictive effect on the cardiovascular system. Plasma levels of endothelins and endothelin-1 mRNA and its receptor are significantly higher in broilers than in layers, especially after 21 d of age (Hassanpour et al., 2010). In addition, unlike in layer hens, intensive genetic selection in broiler breeder flocks compromised reproductive function by diminishing reproductive capacity, reduced egg production, fertility, and hatchability, caused abnormalities in the skeletal system, and increased carcass fatness (Emmerson, 1997; Joseph and Moran, 2005). Considering the high egg production, layer hens can develop diseases such as fatty liver hemorrhagic syndrome, fatty liver, necrotic hemorrhagic hepatitis, osteoporosis, or hypocalcemia (Julian, 2005). In addition, genetic selection had a less detrimental effect on the immune system of layer hens compared to broiler breeders (Koenen et al., 2002; Parmentier et al., 2010; Leshchinsky and Klasing, 2001).

Owing to genetic proximity and different rates of muscle growth and egg production in broiler breeders and layer hens, avian embryos and chicks provide excellent models for the study of developmental mechanisms (Zheng et al., 2009). Therefore, the aim of this review is to discuss the consequences of different growth rates as a result of long-term genetic selection on embryonic development and the metabolic rate of broiler breeders and layer hens.

GROWTH AND DEVELOPMENT

During early embryonic development, chicken embryos rely exclusively on egg components for growth and development (Ho et al., 2011). Egg yolk is made up of a multitude of components, such as lipids, carbohydrates, hormones, and antibodies, that are physiologically relevant to the developing embryo. During the early period of development, egg yolk is an important contributing factor to the rate of embryo growth (Ho et al., 2011). Growth is the most energy-consuming process during embryo development. On average, around 80% of original yolk energy content is directed toward growth. After subtracting the fraction of energy (approximately 5%) lost in metabolic waste products, only about 15% of initial yolk energy is left to support all the other metabolic processes taking place during embryonic development (Rombough, 2011). Perturbations in yolk environment affect the development rate of broiler and layer embryos in the same fashion as growth rate. It was shown *in vitro* that broiler yolk accelerates the development rate of layer embryos, whereas layer yolk has no clear effect on the development rate of broiler embryos (Ho et al., 2011). Broiler eggs, although no different in mean total mass from layer eggs, possess significantly larger yolk mass than layer eggs (Sato et al., 2006a; Ho et al., 2011). The larger yolk mass of broiler eggs is apparently related to the larger body mass of those embryos. This suggests that yolk mass may be useful in predicting embryo mass during early embryonic development (Ho et al., 2011).

The body mass of embryos differs considerably between layer and broiler breeder hens throughout embryogenesis (Figure 1), and the difference is most marked during the late stages of embryogenesis (Druyan, 2010; Ho et al., 2011). Embryo mass gradually increases during embryonic development and is greater in broilers than in layers (Sato et al., 2006a,b, 2007). On day 14 of embryogenesis, embryonic body mass is significantly greater in broilers than in layers (Ohta et al., 2004). On day 16 of embryogenesis, layer embryos exhibit slower development than broiler embryos, which is reflected in the lower body mass of the embryos (Everaert et al., 2008). On embryonic day 19 the body mass of broiler embryos is significantly higher than that of layer embryos (Ohta et al., 2004), and on embryonic day 20 embryo mass depends on egg weight but not on bird type (Sato et al., 2006b). It was also found that a 1-g difference in egg weight results in a 10-g difference in the body weight of a broiler at 56 d of age (Ohta et al., 2004).

The differences in growth of embryos obtained from layer hens and broiler breeders may be associated with differences in the rate of yolk sac utilization. During embryonic development, yolk sac contents are utilized more quickly in broiler than layer embryos (Sato et al., 2006a,b). During the first hours of embryogenesis, yolk sac weight is significantly greater in broiler embryos than in layer embryos, and the difference of around 3 g between the two bird types persists up until day 14 of embryogenesis (Sato et al., 2006a). In turn, on day 15 of embryogenesis, the relative weight of the yolk sac is significantly higher in layers than in broilers. From embryonic days 17 and 18, broiler and layer embryos have a similar yolk sac weight of around 13 g (Sato et al., 2006a; Druyan, 2010). On the day of hatching, the residual yolk sac weight in broilers is lower than in layers. Therefore, the body weight of broiler breeders in which the residual yolk sac was removed from the abdominal cavity is greater than in layer hens on hatching day (Sato et al., 2006b). For the first few days after hatching, chicks rely on the residual yolk sac contents, and problems with their absorption limits the growth potential of broilers (Henderson et al., 2008). These disturbances may lead to incidents of unabsorbed yolk sacs, which is twice as frequent in broilers as in layers (Buhr et al., 2006).

The differences between the development of layer and broiler embryos are reflected in the time of hatch. Broiler embryos hatch beginning on day 20 of embryogenesis, whereas layer embryos hatch a day later,

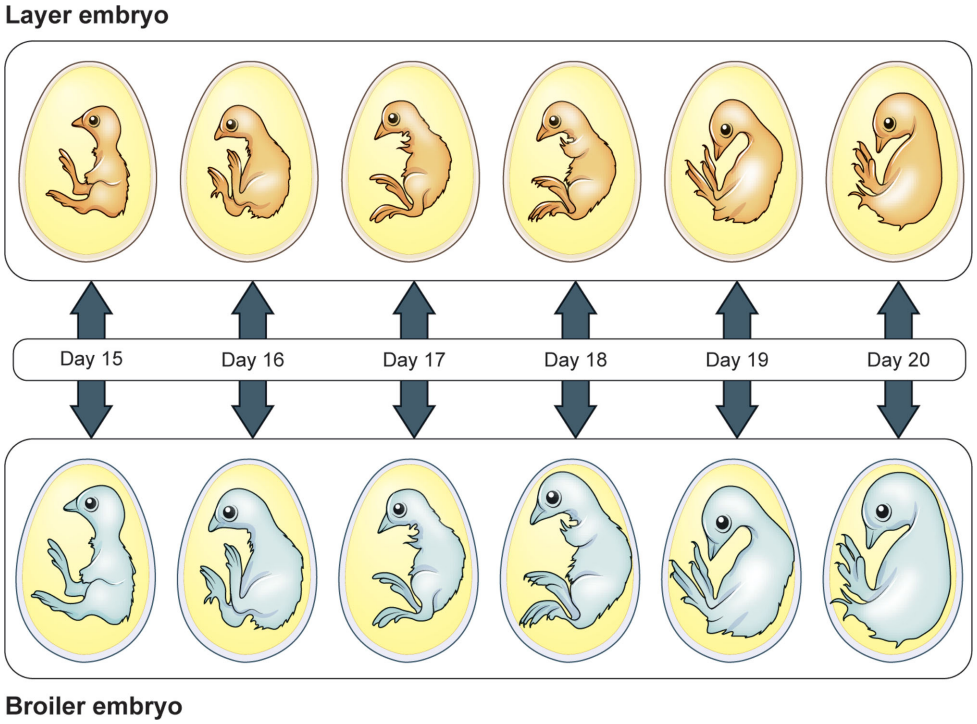

Figure 1. Differences in embryo mass in broiler breeders and layer hens during embryogenesis.

beginning on embryonic day 21 (Janke et al., 2004; Druyan, 2010). The first layer chick hatches from 491 h of incubation, 13 h later than broiler chicks. Broiler chicks achieve 100% hatch at 501 and 502 h. At 504 h (end of incubation time), only 75.5% of the layer chicks hatch (Druyan, 2010). At hatch, layer chicks are significantly lighter than broiler chicks (Ohta et al., 2004; Sato et al., 2006b; Druyan, 2010). Although layer chicks have a lower body weight at hatch compared to broiler chicks, their body weights in relation to yolk are similar. It seems that the layer embryos' delayed hatch enables them to consume additional yolk and reach a relative yolk weight similar to that of broilers at hatch (Druyan, 2010). It was also shown that early embryo mortality (after day 3 of embryogenesis) is higher in broiler breeders (16.4%) than in layer hens (11.9%). Early embryonic mortality is more often associated with chromosomal aberrations in layer embryos than in broiler breeders. The frequency of chromosomal aberrations in all fertilized eggs is similar in both bird types (Thorne et al., 1991).

HORMONE METABOLISM

Maternally produced thyroid hormones, as well as testosterone, which are found in egg yolk, may contribute to phenotypic differences in birds during both the prenatal and postnatal periods. Thyroid hormones play a crucial role in the differentiation and maturation of specific tissues in birds, and their decrease in egg yolk results in smaller offspring. In chick embryos, yolk uptake for the first 13 d of embryogenesis is approximately 350 mg (27 mg/d), between days 13 and 15 it is approximately 230 mg (115 mg/d), and then uptake accelerates rapidly to reach approximately 1 g/d for the last 2 d of the 21-d embryogenesis (McNabb and Wilson, 1997). During the posthatch period, the remaining yolk sac continues to be absorbed. Thus, the yolk also can be a source of thyroid hormones during the first few days of posthatching life (McNabb and Wilson, 1997). The concentration of triiodothyronine (T_3) in the yolk of broiler eggs is approximately twice as low as in layer eggs (Ho et al., 2011). In layer chicks, plasma T_3 was significantly higher than in broiler chicks during embryogenesis. Between 1 and 10 d after hatch, plasma T_3 levels decrease in broilers but increase in layers. In turn, the level of thyroxine (T_4) in both types of hens gradually increases during the embryonic period. After hatching, T_4 levels continue to increase in broilers but decrease in layers, in which it is inversely correlated with changes in T_3 level (Sigui et al., 1999). It was found that significantly lower T_3 concentrations in layer hens compared to broiler breeders may cause differing metabolic rates and oxygen demands, thereby contributing to growth differences in chickens (Druyan, 2010).

Yolk testosterone increases body size and muscle mass, modulates immune function, and differentiates embryonic stem cells into beating cardiomyocytes. It is likely that the significant difference in yolk testosterone between the two types of poultry is responsible for the chronotropic responses and larger body masses found in layer embryos cultured on broiler yolk. The mean concentration of testosterone in the yolk of broiler eggs is significantly higher than in layer eggs. The significant difference in the concentration of these hormones

between broiler breeders and layer hens makes them potential effectors (manipulators) of interbreed variation in chickens (Ho et al., 2011).

A major role in regulating animal growth is also played by the neuroendocrine system, in particular the hypothalamic-pituitary-somatotropic axis (Zhao et al., 2004; Zheng et al., 2009). Growth hormone (GH) has no effect or a negative effect on growth in poultry, especially chicks. GH secretion in broiler breeders and layer hens is under dual control by hypothalamic factors (somatoliberin-/thyrotropin-releasing hormone and somatostatin), of which somatostatin serves an inhibitory function. mRNA expression of hypothalamic somatostatin and pituitary GH and plasma GH levels are higher in layer hens, which have a lower level of GH receptor mRNA in liver (Zhao et al., 2004). The expression of the GH gene in broiler breeders is significantly higher than in layer hens on day 18 of embryogenesis, showing a positive correlation with embryo mass in the period between day 18 of embryogenesis and day 5 of age, but an inverse correlation was found on day 10 of age. Layer hens have higher expression levels of GH gene compared to broiler breeders, showing a negative correlation with the rate of growth after hatching (Ruqian et al., 2001). The growth hormone also stimulates the production of hepatic insulinlike growth factor I (IGF-1), which stimulates growth in birds. In addition, pituitary GH controls IGF-1 and T_3 concentrations in the body; thus, the growth is also dependent on the immediate effect of T_4 and its active form, T_3, along with the interaction between thyroid hormones and the GH-IGF-1 axis (Scanes, 2009).

LIPID METABOLISM

Differences in lipid metabolism between broiler breeder and layer hens can be one of the factors affecting the rate of their growth and development (Sato et al., 2006b). Egg yolk lipids are a major source of energy for growth of chick embryos, because during their development over 90% of total energy comes from oxidation of egg yolk fatty acids (Sato et al., 2006a,b). During embryo development, the main liver lipids are cholesterol esters; after hatching they are replaced with triglycerides (TG), which later accumulate mainly in the liver. Liver TG content increases significantly during embryogenesis in both bird types and is significantly higher in broilers than in layers. Liver TG content is similar in broiler and layer embryos on day 14 of embryogenesis, 1.3-fold higher in broiler compared to layer embryos on day 18 of embryogenesis, and 2.2-fold higher when chicks hatch (Sato et al., 2006b; Druyan, 2010). The higher TG content in broilers may be explained by increased TG absorption from the yolk lipids. In the second week after hatching, TG are the main components of lipids in the chicken liver. Therefore, the higher proportion of TG in the liver of broilers suggests that during embryogenesis liver development can be more rapid in broilers than in layers. It was also found that absolute liver weight is higher in broilers than in layers, whereas relative liver weight shows no significant differences between both types of birds (Sato et al., 2006b; Druyan, 2010). During embryogenesis, plasma concentrations of TG, D-3-hydroxybutyrate and glycerol, which are associated with oxidation of fatty acids, are lower in broilers than in layers, which means that broiler embryos use more lipids. The use of fatty acids as a source of energy also requires carbohydrates. However, because carbohydrates account for less than 1% of the nutrients stored in the egg, conversion of amino acids or glycerol to glucose or glycogen (gluconeogenesis) is essential for supply of carbohydrates. Broiler embryos use more glycerol than layer embryos, which suggests that glyconeogenesis from glycerol may be accelerated in broiler compared to layer embryos (Sato et al., 2006a). In addition, during embryogenesis total plasma and liver concentration of bile acids is low, as is the expression of cholesterol 7α-hydroxylase (CYP7A1), a liver specific enzyme that limits biosynthesis of bile acids. However, their concentration significantly increases on the day of hatch, as does the expression of *CYP7A1* gene, which is significantly higher in layers than in broilers after hatching (Sato et al., 2008).

THERMOGENESIS

Differences in heat production already occur during chick embryonic development (Chwalibog et al., 2007; Everaert et al., 2011). Heat production is lower in broiler than in layer embryos and gradually decreases during embryogenesis in both bird types, and the respiratory quotient is approximately 0.7 (Sato et al., 2006a, 2007). The significantly higher values of heat production and body temperature in broiler embryos compared to layer embryos from day 12 of embryogenesis until hatching, except on days 16, 17, and 18, were probably due to differences in the embryonic growth rate and composition of tissues (Janke et al., 2004). Body temperature in layer chicks is lower than in broilers, which suggests that layer chicks have a more advanced endothermic response than broiler chicks (Andrewartha et al., 2011). The efficiency of metabolizable energy use in birds is determined by the amount of heat produced. The basal metabolic rate in broiler chicks is lower than in layer chicks, starting from day of hatch until a body weight of 500 g is reached (Kuenzel and Kuenzel, 1977). Consequently, whole-body protein turnover is slower in broilers, which is conducive to a more efficient use of feed energy compared to layers (Muramatsu et al., 1987, 1990). In the fed state, whole-body protein synthesis and degradation is higher in layer hens than in broiler breeders. In the starved state, the difference in the rate of protein synthesis between the two bird types virtually disappears, whereas the degradation rates are higher in layer than in broiler birds (Muramatsu et al., 1987). It was confirmed that a bird's food intake per unit metabolic body weight is maximal around 3 weeks of age, which implies a marginal difference between the

capacity to supply oxygen and actual oxygen requirements to metabolize food (Hassanpour et al., 2010). Because broiler breeders utilize a greater proportion of metabolizable energy for growth compared to layer hens, they are more efficient at using this energy for production compared to layers (Swennen et al., 2007). In the first week of life, the resting metabolic rate is lower in broilers than in layers, although they grow 6 times as fast. Later on, the differences between both bird types disappear despite the fact that broilers grow twice as rapidly. Yet broiler breeders have a much higher peak metabolic rate (Konarzewski et al., 2000). Therefore, heat production is different between the two types of hen, which confirms the considerable differences in their development (Sato et al., 2006a).

GAS EXCHANGE

Layer embryos have a lower O_2 consumption rate and demand compared to broiler embryos during embryogenesis (Janke et al., 2004; Druyan, 2010), but an inverse relationship was reported by Sato et al. (2006a). Lower O_2 consumption means that the fat oxidation rate is lower in layer compared to broiler embryos, as reflected in the higher relative yolk weight during embryo growth (Chwalibog et al., 2007; Druyan, 2010). Prior to day 16 of embryogenesis, layer embryos show a slower development, which is reflected in lower air cell and blood CO_2 partial pressure and higher air cell O_2 (Everaert et al., 2008). It was also found that between embryonic days 12 and 18, broiler and layer embryos have a similar mechanism to cope with high CO_2 levels (Everaert et al., 2011). The lower O_2 consumption rate during the development of layer embryos, reflected in the lower demand for O_2, confirms the significantly lower hematocrit and hemoglobin levels in embryos from the layer line compared to broiler embryos (Druyan, 2010). Research by Janicki et al. (2003) demonstrated that broiler embryos show a lower rate of early embryonic development compared to layer embryos, at least with regard to erythropoiesis (Janicki et al., 2003). Although the O_2 consumption rate and the hematocrit and hemoglobin levels in layer embryos are lower than in broiler embryos, layer embryo heart rate is higher (Druyan, 2010). This phenomenon occurs from embryonic day 15, and between days 10 and 14 the mean heart rate in layers is significantly lower than in broilers. On the day of hatch, the heart rate of laying chicks is significantly higher than in broilers (Yoneta et al., 2007; Druyan, 2010). The circulatory system of these two types of hen differentiates very early in embryonic development. At 40 h of embryogenesis, broiler embryos show left ventricular hypertrophy compared to layer embryos (Yoneta et al., 2007). It was shown *in vitro* that broiler embryos developing on layer yolk culture medium had significantly higher heart rates than layer embryos developing on broiler yolk culture medium. Thus, layer yolk composition decelerates the heart rate of broiler embryos (Ho et al., 2011).

CONCLUSION

The differences in growth rate as a result of intensive genetic selection of hens for meat (broilers) and egg production (layers) have led to considerable differences in the mechanisms of growth and development and, thus, in avian metabolism. That intensive genetic selection of broiler breeders and layer hens is effective is already seen during embryonic growth and also after hatching. Breeding work to improve economically important production traits caused a considerable increase in productivity, but it also gave rise to metabolic disturbances. The differences in the metabolism of the yolk sac, hormones, and lipids and in gas exchange and thermogenesis contribute, among others, to differences in the time of hatch and body weight of chicks. Thus, both broiler and layer embryos and chicks, due to the considerable differences in their metabolism as a result of intensive selection, can serve as excellent, easily available, and inexpensive experimental models for fundamental scientific research. However, it would be worth comparing these issues in a meta-analysis.

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