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The Effects of Genetic Line (Broilers vs Layers) On Embryo Development

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#### ABSTRACT

Recent decades were characterized by genetic selection of broiler and layer chickens for enhanced growth rate and meat yield or intensified egg production, respectively. It is to be expected that genetic selection for various traits would also influence embryo development and growth patterns that affect metabolism. The objective of the present study was to examine the effects of broiler (Cobb and Ross) and layer (Lohmann) lines and parent flock age (31 and 38 wk) on embryonic development, heart rate,  $O_2$  consumption, and blood parameters. For each line, 2 incubation sets, from flocks aged 31 and 38 wk, with 500 eggs per set, were studied. Development patterns differed between layers and broilers: layers hatched 1 d later and their relative embryonic weight at hatch was significantly lower, probably because of their longer period until hatch, although yolk relative weights were similar. Oxygen consumption of layer embryos was lower than that of broilers, and plasma triiodothyronine concentration, hematocrit, and hemoglobin levels were lower in layers than in broilers. However, layer embryo heart rate was higher from embryonic d (E) 15 onward. Differenceswere found between the Ross and Cobb lines in embryonic development. Oxygen consumption of Ross embryos was slightly higher than that of Cobb from E16 to E19. Heart rate of Ross embryos was significantly higher than that of Cobb. Furthermore, plasma triiodothyronine concentration of Ross embryos was significantly higher on E14, E16, and hatch. These differences suggest that the genetic selection for rapid growth rate in the 2 broiler lines did not cause differences between their embryonic growth patterns, but it did affect their metabolic rate. Oxygen consumption was higher in embryos from the 38-wk-old flock. The results suggest that genetic selection affected not only production traits but also the developmental pattern of the embryo and its metabolic characteristics.

Key words: broiler, laying hen, embryogenesis, metabolic rate

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#### INTRODUCTION

Recent decades have seen the development of genetic selection of broiler and layer chickens for different traits. Although selection of broilers for enhanced growth rate and meat production has achieved 50- to 60-fold increases in BW from hatch to marketing (Havenstein et al., 2003), selection of layers for commercial egg production and high feed conversion efficiency has resulted in a bird that produces over 300 eggs per year (Appleby et al., 2004). Several comparative studies between layers and broilers (Jackson and Diamond, 1996; Mahagna and Nir, 1996; Koenen et al., 2002) revealed differences between the breeds in several production traits. For example, at 6 wk of age, BW of broilers was found to be 5 times that of layers (Zhao et al., 2004). Most of the difference in BW between the 2 breeds was due to a marked increase in broiler growth rate during the first 2 wk posthatch (Vieira and Moran, 1999). In addition, basal metabolic rate of broiler chicks was found to be lower than that of layer chicks from day of hatch to reaching 500 g of body mass (Kuenzel and Kuenzel, 1977).



Daily rates of total energy utilization by growing chicks may be limited by the amount of energy available in the environment, by physiological or anatomical growth constraints, or by constraints imposed by digestive processes (Konarzewski et al., 1990). Recently, however, it has been accepted that incubation-related factors also influence the performance and growth of chicks (Decuypere et al., 2001; Tona et al., 2004).

It seems that the intensive genetic selection for production traits has also influenced the embryo development pattern and metabolism, as well as their postnatal growth (Hulet and Meijerhof, 2001), all of which are determined by the tissue biosynthesis rate, which depends, in turn, on the accessibility of nutrients and  $O_2$  during incubation. Ohta et al. (2004) found that embryo growth and protein accumulation, as well as yolk consumption, differed between broilers and layers. Sato et al. (2006) also found differences in heat production and lipid metabolism between the broiler and layer embryos. All of these factors may determine the developmental differences between broiler and layer embryos.

Janke et al. (2004) found that  $O_2$  consumption of Ross embryos matched that measured in experiments conducted over 2 decades previously (Tullett and Deeming, 1982; Burton and Tullett, 1983), in spite of the tremendous progress in genetic selection, whereas Lohmann White Leghorn embryos had lower heat production than Blue North Holland, as measured over 4 decades previously (Romijn and Lokhorst, 1960; Wangensteen and Rahn, 1970–1971).

It is to be expected that the genetic selection for various traits would cause different strains to exhibit differing patterns of embryonic development and growth and that their actual metabolic rates and  $O_2$  consumption would probably be different, as was reported by Sato et al. (2006), who found that different strains applied differing metabolic strategies throughout incubation and hatching.

The objectives of the present study were to examine the effects of broiler and layer genetic strains and of parent flock age on embryo development, heart rate (**HR**),  $O_2$  consumption, and blood parameters.

# MATERIALS AND METHODS

# **Experimental Design**

All procedures in this study were carried out in accordance with the accepted ethical and welfare standards of the Israeli Ethics Committee (IL-156/08). Two incubation sets were used: the first for eggs from breeders that were 31 wk of age, the second for those from breeders aged 38 wk. Eggs from commercial lines of Lohmann White Leghorn layer strains and from Cobb 500 and Ross 308 broiler strains were studied. Five hundred eggs from each line were used.

All eggs were numbered and weighed individually before the beginning of incubation. They were incubated under standard incubation condition, at 37.8 °C and RH 56%, and were turned once per hour. All eggs were incubated in the same Danki medium-size incubator for 2,500 eggs (Danki ApS, Ikast, Denmark), and on embryonic d (**E**) 10, they were candled and unfertilized eggs and dead embryos were removed. At E18, the eggs were transferred to a separate Danki Hatcher Type 3 at 37.2 °C and RH 60%. During hatching, the number of chicks hatched was recorded every hour. Nonhatched eggs or those that were externally pipped were also recorded.

Based on the first trial results, blood samples in the second trial were collected from the Cobb, Ross, and Lohmann embryos. Blood was used to determine hematocrit levels and hemoglobin and triiodothyronine  $(T_3)$  concentrations.



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# Egg, Yolk, Embryo, Liver, Breast Muscle and Heart Weights

At each of the stages E15, E17, E18, internal pipping (**IP**), external pipping (**EP**), and hatch, a sample of 10 eggs per line was opened each day. Yolk-free embryo weights were recorded and the embryonic BW (**EW**) was used to calculate the relative EW (%):

Relative embryonic BW (%) = Embryo weight ------ x 100 Initial egg weight

The yolk sac was separated from the embryo, amniotic fluid, and egg white, and the yolk sac weight was measured and used to calculate the relative yolk sac weight (%):

Relative yolk sac weight =	Yolk sac weight x 100 Embryo weight
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Data of embryo relative weights and yolk relative weights were corrected by analysis of covariance with egg initial weight.

Liver, breast muscle, and heart were dissected and weighed, and these weights were used to calculate the relative weight of each organ, determined as the ratio of organ weight to EW.

# HR

From E12 onward, the HR of 15 embryos from each line was measured daily with the Buddy Digital Egg Monitor (Avitronics, Torquay, UK). Using infrared transmitters and sensors, Buddy is capable of amplifying the cardiovascular signal of an embryo within the egg by as much as 20,000 times. This allows detecting the actual heartbeat of the embryo as early as 12 d (for a chicken embryo) after incubation has started. The egg is placed on its side, on the sensor pad at the bottom of the egg compartment, the lid is closed, and the Buddy is turned on. Instantly, the Buddy gives information on the onboard screen via a flashing heart, pulse readout, and 3-digit HR. The monitor will also indicate movement of the embryo within the egg. When the embryo settles, the readout reverts back to HR. It all can take around 1 min per egg. All of the measurements were performed at incubation temperature.

# O<sub>2</sub> Consumption

To measure  $O_2$  consumption of the embryos during incubation, 6 eggs from each line were placed, each day from E10 onward, in a small cylindrical metabolic chamber measuring 7 cm in diameter and height, which was placed in a water container maintained at 37.8 °C. Oxygen consumption was measured according to Buffenstein and Yahav (1991). Briefly, dried air was pumped into the metabolic chamber at a flow rate of 50 mL/min with a flow meter scaled from 0 to 60 mL/min (Aalborg Instruments and Controls, Orangeburg, NY). Dried air from the metabolic chamber was measured for  $O_2$  partial pressure with an  $O_2$  analyzer S-3A/I (Ametek, Pittsburgh, PA). Oxygen consumption was measured for 15 min continuously according to previous measurements demonstrating that during 15 min, there are no changes in  $O_2$  consumption.



#### **Blood Parameters**

Starting on E12 and continuing until E19, about 0.5 mL of blood was collected each day from the allantoic vein into a heparinized 1.0-mL syringe via a 25-gauge needle, but on hatching day, blood was sampled by cardiac puncture. Samples were collected from 10 embryos per line on each day of embryo development. The blood samples were used to determine hematocrit levels and hemoglobin and  $T_3$  concentrations. Blood for hematocrit measurements was drawn into heparinized microcapillary tubes and centrifuged in a microliter centrifuge (Hettich, Tuttlingen, Germany) at 4,000 × *g* for 8 min. Hemoglobin concentration was determined calorimetrically with the Pointe Scientific Hemoglobin Reagent Set (H7504, Pointe Scientific, Canton, MI) according to the manufacturer's instructions. Plasma samples were radioimmunoassayed for total  $T_3$  with the RIA Kit (Diagnostic Products Corporation, Los Angeles, CA; Yahav et al., 2004). The intraassay and interassay CV of the  $T_3$  assay were 7.0 and 9.4%, respectively.

#### Statistical Analysis

Although  $O_2$  consumption and HR were recorded as repeated measures, they were analyzed in a single dependent data file with the same generalized linear model that was used to analyze the rest of the data. Incubation data were subjected to factorial 3-way ANOVA with the parental flock age (31 or 38 wk), line (Ross, Cobb, or Lohmann), and day of development (according to day of data collection) as fixed main effects; the model included all interactions between these effects. The Tukey-Kramer honestly significant difference test was used to test the separation of the means, in comparing the lines on each day of development. These statistical analyses were conducted with JMP software (SAS Institute, 2005).

### RESULTS

#### Embryonic Development: Relative Weights of Body, Yolk, Breast Muscle, Liver and Heart

Although the breeders' ages were equal, within each incubation set, the initial egg weights differed significantly between the 3 lines. In the first incubation set, 31-wk parental flock mean egg weights were  $63.0 \pm 0.43$ ,  $55.9 \pm 0.37$ , and  $57.0 \pm 0.41$  g for the Cobb, Ross, and Lohmann eggs, respectively. In the second set, 38- wk parental flock mean egg weights were  $63.4 \pm 0.45$ ,  $61.3 \pm 0.39$ , and  $62.2 \pm 0.50$  g for Cobb, Ross, and Lohmann eggs, respectively.

There was no influence of flock age on embryos hatch time. Cobb and Ross embryos started to hatch at a similar time, with first chicks for both lines recorded at h 478 from the beginning of incubation. The first hatching chick from the Lohmann line was recorded at h 491, 13 h later than the broiler lines. Cobb and Ross chicks achieved 100% hatch at h 501 and 502, respectively. At h 504 (end of incubation time), only 75.5% of the Lohmann chicks hatched.

The interactions with flock age had no significant effect on relative embryo weight, which generally increased as the flock aged (P < 0.001 for parental flock age). Relative EW (%) of the various strains on each developmental day are compared in Figure 1a and b.

Relative EW gradually increased with the developmental stages. In the first incubation set (flock age 31 wk, Figure 1a), there was a significant interaction (P = 0.0066) between line and embryo day of development of relative EW. This was significantly higher in the broiler strains (Cobb and Ross) than in the layer (Lohmann) strain (25.4 and 26.2% vs. 21.1%) on E15. Thereafter, only the Cobb embryos exhibited significantly higher relative EW. No differences were found between the Ross and the Lohmann lines from E17 onward until EP. At hatch, Lohmann chicks had a nonsignificantly lower BW than the broiler chicks ( $42.7 \pm 0.47$ ,  $42.6 \pm 0.50$ , and  $41.6 \pm 0.58$  g for Cobb, Ross, and Lohmann chicks, respectively), but their relative EW was significantly lower (P < 0.0001). In the second incubation set (flock aged 38 wk, Figure 1b), significant differences in relative EW were found between Lohmann embryos and both Cobb and Ross embryos on all development days. At hatch, Lohmann chicks had significantly lower BW and relative EW than those of both broiler lines:  $45.7 \pm 0.45$ ,  $46.1 \pm 0.40$ , and  $42.8 \pm 0.41$  g for Cobb, Ross, and Lohmann chicks, respectively. In both incubation sets, no significant difference in relative EW was found between Cobb and Ross lines.



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Yolk relative weight (% of EW) decreased gradually as development progressed, with no interaction between flock age, line, and age of development. The relative yolk weight patterns were similar for the 31-wk and 38-wk flocks (Figure 2). However, in the 38-wk broiler lines, relative yolk weights decreased significantly compared with those of embryos from the 31-wk flock, causing a significant interaction (P = 0.008) between line and flock age. A significant interaction (P < 0.001) between line and day of development was also found; this was caused by the faster decrease of the yolk relative weight in the Lohmann line. In the first incubation set (31-wk flock, Figure 2a), at E15, relative yolk sac weight of the Lohmann line was significantly higher than those of Cobb and Ross broiler lines (93.8, 85.6, and 81.7%, respectively). From E17 onward, all 3 lines exhibited similar yolk relative weights. In the second incubation set, from E15 until IP, the relative yolk weight was significantly higher in the layer than in the broiler lines (Figure 2b). Again, a faster decrease was observed in the Lohmann line, which reached a similar yolk relative weight to those of the broiler lines at EP and hatch. In each of the incubation sets, the yolk relative weights of the Cobb and Ross embryos were similar.

No differences among the 3 lines were recorded, in liver, breast muscle, and heart relative weights, at any developmental stage (data not shown).



Figure 1: Relative embryo weight: yolk-free embryo weight as a percentage of initial egg weight (n = 10) from embryonic d (E) 15 to hatch for Cobb, Ross, and Lohmann embryos (panel a = 31-wk-old parental flock; panel b = 38-wk-old parental flock). On each day of incubation, different letters designate significant differences (P  $\leq 0.05$ ) among treatments. IP = internal pipping; EP = external pipping.



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#### Embryo HR and O<sub>2</sub> Consumption

Embryo HR were measured from E13 to E19. Figure 3a and b presents the changes in HR of the 3 lines as related to development day. All 3 lines of embryos from the second incubation set (38-wk parent flocks) had significantly (P < 0.001) lower HR than those from the first incubation set (31-wk parent flocks). No other significant interaction with flock age was found. Throughout the days of measurement, Ross embryos exhibited higher HR than Cobb embryos, and this difference was found to be significant on E14, E15, E16, E17, and E18 in the first incubation set (Figure 3a) and on E14, E15, E17, and E18 in the second set (Figure 3b). On E13 and E14, HR of the Lohmann embryos was similar to that of the Cobb embryos increased and was significantly higher than that of the Cobb embryos; however, it was significantly higher than that of the Ross embryos only on E17 in the first incubation set (Figure 3a) and on E17 and E18 in the second set (Figure 3b). Thus, there was a significant interaction (P < 0.0001) between line and day of development.

Oxygen consumption was detectable from E10 onward (Figure 4a and b). In general, embryos from the second incubation set (38-wk parent flock) had significantly higher  $O_2$  consumption (P = 0.025) than those from the first set (31-wk parent flock). In both incubation sets, embryo  $O_2$  consumption gradually increased with embryo growth and development up to E17, followed by a plateau until E19. The Ross and Cobb embryos exhibited similar patterns of  $O_2$  consumption in both incubation sets, with slightly higher consumption in the Ross embryos, whereas in the first incubation set (Figure 4a), the Lohmann embryos exhibited a lower  $O_2$  consumption than the Ross and Cobb embryos throughout the days of development. In the second set (Figure 4b), Lohmann embryos exhibited until E15 a lower  $O_2$  consumption in comparison to Ross and Cobb embryos. Thereafter,  $O_2$  consumption was similar among all lines.



**C.H.I.C.K**. Program **Figure 2:** Relative yolk weight as a percentage of embryo weight (n = 10) from embryonic d (E) 15 to hatch for Cobb, Ross, and Lohmann embryos (panel a = 31-wk-old parental flock; panel b = 38-wk-old parental flock). On each day of incubation, different letters designate significant differences ( $P \le 0.05$ ) among treatments. IP = internal pipping; EP = external pipping.

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#### **Blood Parameters**

Plasma  $T_3$  concentration increased slightly between E13 and E19 but more rapidly between E19 and hatch in all 3 lines (Figure 5). At E13 and E19, there was no significant difference among lines. Higher levels of  $T_3$  were observed in the Ross embryos at E14 and E16, whereas at E15, E17, E18, and at hatch,  $T_3$  level of both broiler lines was significantly higher than that of Lohmann embryos.

No difference was found between Ross and Cobb embryos in mean hematocrit values throughout the days of development (Figure 6). In the Lohmann embryos, the hematocrit level was significantly lower than that in the Ross embryos on all measurement days. A similar but less pronounced difference was found between the Lohmann and Cobb embryos, which differed significantly on E13, E14, E16, E17, and E18 (Figure 6).

Hemoglobin concentrations in the whole blood tended to be similar in the Ross and Cobb embryos except at E16 (Figure 7). At E14, E18, and E19, hemoglobin concentration of the Lohmann embryos was significantly lower than that of the broilers (Figure 7), whereas at E17, Lohmann embryos only differed significantly from Ross embryos. No differences in hemoglobin level were found between the 3 embryos lines on the other measurement days.

#### DISCUSSION

This study revealed differences between the development patterns and metabolism during embryogenesis of broilers and lavers from parental flocks aged 31 and 38 wk. Genetic selection for various traits has caused different strains to have differing growth patterns, not only posthatch but also during embryonic development. They differ in their metabolic rates and O<sub>2</sub> consumption patterns. Layer embryos developed more slowly and differed from broilers in their development patterns. The most noticeable parameter that indicated differences between the development patterns of broilers and layers during embryogenesis was the time of hatch. Although embryos of the 2 broiler lines, which had been selected for high growth rate and meat yield, hatched during the same period that started at the beginning of E20, those from the layer line, which had been selected for egg production, began hatching 1 d later, at the beginning of E21. These results are in agreement with Janke et al. (2004), who found that Lohmann White Leghorns hatched on E21, one day after the broilers. At hatch, layer chicks from incubation sets 1 and 2 had mean BW that were lower and significantly lower, respectively, than those of broiler embryos. This difference in BW followed continuing differences between relative embryo weights of broilers and layers that already were observed on E15. These results are consistent with findings of Everaert et al. (2008), who reported that layer embryos from a 48-wk-old flock showed slower development than broiler embryos, and this reflected their lower embryo weight through E16. The present findings are also consistent with those of Ohta et al. (2004), who also found a difference in embryonic growth between broilers and layers.

The cause for the difference in embryonic relative growth between the layer and broiler lines might be related to their rates of yolk consumption. In the present study, although layer chick weight at hatch was lower than that of broiler embryos, their yolk relative weight was similar. In the first incubation set, yolk relative weights in all 3 lines were similar from E17 onward, whereas in the second set, yolk relative weights in all lines were similar only from EP onward. It seems that the layer embryos' delayed hatch enabled them to consume additional yolk and reach a relative yolk weight similar to that of broilers at hatch. The substantial differences between broilers and layers in relative embryo weight and in yolk consumption are probably associated with their differences in  $O_2$  consumption rates. The  $O_2$  consumption rate of layer embryos was, in general, significantly lower than those of broiler line embryos, in agreement with Janke et al. (2004). The lower  $O_2$  consumption rate implies that fat orbidition by layer embryos was less than that of broilers, as manifested in the higher relative yolk weight of the former during embryo growth according to Chwalibog et al. (2007).

In the present study,  $O_2$  consumption data were collected only until E19 (i.e., before the IP phase); there are no  $O_2$  consumption data for the hatching period. However, the relative yolk weight data seem to indicate that although the broiler embryos found it hard to continue to use fat, probably because of  $O_2$  supply limitation, layer embryos could still satisfy their  $O_2$  demand. During their longer incubation period, the layer embryos probably had not yet reached their  $O_2$  supply limitation and continued to absorb yolk. When the layer embryos could no longer obtain enough  $O_2$ , their hatching process was triggered, and this occurred 1 d later than in the broiler embryos.





**Figure 3**: Heart rate (beats/min) of Cobb, Ross, and Lohmann embryos (n = 15) incubated together under standard incubation condition from embryonic d (E) 13 to E19 (panel a = 31-wk-old parental flock; panel b = 38-wk-old parental flock). On each day of incubation, different letters designate significant differences ( $P \le 0.05$ ) among treatments. Within each line, different capital letters designate significant differences (P < 0.05) between days.

The lower  $O_2$  consumption and lower relative weights of the layer embryos than those of the broilers were found to be linked to their lower plasma  $T_3$  concentrations, and this despite the similarity of their respective patterns of changes in plasma  $T_3$  concentrations. It can be speculated that the lower  $T_3$  concentrations in the layers caused differing metabolic rates and  $O_2$  demands. All of those differences between the layer and broiler lines indicate a difference between their embryonic growth patterns, as was reported by Pal et al. (2002).





**Figure 4**: Oxygen consumption (mL·g–1·h–1) of Cobb, Ross, and Lohmann embryos (n = 6) incubated together under standard incubation condition from embryonic d (E) 10 to E19 (panel a = 31-wk-old parental flock; panel b = 38-wk-old parental flock). On each day of incubation, different letters designate significant differences ( $P \le 0.05$ ) among treatments. Within each line, different capital letters designate significant differences (P < 0.05) between days.



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*Figure 5 :* Plasma triiodothyronine ( $T_3$ ) concentration ( $ng \cdot mL-1$ ) of Cobb, Ross, and Lohmann embryos (n = 10) incubated together under standard incubation condition from embryonic d (E) 13 to hatch. On each day of incubation, different letters designate significant differences ( $P \le 0.05$ ) among treatments.



**Figure 6 :** Hematocrit level of Cobb, Ross, and Lohmann embryos (n = 10) incubated together under standard incubation condition from embryonic d (E) 13 to hatch. On each day of incubation, different letters designate significant differences ( $P \le 100$ )



In the present study, hematocrit and hemoglobin levels of embryos from the layer line were significantly lower than those of embryos from both broiler lines. This is a further indication that layer embryos had a lower demand for  $O_2$  during their development, as manifested in their lower  $O_2$  consumption rate.

Surprisingly, although  $O_2$  consumption rate and hematocrit and hemoglobin levels in layer embryos were lower than those in broiler embryos, the HR of the former was found to be higher. This phenomenon was observed from E15 onward, whereas from E10 to E14, the HR of the Lohmann embryos was lower than that of the Ross embryos and similar to that of Cobb embryos. These results were in agreement with those of Yoneta et al. (2007), who reported that although on E10 to E14 mean HR was significantly higher in broilers than in Leghorns, at hatch, broiler mean HR was significantly lower than that of Leghorn. Yoneta et al. (2007) suggested that the reversal of the difference in HR between the broiler and layer strains indicated that the HR development patterns during incubation and at hatch differ between strains. It may be that HR of the layer is faster because of a smaller stroke volume, but this must be elucidated.

In the present study, comparison between Ross and Cobb embryos revealed differences in embryonic development between these 2 lines. From the results of this study, it does not appear that genetic selection for rapid growth had a significant influence on the overall embryonic relative growth of the 2 broiler lines examined. The 2 lines had similar relative EW and similar yolk relative weights, but the  $O_2$  consumption rate of Ross embryos was slightly higher. The broiler lines differed in mean HR, which was significantly higher in Ross than in Cobb embryos, and this suggests that although the genetic selection for rapid growth in these 2 lines did not cause differences between their growth patterns, it may, however, affect their metabolic rates. Support for this hypothesis can be found in the findings for plasma  $T_3$ , hematocrit and hemoglobin concentrations. Even though the same pattern of changes in plasma  $T_3$  concentrations than those of Cobb, especially on the day of hatch; Ross embryos also exhibited higher hematocrit and hemoglobin levels. All of these findings can be attributed to the higher  $O_2$  consumption of the Ross embryos, which again indicates the possibility that the Ross and Cobb embryos have differing metabolic demands during embryogenesis.



**Figure 7**: Hemoglobin concentration (g·dL-1) of Cobb, Ross, and Lohmann embryos (n = 10) incubated together under standard incubation condition from embryonic d (E) 10 to E19. On each day of incubation, different letters designate significant differences ( $P \le 0.05$ ) among treatments.



Embryonic relative weight was affected by flock age: it increased as the flock aged. The increase in relative EW mostly enhanced the difference between the broiler and the layer embryos. Although the relative EW of Ross embryos was slightly lower than that of Cobbs in the first incubation set, it was similar in the second set, embryos to become more significant. Indeed, broiler chicks from 38-wk-old parental flocks had significantly higher BW at hatch than layer embryos from 38-wk-old flocks, whereas there was no such difference between the respective embryos from 31-wk-old parental flocks.

Mean relative yolk weights differed significantly between the 2 incubation sets, with that of the second set being 6% smaller than that of the first set: 43.3 and 40.7%, respectively. These results indicate that yolk consumption by the embryos in the second incubation set was higher than that of the first incubation set. Because the yolk yield increases with increasing flock age (Fletcher et al., 1981), yolk content improved as well. Although in young parent flocks the yolk content might be adequate for embryonic development, in older flocks it also supports maximum growth of the embryo. Because most of the  $O_2$  consumption is used for fat oxidation,  $O_2$  consumption influences the amount of yolk fat that is used (Chwalibog et al., 2007). Indeed,  $O_2$  consumption of embryos from the second incubation set was significantly higher than that of embryos from the first set because more energy was allocated to yolkconsumption by the embryos.

It can be concluded that genetic selection affects not only production traits but also the developmental pattern of the embryo and its metabolic characteristics. Hence, it may be beneficial to adjust incubation environment according to the line being used.



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