

# Energy partitioning during incubation and consequences for embryo temperature: A theoretical approach

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**ABSTRACT** In practice, many hatchability and chick quality problems have been related to the control of embryo temperature (ET) during incubation. Within an incubator, set at a constant machine temperature (MT), ET can vary substantially. Embryo temperature is the result of the balance between heat transfer to and from the embryo and heat production (HP) of the embryo. We investigated which factors theoretically could account for the variation in ET within an incubator. First, the effects egg weight, MT, and oxygen availability on HP of embryos were quantified. Differences in HP could be due only to differences in the amount of energy utilized from the egg or to differences in the efficiency of the conversion of energy in the egg to energy in the chicken, indicated as  $E_{YFB}$ . Results of these analyses showed that differences in HP attributable to egg weight or oxygen availability were mainly a result of the amount of energy used from the egg constituents and not of a change in  $E_{YFB}$ . However, at a given MT, this

variation in HP could account for a maximum increase in ET of only 1.21°C, suggesting that other factors played a role because in practice within an incubator, larger differences in ET have been found. The most important factor was probably the difference in air velocity within an incubator, resulting in differences in heat transfer. Because of this variation, ET varied within an incubator and with increasing ET,  $E_{YFB}$  decreased, resulting in an even higher HP and consequently ET. We concluded that this theoretical approach could explain the wide variation in ET, and consequently could explain the negative effects of high ET on hatchability and chick quality found in the literature. This indicates that, in both practice and in incubation experiments, it is of great importance to realize that any factor affecting HP or heat transfer influences ET. We strongly suggest that ET (or eggshell temperature) be controlled in any incubation experiment involving hatchability or energy utilization.

**Key words:** embryo temperature, heat production, heat loss, energy utilization, efficiency of energy transfer

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## INTRODUCTION

In practice, many hatchability and chick quality problems have been related to the control of embryonic temperature (ET) during incubation (French, 1997). Lourens et al. (2005) and Joseph et al. (2006) used eggshell temperature (EST) measurements as a nondestructive means to measure ET, and it has been shown that even small deviations from a constant EST of 37.8°C can have a serious effect on embryonic development [up to a 10% difference in yolk-free body mass (YFB mass = BW – residual yolk) at hatching; Lourens et al., 2005] and hatchability (up to 10%; Lourens et al., 2005). Be-

cause EST can vary largely within an incubator (Lourens, 2001: 1.5°C at embryonic d 18; Elibol and Brake, 2008: 0.7°C at embryonic d 18), and consequently affect hatchability and chick quality (Elibol and Brake, 2008; Lekrisompong et al., 2009), it was necessary to investigate causes for this variation in EST. Eggshell temperature (or ET) has been shown to be the result of the balance between 1) the transfer of heat to and from the embryo and 2) the heat production (HP) of the embryo. It has been reported that when either heat transfer or HP is changed, ET is changed from a given state to a new value (Meijerhof, 2002). Heat transfer has been shown to be mainly determined by the temperature difference between the egg and its environment and air velocity across the egg, and to a lesser extent by humidity of the air (Kashkin, 1961; Meijerhof and Van Beek, 1993; Van Brecht et al., 2005). Heat production has been reported to be determined by 1)

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the total amount of energy utilized from the egg and 2) the efficiency of this energy utilization (Ar et al., 1987; Pearson et al., 1991).

The aim of this study was to investigate which factors theoretically could account for the variation in ET within an incubator. Both egg (egg weight) and incubation (temperature, oxygen availability) factors were evaluated for their effect on maximum HP. Additionally, the effect of maximum HP on ET with variable levels of heat transfer was calculated using a theoretical model, based on Meijerhof and Van Beek (1993). Finally, the theoretical maximum levels of ET were compared with EST found in practice and potential reasons for reported differences are discussed. All calculations were based on chicken eggs and d 18 of incubation was used as the moment to compare differences between the factors to be studied.

## FACTORS AFFECTING EMBRYONIC HP

During incubation, the developing embryo was shown to utilize energy from egg nutrients, mainly from the oxidation of yolk fats (Romanoff, 1967; Noble and Cocchi, 1990) and, to a lesser extent, from the oxidation of carbohydrates and proteins (Fiske and Boyden, 1926). Not all egg nutrients were utilized during incubation because a certain amount of energy remained unused in the residual yolk (RY) or was lost as extra embryonic membranes, meconium (Ar et al., 1987), and urates (Fiske and Boyden, 1926). The latter amount was reported to be relatively limited (Romanoff, 1967: at hatching, 110 mg), and although in overheated embryos this amount might be somewhat increased, it was neglected in the current study. Furthermore, part of the energy was lost as heat (HP) as a by-product of embryonic growth, maintenance, and development (Ar et al., 1987; Pearson et al., 1991). Heat production was determined by 1) the amount of energy utilized from the egg and 2) the efficiency of this energy utilization (the efficiency of the conversion of energy in the egg to energy in the chicken). The efficiency of energy utilization was indicated as  $E_{YFB}$ , and was calculated according to Kleiber (1961) as

$$E_{YFB} = \frac{\text{yolk-free body (kJ)}}{\text{albumen (kJ) + yolk (kJ) - RY (kJ)}} \times 100\%. \quad [1]$$

Variation in HP could be due to egg and incubation factors. In this study, egg weight as an egg factor and incubation temperature and oxygen availability as incubation factors were investigated for their effect on HP.

### Egg Weight

Vleck et al. (1980) and Hoyt (1987) demonstrated an increase in HP just before internal pipping of between 1.5 and 2.0 mW/egg per extra gram of egg weight (with

eggs of different species ranging from 1.5 to 1,450 g). Large eggs not only exhibited more HP than small eggs in late incubation, but they also faced more difficulties in transferring heat away from the egg because of their smaller surface-to-volume ratio and larger layer of non-moving air surrounding the egg (Vogel, 1984; French, 1997). Consequently, at a constant machine temperature (MT) and heat transfer rate, large eggs experienced a higher ET than small eggs, especially in the last week of incubation. Because ET affected energy utilization and consequently HP, it could be assumed that differences in HP attributable to differences in egg weight might be confounded by differences in ET. To correct for this confounding effect of egg weight on ET, EST should be kept the same when comparing the effects of egg weight on HP. When eggs were incubated at a constant EST of 37.8°C, HP at d 18 of incubation in small (55.7 g) and large eggs (70.4 g) was 137 and 155 mW/egg, respectively (Lourens et al., 2006; Table 1). In the range of egg weights used, HP at d 18 of incubation increased by 1.2 mW/egg per gram of egg weight. This value was substantially lower than the values found by Hoyt (1987) and Vleck et al. (1980), which might have been because, in their studies, eggs were incubated on a MT basis, instead of an EST basis; consequently, the effect of egg weight was probably confounded by a difference in EST.

Because HP was a result of the amount of energy utilized from the egg and the  $E_{YFB}$ , Table 1 also shows the energy partitioning between egg, hatchling, and HP. Embryos in large eggs utilized 58 kJ more energy than embryos in small eggs, and the YFB of hatchlings from large eggs contained 23 kJ more energy at hatching than those from small eggs. The  $E_{YFB}$  was comparable for both egg weight classes, meaning that if EST remained the same, differences in HP attributable to differences in egg weight were due only to the amount of energy utilized and not to differences in efficiency of this energy utilization. In cases in which EST did not remain the same, differences in  $E_{YFB}$ , and consequently HP, would be expected.

**Table 1.** Energy partitioning between egg, hatchling, and heat production (HP) at d 18 of incubation in small (55.7 g) and large eggs (70.4 g)<sup>1</sup>

Item <sup>2</sup>	Small eggs	Large eggs
Albumen (kJ)	69 <sup>b</sup>	90 <sup>a</sup>
Yolk (kJ)	259 <sup>b</sup>	320 <sup>a</sup>
YFB (kJ)	155 <sup>b</sup>	178 <sup>a</sup>
RY (kJ)	27 <sup>b</sup>	51 <sup>a</sup>
Utilized (kJ)	301 <sup>b</sup>	359 <sup>a</sup>
$E_{YFB}$ (%)	51.6	49.6
HP at d 18 (mW/egg)	137 <sup>b</sup>	155 <sup>a</sup>

<sup>a,b</sup>Values within a row lacking a common superscript differ ( $P < 0.05$ ).

<sup>1</sup>Based on Lourens et al. (2006).

<sup>2</sup>YFB = yolk free body; RY = residual yolk;  $E_{YFB}$  = efficiency of energy utilization.

**Table 2.** Energy partitioning between egg, hatchling, and heat production (HP) at d 18 of incubation in eggs incubated at 37.8 and 38.9°C and at 17, 21, or 25% oxygen (O<sub>2</sub>) from d 9 to 19 of incubation<sup>1,2</sup>

Item	EST (°C)		Oxygen (%)			Significance		
	37.8	38.9	17	21	25	EST	O <sub>2</sub>	EST × O <sub>2</sub>
Albumen (kJ)	73	76	73	75	76	NS	NS	NS
Yolk (kJ)	280	282	282	281	281	NS	NS	NS
YFB (kJ)	170 <sup>a</sup>	158 <sup>b</sup>	150 <sup>b</sup>	172 <sup>a</sup>	171 <sup>a</sup>	*	*	NS
RY (kJ)	48	46	68 <sup>a</sup>	43 <sup>b</sup>	31 <sup>c</sup>	NS	*	NS
Utilized (kJ)	305	311	286 <sup>c</sup>	313 <sup>b</sup>	326 <sup>a</sup>	NS	*	NS
E <sub>YFB</sub> (%)	55.7 <sup>a</sup>	50.8 <sup>b</sup>	52.5	54.9	52.4	*	NS	NS
HP at d 18 (mW/egg)	131 <sup>b</sup>	148 <sup>a</sup>	119 <sup>c</sup>	138 <sup>b</sup>	152 <sup>a</sup>	*	*	NS

<sup>a-c</sup>Values within a factor and within a row lacking a common superscript differ ( $P < 0.05$ ).

<sup>1</sup>Based on Lourens et al. (2007).

<sup>2</sup>EST = eggshell temperature; YFB = yolk free body; RY = residual yolk; E<sub>YFB</sub> = efficiency of energy utilization.

\* $P \leq 0.05$ .

## Incubation Conditions

It has been estimated that more than 90% of the total energy requirement of the hatchling is derived from fatty acid oxidation of the yolk lipids (Noble and Cocchi, 1990). To be able to oxidize yolk nutrients, embryos require sufficient oxygen for aerobic metabolism. When embryos turned to anaerobic metabolism because oxygen was limiting (Bjønnes et al., 1987), they gradually decreased fat metabolism and increased glycogen metabolism (Bell and Freeman, 1971). Depressed oxygen concentrations or elevated incubation temperatures are 2 factors that can induce a change from aerobic to anaerobic metabolism, resulting in decreased yolk utilization (Wineland and Christensen, 2001). In a 2 × 3 experimental design, Lourens et al. (2007) investigated the effects of temperature and oxygen concentration on yolk utilization and embryonic development. From d 9 until d 18, EST was set at either 37.8°C (normal) or 38.9°C (high), in combination with oxygen concentrations of 17% (low), 21% (normal), or 25% (high). The HP at d 18 ranged between 114 and 154 mW/egg, depending on the EST and oxygen concentration. The effects of EST and oxygen concentration on energy partitioning at d 18 of incubation are shown in Table 2.

High EST decreased YFB energy content, but did not affect total energy utilization or RY energy content. High EST also decreased E<sub>YFB</sub>, which explained the higher HP observed for eggs incubated at high EST compared with normal EST. The total amount of energy used increased with increased oxygen concentration, which was also reflected in a lower energy content of the RY at hatching. Oxygen concentration had no effect on E<sub>YFB</sub>, but HP at d 18 increased with higher oxygen concentration because of a higher amount of energy utilized from the egg.

In summary, HP could be affected by both the amount of energy utilized from the egg and E<sub>YFB</sub>. The amount of energy utilized could be affected by egg weight and oxygen concentration, whereas ET had no effect on the amount of energy utilization (Table 3). The E<sub>YFB</sub> was affected by EST, but not by egg weight or oxygen

supply. We concluded that when eggs were incubated at the same EST, differences in HP were determined mainly by differences in energy utilization and not by differences in the efficiency of this utilization.

One aspect that probably also affects energy utilization and HP is breed. Broilers and layers are selected for different performance purposes, which may affect egg energy utilization and HP during incubation (Janke et al., 2004; Sato et al., 2006; Everaert et al., 2008; Druyan, 2010). Furthermore, within a breed, different strains can differ in energy utilization and HP (Tona et al., 2010). However, all these studies were conducted when eggs were incubated in the same incubator, meaning that eggs of different breeds and strains probably experienced different ET and consequently had different levels of energy utilization and HP. However, experiments studying energy utilization in different breeds when incubated at the same EST are lacking.

## EFFECTS OF INCREASED ENERGY UTILIZATION ON HP

In the previous paragraph, we concluded that in eggs incubated at the same EST, HP was determined mainly by energy utilization. According to Romanoff (1967), energy utilization increased substantially from d 13 of incubation onward, reaching its maximum at d 16 of incubation, after which it remained more or less constant. Based on HP (Lourens et al., 2006), differences in energy utilization between small and large eggs mainly occurred from d 15 onward. Consequently, changes in HP were especially important during the last week

**Table 3.** Factors affecting heat production through the amount of energy utilization and efficiency of energy utilization between egg and hatchling (E<sub>YFB</sub>)

Item	Energy utilization	E <sub>YFB</sub>
Egg weight	Yes	No
Oxygen	Yes	No
Eggshell temperature	No	Yes

of incubation. Theoretically, HP can increase further when the embryo is also able to utilize all the energy in the egg during incubation, resulting in a lack of RY at hatching. In the following paragraph, a theoretical calculation of HP was made, based on the assumption that all RY was utilized in the period from d 0 to 21, d 15 to 21, or even d 18 to 21 of incubation (Figure 1).

Romanoff (1967) showed how energy from the albumen and yolk during incubation was distributed between the embryo and HP. From the total amount of energy available in an average 62-g Leghorn hatching egg (361 kJ), 248 kJ was deposited in the hatchling and 113 kJ of the initial energy was lost. The energy in the hatchling was divided between YFB (130 kJ) and RY (118 kJ). The total amount of energy utilized was  $361 - 118 = 243$  kJ, and  $E_{YFB}$  was 53.5%. Romanoff (1967) also determined the relative energy utilization per day. At d 18 of incubation, only 10.5% of the available energy (243 kJ) was utilized. Theoretically, when all energy that remained in the RY at hatching would have been utilized with the same  $E_{YFB}$ , evenly distributed across the 21-d incubation period, energy utilization at d 18 would increase from 10.5 to 15.7% (Figure 1). When the 118 kJ extra available energy in the RY would be utilized in a shorter period of time, for example, between 15 and 21 d or 18 and 21 d, relative energy utilization at d 18 would increase to 17.4 and 22.0%, respectively (Figure 1).

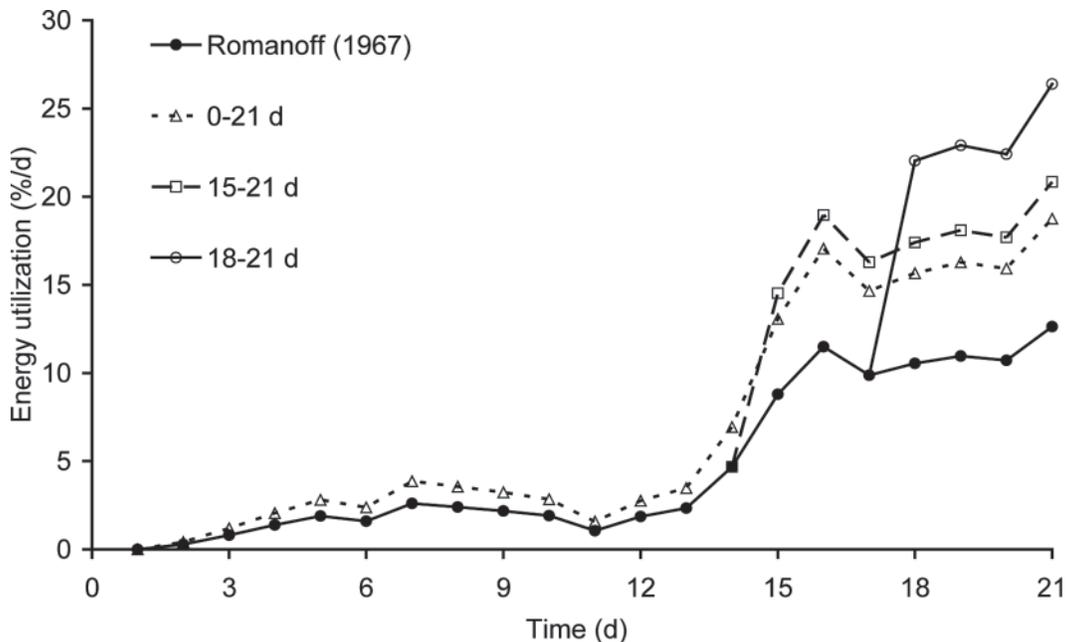
Embryos that utilized a total amount of energy of 243 kJ would reach an HP of  $243 \times 0.105 \times (1 - 0.535)/(24 \times 60 \times 60) = 137$  mW/egg at d 18. If the remaining energy in the RY at hatching (118 kJ) would

have been utilized, evenly distributed across the 21-d incubation period, HP at d 18 would increase to 183 mW/egg. If energy utilization would have been intensified between 15 and 21 d or between 18 and 21 d, HP at d 18 would increase further to 188 and 202 mW/egg, respectively. This means that from an egg of 62 g, with a given  $E_{YFB}$  of 53.5%, theoretically HP could reach a maximum level of 202 mW/egg.

The theoretical effect of increased energy utilization on HP at d 18 was calculated for eggs in the studies by Romanoff (1967), Lourens et al. (2006, 2007), and Sato et al. (2006). Based on these results, we calculated the increase in HP at d 18. When the increased energy utilization was equally distributed over the period of d 1 to 21 of incubation, HP at d 18 increased on average by 3.2 mW/egg for each 10-kJ increase in energy utilization ( $R^2 = 0.94$ ). When each 10-kJ increase in energy utilization was distributed over the period of 15 to 21 d or over the period of 18 to 21 d of incubation, HP at d 18 would increase by 4.2 and 7.1 mW/egg, respectively, with each 10-kJ increase in energy utilization.

## CONSEQUENCES OF INCREASED HP FOR ET

To estimate the effect of HP on ET, we used the mathematical model of Meijerhof and Van Beek (1993). We verified this model using data from Lourens et al. (2006). Additionally, this model was used to estimate the effect of HP on ET, depending on heat loss variables. Finally, we compared the theoretical results with observations of EST in practice.



**Figure 1.** Relative energy utilization per incubation day according to Romanoff (1967), and relative energy utilization in the theoretical situation in which energy remained in the residual yolk at hatching that also would have been utilized between 0 and 21 d, 15 and 21 d, or 18 and 21 d of incubation.

### Calculation of ET

To determine the effect of HP on ET, the heat transfer coefficient from the egg to the environment needed to be quantified. Next, ET was calculated based on mathematical relationships among egg characteristics, air temperature, heat transfer, and thermal conductivity, as described by Meijerhof and Van Beek (1993):

$$ET = T_{\text{air}} + \frac{Po}{6} \times \left(1 + \frac{2}{Bi}\right), \quad [2]$$

in which the Pomerantsev number (Po; dimensionless HP) was defined as

$$Po = \frac{q \times R^2}{\lambda (ET - T_{\text{air}})}, \quad [3]$$

and the Biot-number (Bi) was defined as

$$Bi = \frac{\alpha \times R}{\lambda_{\text{egg}}}, \quad [4]$$

so the temperature difference between the embryo and air could be calculated as

$$ET - T_{\text{air}} = \frac{q \times R^2}{6\lambda_{\text{air}}} \times \left(1 + \frac{2\lambda_{\text{egg}}}{\alpha \times R}\right). \quad [5]$$

In these equations,  $q$  was the amount of heat produced by the embryo ( $\text{W}/\text{m}^3$ ),  $R$  was the radius of a sphere (m), and  $\lambda_{\text{air}}$  was the thermal conductivity of air ( $\text{W}/\text{m}$  per  $^{\circ}\text{C}$ ). A thermal conductivity of air ( $\lambda_{\text{air}}$ ) of  $0.027 \text{ W}/\text{m}$  per K was used for commercial incubation (Van Brecht et al., 2005). The thermal conductivity of an egg during incubation was not known, but for calculations, it was estimated to increase from  $0.5$  to  $50 \text{ W}/\text{m}$  per K with increasing HP because of the increasing blood flow in a developing embryo (Meijerhof, 1994). Furthermore, for the calculation of heat transfer ( $\alpha$ ), the relationship between the Nusselt number (Nu; dimensionless heat transfer) and the Reynolds number (Re; dimensionless air velocity) was used:

$$Nu = 2 + 1.3Pr^{0.15} + 0.66\sqrt{Re} \times Pr^{0.33}. \quad [6]$$

where Pr is the Prandtl number (dimensionless air velocity).

The dimensionless numbers used in equation 6 were defined as

$$Nu = \frac{2\alpha \times R}{\lambda_{\text{air}}},$$

$$Pr = \frac{\nu}{a_{\text{air}}},$$

$$Re = \frac{2V \times R}{\nu}, \quad [7]$$

where  $\nu$  is the kinematic viscosity of air of  $2.5 \cdot 10^{-5} \text{ m}^2/\text{s}$ ,  $a_{\text{air}}$  is the thermal diffusivity of  $1.2 \cdot 10^{-5} \text{ m}^2/\text{s}$ , and  $V$  is the air velocity (m/s) across the eggs (ASHRAE, 1990). The latent HP by moisture loss was described by equation 8 (Meijerhof and Van Beek, 1993), and resulted in a negative effect on ET:

$$ET = T_{\text{air}} + \frac{-k_a \times dp \times h}{\alpha}. \quad [8]$$

where  $dp$  is the water vapor pressure deficit (Pa) and  $h$  is the latent heat of evaporation ( $\text{J}/\text{kg}$ ).

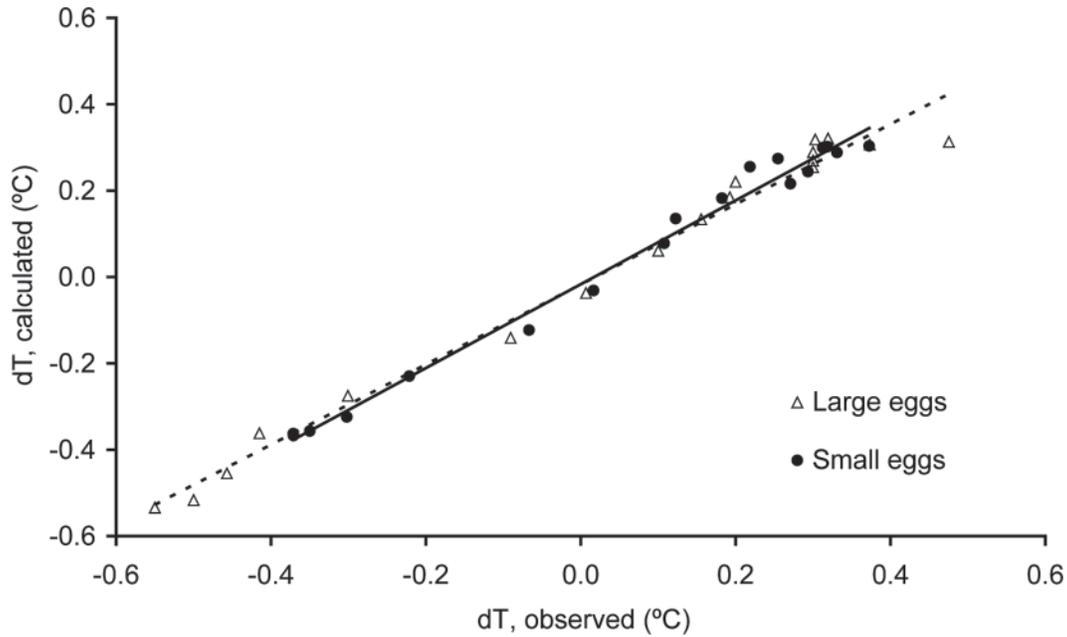
In equation 8, the respiration coefficient  $k_a$  (based on surface of the egg) was calculated from the transpiration coefficient based on mass ( $k_m$ ), as explained by Meijerhof and Van Beek (1993). The weight loss of an egg depended on the water vapor pressure gradient between the egg and the environment and the conductance of the eggshell. Therefore, weight loss of an egg was largely determined by the specific weight loss coefficient of an egg, the ambient temperature, the RH of the air and, to a lesser extent, the temperature difference between the egg and the environment in a situation in which HP was high (Meijerhof and Van Beek, 1993).

To validate the model described above, we used HP data on small and large eggs (Lourens et al., 2006) and the MT that was required to maintain the EST constant at  $37.8^{\circ}\text{C}$ . An average air velocity across the eggs of  $0.3 \text{ m}/\text{s}$  was measured during the experiment. Based on total egg weight loss at d 18 of incubation and the calculated water vapor pressure gradient between the egg and the environment, we estimated the latent heat loss per day. Using the HP data and heat loss calculations (equation 8), we calculated the difference between MT and ET. Calculated and observed values for the difference between MT and ET fitted well (small eggs:  $R^2 = 0.99$ ; large eggs:  $R^2 = 0.98$ ; Figure 2).

Because of this good fit, the model was used to estimate the effect of increased HP on ET, based on energy utilization and  $E_{\text{YFB}}$  in eggs of different weights and incubated at different EST and oxygen concentrations.

### Effect of HP on ET

The effect of HP on ET was largely determined by air velocity (Meijerhof and Van Beek, 1993), so air velocity was taken into account, calculating the effect of HP on ET. The simulated effect of a theoretical increase in HP, because of increased utilization (see Figure 1) on ET at d 18 of incubation at different air velocities,

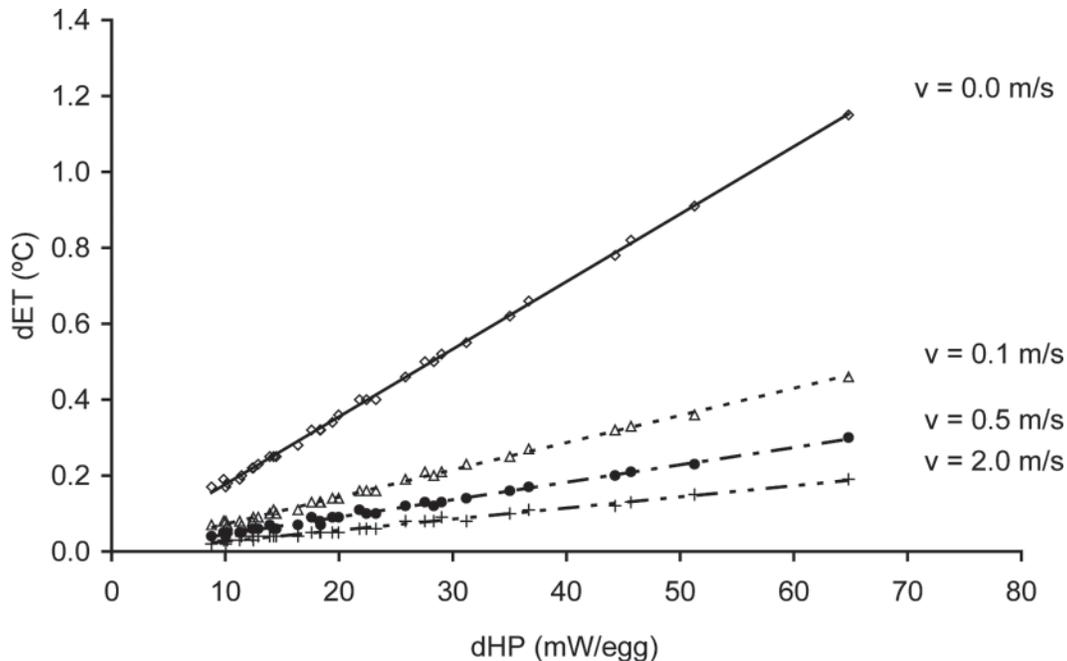


**Figure 2.** Relationship between observed and calculated difference ( $dT$ ) between machine temperature and eggshell temperature in small and large eggs (based on Lourens et al., 2006).

is shown in Figure 3. In this figure, HP data from Romanoff (1967), Lourens et al. (2006, 2007), and Sato et al. (2006) were used.

At a constant air velocity, the calculated changes in HP were linearly related to changes in ET ( $R^2 > 0.99$ ). The largest effect of increased HP on ET was observed in eggs incubated in still air. In still air, an increase in HP of 10 mW/egg at d 18 of incubation increased ET by 0.18°C. When the air velocity was 0.1, 0.5, or 2.0 m/s, an increase in HP of 10 mW/egg increased the ET

by 0.07, 0.05, and 0.03°C, respectively. The theoretically maximum increase in HP at d 18 of incubation was estimated to be 65 mW/egg (202 – 137 mW/egg; see above). In still air, this would increase the ET by 1.21°C. When eggs were exposed to air velocities of 0.1, 0.5, or 2.0 m/s, an increase in HP of 65 W/egg resulted in an increase in ET of 0.47, 0.30, or 0.19°C, respectively. Based on these calculations, we concluded that in the theoretical situation in which all RY was utilized in a short period (d 18 to 21 of incubation) with a given



**Figure 3.** Calculated effects of increased heat production ( $dHP$ ) at d 18 of incubation on the change in embryo temperature ( $dET$ ) as affected by air velocity ( $v$ ).

$E_{YFB}$  of 53.5% and an air velocity of 0 m/s, the ET of 1 single egg increased by a maximal 1.21°C.

### EST in Practice and Experiments

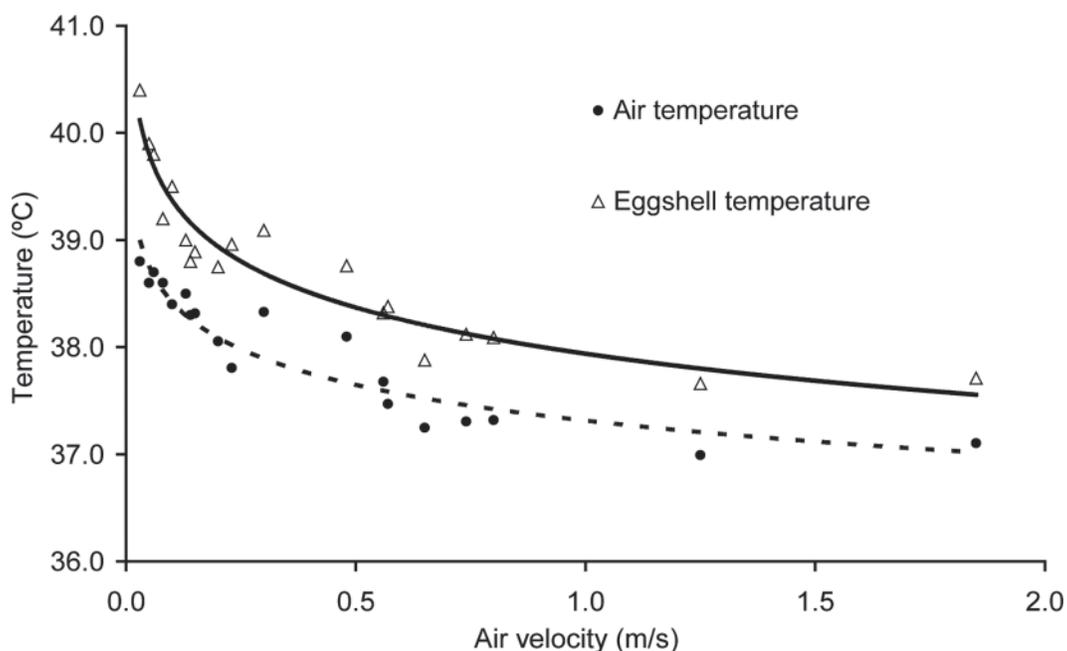
We calculated a maximal increase in ET of 1.21°C above a given ET of 37.8°C, resulting in a theoretically maximal ET of 39°C. However, in practice, EST at d 18 of 40°C or more have been observed (Lourens, 2001). In that study, the MT set point was 37.2°C, but depending on the position of the eggs in the incubator, the EST at d 18 of incubation varied between 37.6 and 40.4°C. This variation largely depended on the variation in air velocity within the incubator. In the corners of the incubator, air velocity was <0.2 m/s, whereas close to the ventilator, air speeds of almost 2.0 m/s were observed (Figure 4). In places where air velocity was low, both EST and air temperature were (substantially) increased. This fits well with the experimental results obtained by Elibol and Brake (2008), who found that eggs of on average 68.9 g had an average EST of 39.4°C when they were placed far from the incubator fan, whereas eggs of the same weight, placed near the incubator fan, showed an average EST of 38.7°C. These EST values were found at an MT setting of 37.4°C.

Hence in practice, embryos in the same single-stage incubator experienced ET that exceeded the range of our calculated theoretical upper limits for ET. The discrepancy between the calculated maximal ET and the observed EST in practice can probably be explained with the following reasoning. The theoretical calculations described above were based on 1 single egg without interactions with other eggs. However, in practice an incubator is filled with up to 100,000 eggs or more,

each with their own HP and heat transfer to each other. As a consequence, air temperature surrounding the egg was higher than with only 1 single egg, as expressed in Figure 4. When EST is not maintained at a set level, this results in a smaller temperature gradient between the egg and the environment, and consequently lower heat loss, resulting in an increased EST. As explained above, a higher EST resulted in a lower  $E_{YFB}$  with the same amount of energy utilized, resulting again in a higher HP and consequently a higher ET. This resulted in a vicious circle. When calculations as described in this study were performed using an MT of 38.8°C (Figure 4), calculated ET increased to 40.2°C in still air, when all energy in the remaining RY would be used in the period from d 18 to 21. In conclusion, the higher EST, as found in practice and in experiments, fits with the theoretical model, as described in this paper, and is probably due to reduced  $E_{YFB}$  and consequently higher HP.

We concluded that, during incubation, embryonic HP was determined by the amount of energy utilized during incubation and the efficiency of this utilization. The amount of energy utilized depended on egg weight and oxygen availability, but not on EST, whereas the effect of breed and strain is currently not known. The efficiency of energy utilization depended on EST. This all means that within a given EST, HP depended only on the amount of energy utilized.

Because of a higher HP, ET can increase. An increase in ET can affect hatchability and hatchling quality. Therefore, it is of great importance to realize that any factor that affects either HP or heat transfer directly influences ET. Especially during incubation experiments, it should be realized that changes in ET may have a



**Figure 4.** Effect of air velocity at a given machine temperature of 37.2°C on air (5 cm from the egg) and eggshell temperature in a commercial incubator at d 18 of incubation (Lourens, 2001).

greater effect on results than the factor investigated itself; therefore, we strongly suggest that ET (or EST) be controlled in any incubation experiment involving hatchability and energy utilization.

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