

# Modeling Incubation Temperature: The Effects of Incubator Design, Embryonic Development, and Egg Size

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**ABSTRACT** A simple model to describe the relationship between the temperature of the developing embryo, incubator temperature, embryo heat production, and thermal conductivity of the egg and surrounding air is presented. During early incubation, embryo temperature is slightly lower than incubator temperature because of evaporative cooling. However, from mid-incubation onwards, metabolic heat production from the embryo raises embryo temperature above incubator temperature. The extent of the rise in embryo temperature depends on thermal conductivity, which, in turn, is mainly influenced by the air speed over the egg. The importance of air speed and restrictions to air flow within artificial incubators is discussed.

Exact determinations of optimum incubation temperatures from studies reported in the literature are difficult

because only incubator temperatures are reported. Embryo temperatures can differ from incubator temperature because of differences in thermal conductivity between different incubation systems and differences between incubators in their ability to control temperatures uniformly. It is suggested that shell surface temperatures are monitored in experiments to investigate temperature effects to allow consistent comparisons between trials. Monitoring shell temperatures would also make it easier to translate optimum temperatures derived in small experimental incubators to the large commercial incubators used by the poultry industry. The relationship between egg temperature, the metabolism of the developing embryo and egg size is discussed.

(Key words: temperature, incubation, model, embryo metabolism, egg size)

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## INTRODUCTION

Most poultry species have an optimum incubation temperature of 37 to 38 C and small deviations from this optimum can have a major impact on hatching success and embryo development (Wilson, 1991). The vast majority of poultry hatching eggs are artificially incubated in incubators that must be designed to accurately control the temperature inside the machine to ensure that the temperature of the developing embryo does not deviate from this optimum.

The temperature experienced by the developing embryo is dependent on three factors: 1) the incubator temperature, 2) the ability of heat to pass between the incubator and the embryo, and 3) the metabolic heat production of the embryo itself. The purpose of this review is to use a simple thermal energetics model of the artificial incubation process to describe the interrelationships among the three factors that determine embryo temperature and discuss some of the implications for the design of incubators.

## THEORY OF HEAT EXCHANGE

The thermal energetics of incubation have been modeled by Kashkin (1961), Kendeigh (1963), Sotherland *et al.* (1987), Turner (1991, 1994), and Meijerhof and van Beek (1993). A simple form of the model can be given as

$$T_{\text{egg}} = T_{\text{inc}} + (H_{\text{emb}} - H_{\text{water loss}})/K \quad [1]$$

where  $T_{\text{egg}}$  = temperature of the egg (Celsius);  $T_{\text{inc}}$  = temperature of incubator (Celsius);  $H_{\text{emb}}$  = heat production of embryo at a given moment of incubation (Watts);  $H_{\text{water loss}}$  = heat loss from evaporative cooling (Watts); and  $K$  = thermal conductance of egg and surrounding boundary of air around the egg (Watts per degree Celsius).

The heat balance of an animal is described by (Schmidt-Nielsen, 1975)

$$H_{\text{emb}} = H_{\text{water loss}} \pm H_{\text{rad}} \pm H_{\text{conv}} \quad [2]$$

or rewritten,

$$H_{\text{emb}} - H_{\text{water loss}} = H_{\text{rad}} + H_{\text{conv}} \quad [3]$$

where  $H_{\text{rad}}$  and  $H_{\text{conv}}$  are the heat lost or gained by

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radiation and convection respectively (Watts). Equation 1 uses the terms  $H_{\text{emb}} - H_{\text{water loss}}$  to describe the heat loss or gain from an egg because they are easier to measure than either  $H_{\text{rad}}$  or  $H_{\text{conv}}$ . Heat transfer through radiation is assumed to be small because all the surfaces within the machine will be at temperatures close to (within approximately 1 to 2 C of) the surface temperature of the egg. Kashkin (1961) estimated that 40 to 45% of the total heat loss from a duck's eggs was by radiation; however, this estimate has assumed that the total egg surface would be able to radiate heat to the surface of the incubator. In a commercial incubator an egg would be surrounded by other eggs at the same temperature, thereby reducing the effective radiative surface of the egg (Kashkin, 1961). It is therefore assumed that the main transfer of heat occurs through convection.

Equation 1 contains the term  $H_{\text{water loss}}$  because eggs continually lose water through incubation, typically amounting to 12% of the fresh egg weight between the onset of incubation and the start of pipping (Ar, 1991). The phase change from liquid water to water vapor requires heat and at incubation temperature this equates to approximately 580 cal/g of water lost (Schmidt-Nielsen, 1975). For example, a 60-g chicken egg loses approximately 0.4 g of water/d, which equates to a heat loss of 232 cal/d or 11.2 mW.

Embryo heat production can be measured directly, but Romijn and Lokhurst (1960) showed that it can be estimated by measuring  $O_2$  consumption. Every liter of  $O_2$  consumed by the embryo is equivalent to the production of 4.69 kcal of heat (Vleck *et al.*, 1980). Typical  $O_2$  consumption of a chicken egg just before pipping is 570 mL/d (Vleck and Vleck, 1987), equivalent to heat production of 2.67 kcal/d or 130 mW.

At the onset of incubation,  $H_{\text{emb}}$  is negligible and therefore  $T_{\text{egg}} < T_{\text{inc}}$  because  $H_{\text{emb}} < H_{\text{water loss}}$ . However, at the end of incubation,  $H_{\text{emb}} \gg H_{\text{water loss}}$  and therefore  $T_{\text{egg}} > T_{\text{inc}}$ . Figure 1 shows  $H_{\text{emb}}$  and  $H_{\text{water loss}}$  of chicken eggs measured by Romijn and Lokhurst (1960).  $H_{\text{emb}}$  was observed to exceed  $H_{\text{water loss}}$  midway through the incubation period. Direct measurements of  $T_{\text{egg}}$  have also observed that it exceeds  $T_{\text{inc}}$  midway through incubation in both chicken (Tazawa and Nakagawa, 1985) and turkeys (Figure 2). The result is that during the first half of incubation, eggs will be gaining heat from the surrounding air, whereas during the second half of incubation, eggs will lose heat.

The thermal conductivity term,  $K$ , used in Equation 1 combines the thermal conductivity of the egg ( $K_{\text{egg}}$ ) and the boundary layer of air around the egg ( $K_{\text{air}}$ ). Sotherland *et al.* (1987) determined values for  $K_{\text{egg}}$  and  $K_{\text{air}}$  and showed that the air boundary layer around the egg was approximately  $100 \times$  greater a barrier to heat loss than the egg itself. These authors also showed that the value of  $K_{\text{air}}$  is dependent on the air speed over the eggs and the relationship could be estimated as follows

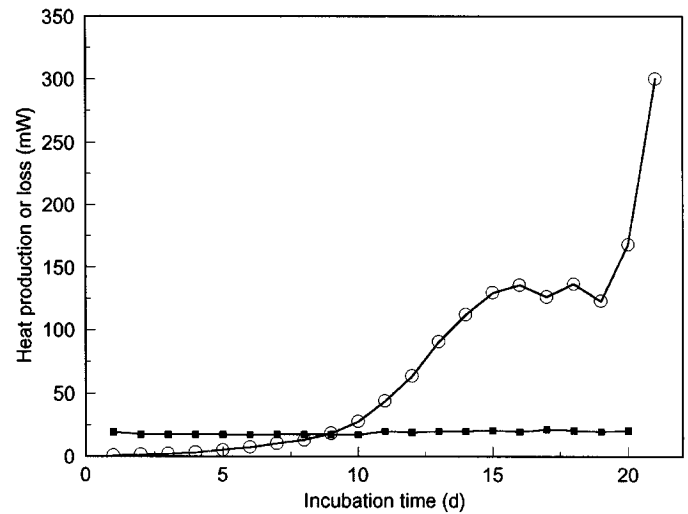


FIGURE 1. Metabolic heat production (○) and evaporative heat loss (■) of chicken eggs during incubation. Data from Romijn and Lokhurst (1960).

$$K = (0.97 U^{0.6}) M^{0.53} \quad [4]$$

where  $U$  = air speed (centimeters per second); and  $M$  = egg mass (grams). The effect of changing air speed from 0 to either 100 or 400 m/s increased thermal conductance by approximately  $2.5 \times$  and  $6 \times$ , respectively. A similar relationship was found by Meijerhof and van Beek (1993).

An important consequence of the relationship between  $K_{\text{air}}$  and air speed is that the differential between  $T_{\text{egg}}$  and  $T_{\text{inc}}$  during the second half of incubation will become greater at slower air speeds. Meijerhof and van Beek (1993) estimated the increase in  $T_{\text{egg}}$  over  $T_{\text{inc}}$  for eggs of different weights and  $H_{\text{emb}}$  at two air speeds, 0.5

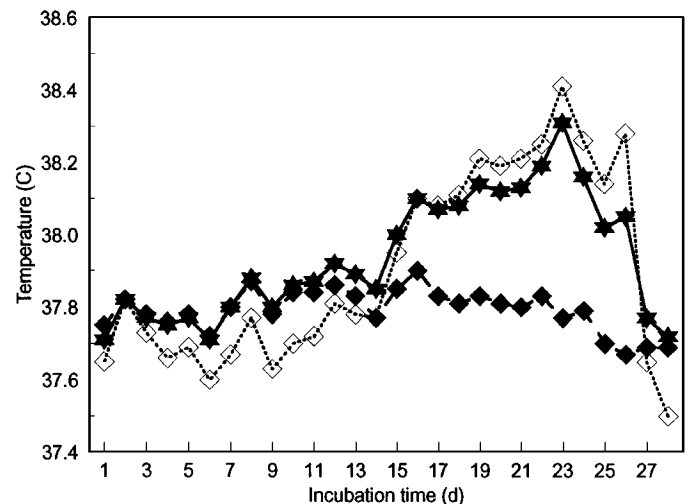
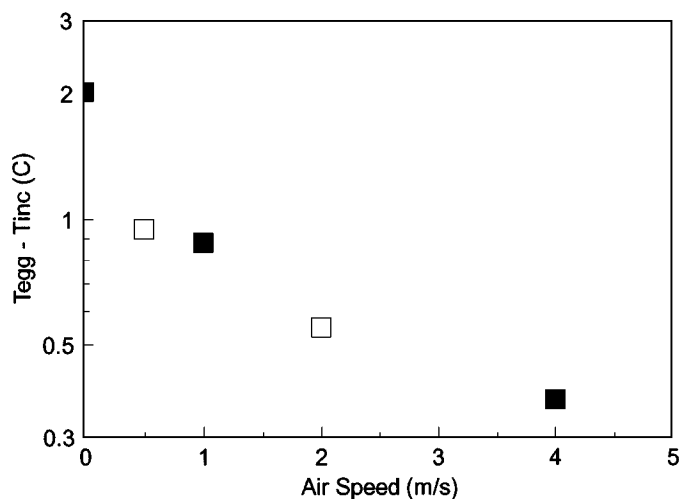


FIGURE 2. Temperature of a turkey egg incubated at 37.5 C; temperature measured inside the egg (○), on the surface of the eggshell (★) and incubator air temperature approximately 10 mm from the egg (◆). The poult hatched on the 26th d of incubation. Data from French (unpublished observations).



**FIGURE 3.** The effect of air speed on the difference between internal egg temperature ( $T_{\text{egg}}$ ) and incubator temperature ( $T_{\text{inc}}$ ) plotted on a log scale. Estimates based on the models of Sotherland *et al.* (1987, ■) and Meijerhof and van Beek (1993, □), using a 50-g chicken egg with a metabolic heat output of 100 mW.

and 2 m/s. Similarly, it is possible to use the values of  $K$  derived by Sotherland *et al.* (1987) for air speeds of 0, 1, and 4 m/s in Equation 1 to estimate  $T_{\text{egg}} - T_{\text{inc}}$ . Figure 3 plots the relationship between air speed and  $T_{\text{egg}} - T_{\text{inc}}$  derived from the two studies based on a 50-g egg with a  $H_{\text{emb}}$  of 100 mW. As can be seen, there is good agreement between the estimates of  $T_{\text{egg}} - T_{\text{inc}}$  between the two studies.

The value of  $K_{\text{egg}}$  has been shown to increase during incubation because the development of the network of blood vessels in the chorioallantoic membrane underlying the shell improves heat flow (Tazawa *et al.*, 1988). The effect of blood flow on  $K_{\text{egg}}$  will increase as egg size increases but the overall effect on  $K$  will only become significant if air resistance to heat transfer becomes small (Turner, 1987). In chicken eggs, blood flow increased  $K_{\text{egg}}$  by approximately 20% (Tazawa *et al.*, 1988).

The thermal energetic model of artificial incubation is relatively simple because heat is transferred between the egg and air totally surrounding the egg. The situation is more complicated in natural incubation, in which heat is applied by the bird sitting on the egg (see Turner, 1991 for further discussion on this subject).

## TEMPERATURES IN INCUBATORS

The use of thermal conductance,  $K$ , in Equation 1 has assumed a simple incubator, that is an egg surrounded by warm air. However, in commercial incubators the situation is much more complicated, as each egg will be surrounded by many other eggs that may (in a single-stage incubator) or may not (in a multi-stage incubator) be at the same developmental stage. Although it is not the intention of this paper to discuss the design requirements of an incubator (see Owen, 1991), clearly the design of the incubator will have an effect on the transfer of heat between the egg and the incubator air.

Incubators require an air conditioning unit to provide heat or cooling and humidification and a fan to circulate the conditioned air through the eggs before being returned to the conditioning unit. The volume of air that passes the eggs to transfer heat can be estimated using (Owen, 1991)

$$(T_{\text{off}} - T_{\text{on}}) = F.H_{\text{eggs}}/V_{\text{eggs}} \quad [5]$$

where  $(T_{\text{off}} - T_{\text{on}})$  = the temperature rise in air flowing over the eggs (Celsius);  $F$  = factor, approximately 3.25 for incubator air at 37.5 C and 50% RH;  $H_{\text{eggs}}$  = heat production of eggs in flow path (Watts); and  $V_{\text{eggs}}$  = flow rate of air over eggs (cubic meters per hour). The rise in air temperature as it passes over the eggs is inversely proportional to air volume flow and therefore uniform control of egg temperature within the incubator depends on uniform air movement around the eggs. As air flow has a negligible effect on water loss from the eggs (Kaltofen, 1969; Spotila *et al.*, 1981) there appears to be no limit to increasing air flow to control temperature (Owen, 1991).

The uniformity of air flow within an incubator will depend on how easy it is for the air to pass between the trays of eggs. This may be the path of greatest resistance to air movement and air may pass around the mass of eggs, through spaces next to machine walls or between egg trolleys (Owen, 1991). Eggs must be turned through 90° every hour for normal embryo development to take place (Tullett and Deeming, 1987) and this is achieved in an incubator by tilting the egg trays at 45° from horizontal, the direction changing every hour. In most incubators, turning is achieved by pivoting the individual trays around a fulcrum at the center of the tray. The effect of the turning is to reduce the space between the trays significantly from the spacing when the trays are horizontal (Figure 4).

Using Equation 5, it is possible to estimate the effect of tray spacing on the air speed required over 18 d for chicken eggs to obtain an acceptable air temperature rise (for calculation purposes 0.5 C). Assumptions made in the calculations were: height of tray and eggs = 60 mm; tray dimensions = 0.9 m × 0.31 m, air assumed to pass across the width of the egg tray; heat output per egg = 120 mW; and tray capacity = 132 eggs, of which 22 are exposed to open air when tray is turned and therefore excluded from the calculation. The relationship between tray spacing and required air speed to maintain egg temperature is shown in Table 1. Two estimates are given, one assuming that both trays contain eggs at 18 d of incubation and one assuming that one tray contains eggs that are less than midway through incubation and therefore producing no heat.

As can be seen from Table 1, as the spacing between the trays increases, there is an exponential decline in required air speed. Although actual spacing between trays in commercial incubators is highly variable, with many of the newer machine designs incorporating greater tray spacing, it is not uncommon to see trays

TABLE 1. The required air speed between egg trays in an incubator to maintain the same internal egg temperature at different tray spacings

Distance between trays		Air speed	
		One tray with 18-d eggs	Both trays with 18-d eggs
Horizontal	Turned 45°	(m/s)	
(mm)			
30	3	4.8	9.6
35	7	2.1	4.1
40	11	1.3	2.6
50	18	0.8	1.6
60	25	0.6	1.2

that are sufficiently close together that large eggs on the tray are damaged by the tray above.

There are little reported data on air speeds between trays in incubators, but values between 0.1 and 3.0 m/s have been observed in chicken incubators (Kaltofen, 1969), less than 0.1 m/s in duck incubators (Kashkin, 1961) and between 0.2 and 2.2 m/s in a turkey incubator (French, unpublished observations). The considerable variation in air speed between different locations within chicken and turkey incubators would suggest that temperature variation would be observed in these machines.

Kaltofen (1969) investigated the relationship between air speed over the eggs, temperature of the air surrounding the eggs and subsequent hatchability at different locations within a commercial incubator (700 egg drum type, make not specified, operated single stage). As part of the study, incubator fan speeds were changed to give different air speeds over the eggs. Table

2 summarizes the main observations from this study. Increasing the incubator fan speed resulted in faster air speeds over the eggs and lower air temperatures, supporting the predictions of Sotherland *et al.* (1987) and Meijerhof and van Beek (1993) that air speed has a major influence on thermal conductivity. Air speed also varied between tray locations within the machine, although only at the lowest fan speed did this result in a temperature difference between the trays. The increase in temperature at the lowest fan speed was also sufficient to depress hatchability.

Mauldin and Buhr (1995) measured temperatures on top of eggs in a multi-stage chicken incubator and observed that temperature was on average 1 C warmer on the trays than at the temperature controller of the incubator. Temperature on the trays also changed with time depending on the age of the eggs within the incubator. Every 3 or 4 d, 18-d-old eggs were moved out of the incubator to be transferred into a hatcher and they were replaced with fresh eggs. The initial effect of the movement of eggs was to lower temperature just after the transfer. An increase of approximately 0.5 C over the following 3 or 4 d was then observed, until temperature fell again at the next transfer. The study illustrates the effect that the presence and management of other eggs within the incubator can have on the temperature experienced by an individual egg.

The observation of Kaltofen (1969) and Mauldin and Buhr (1995) that temperatures recorded among the eggs can differ markedly from the operating temperature of the incubator has also been observed in a wide range of turkey incubators (Table 3). Maximum temperatures were recorded normally on eggs at the end of incubation and were between 0.4 to 3.1 C above the machine operation temperature. It is clear from these studies that many commercial incubators are not able to maintain a uniform temperature surrounding the incubating egg, principally due to uneven air flow within the machine. Improving incubator design by improving air flows within the machines is an important goal for incubator manufacturers. Techniques to directly measure K within incubators have been described by Meijerhof and van Beek (1994).

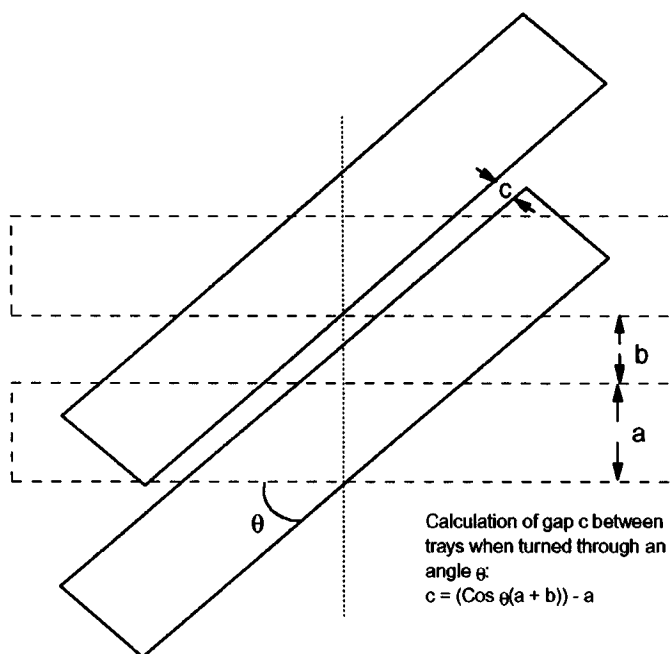


FIGURE 4. The effect of turning on the spacing between egg trays.



**TABLE 2. The effect of altering incubator fan speed, in revolutions (rev) per minute, on air speed over eggs, temperature among the eggs, and hatchability at two locations within the incubator (Kaltofen, 1969)**

Variable	Tray position	Fan speed		
		60 rev/min	120 rev/min	180 rev/min
Air speed, m/s	Center	0.20	0.45	0.62
	Bottom	0.99	2.10	2.80
Temperature, C	Center	39.4	38.6	38.0
	Bottom	38.9	38.7	38.1
Hatchability variance from 120 rev/min treatment, % points	Center	-23.2	0	+0.4
	Bottom	-2.9	0	-0.1

## OPTIMUM INCUBATION TEMPERATURE

Optimum incubation temperature is normally defined as that required to achieve maximum hatchability. However, Decuyper and Michels (1992) have argued that the quality of the hatchling should also be considered. The effect of temperature on length of incubation has been observed in several studies (Romanoff, 1935, 1936; Romanoff *et al.*, 1938; Michels *et al.*, 1974; French, 1994a) and on the rate of embryo growth (Romanoff *et al.*, 1938; Decuyper *et al.*, 1979). Incubation temperature has been found to affect the hatchling's thermoregulatory ability, hormone levels, and posthatching growth rate (see reviews by Wilson, 1991; Decuyper, 1994). Of potentially greater commercial importance, Ferguson (1994) has suggested that temperature may be able to alter the sex ratio by altering the phenotypic sex of a proportion of chick embryos.

Studies investigating the effect of incubation temperature on the hatchability of poultry species have been reviewed by Lundy (1969) and Wilson (1991). Several broad conclusions were drawn in these reviews: 1) optimum continuous incubation temperature for poultry species is between 37 to 38 C, although hatchability is possible between 35 to 40.5 C; 2) embryos are more sensitive to high than to low temperature; 3) the effect of a suboptimal temperature will depend on both the

degree of deviation from optimum and the length of time applied; 4) embryos appear to be more sensitive to suboptimal temperatures at the beginning of incubation than at the end of incubation. Recent studies suggest that optimum temperature may differ between poultry strains (Decuyper, 1994; Christensen *et al.*, 1994) or eggs of different sizes (French, 1994b).

Interpretation of incubator temperature studies is difficult because they use incubator operation temperature as the temperature treatment applied to the egg. The data from both chicken and turkey incubators show that the temperature indicated on the incubator control may be significantly different from the temperature of the air surrounding the egg. The implication of Equation 1 is that the embryo inside the egg may be subjected to a different temperature to the air surrounding the egg depending on the thermal conductivity of the boundary layer of air around the egg. It is therefore possible that two studies using different incubation systems can apply the same incubator temperature treatments but for widely different  $T_{emb}$  results to be observed.

The problem is illustrated by the elegant study of Ono *et al.* (1994). Chicken embryos between 12 and 20 d of incubation were subjected to a temperature of 48 C and the time taken for the embryos' hearts to stop beating was measured. As the embryos got older their

**TABLE 3. Temperatures recorded in turkey incubators in Europe and North America (French, unpublished observations)**

Hatchery	Type of incubator	Operation temperature	Temperature among eggs	
			Mean	Maximum
(C)				
A	Drum multi-stage	37.5	37.9	38.7
B	Drum multi-stage	37.4	37.5	38.2
C	Tunnel multi-stage	37.0	37.2	37.8
D	Fixed rack multi-stage	37.6	37.8	38.0
E	Fixed rack multi-stage	37.4	37.4	38.0
F	Fixed rack multi-stage	37.4	37.4	38.2
G	Fixed rack multi-stage	37.5	37.6	38.2
H	Cabinet multi-stage	37.4	37.7	38.0
I	Cabinet single-stage	37.3	37.4	37.7
J	Cabinet single-stage	37.3	37.6	40.4
K	Cabinet single-stage	37.6	37.6	38.1
K	Cabinet single-stage	37.1	37.1	38.6

tolerance time decreased from 100 min at 12 d to 56 min at 20 d. From this finding, it could be concluded that older embryos are less tolerant to high temperature. However, internal egg temperatures were also measured in this study and it was found that, at all ages, embryos were dying when their internal egg temperature reached 46.5 C. Tolerance time became shorter with embryo age because older embryos had higher internal temperatures at the start of the experiment.

The important conclusion is that incubator temperature studies should measure the temperature experienced by the embryo if the observations are to have wider relevance than to the particular incubator used in the experiment. Most research work is undertaken in small incubators containing hundreds of eggs, in which the difference between incubator temperature and that experienced by the embryo may not be high. However, commercial incubators contain thousands of eggs and results from research may not be transferable to the practical situation unless a common standard of egg temperature is used.

Measuring internal egg temperature is problematic because the structural integrity of the shell becomes damaged, risking bacterial contamination and damage to the developing embryo. An alternative is to measure shell surface temperature, as  $K_{\text{egg}}$  is high in comparison to  $K_{\text{air}}$ , resulting in only small differences between internal and shell surface temperature (Sotherland *et al.*, 1987; Figure 2). Unfortunately, the author is unaware of any studies that have investigated the relationships between either internal or shell temperature and subsequent hatching success, and this question would be an appropriate topic for investigation.

## TEMPERATURE AND EMBRYO METABOLISM

Studies on the effects of incubation temperature on embryo metabolism have been reviewed by Deeming and Ferguson (1991). As temperature changes, so does the oxygen consumption of the embryo and, hence, its heat production,  $H_{\text{emb}}$ . Avian embryos for the majority of the incubation time are poikilothermic and therefore do not increase their metabolic heat output to maintain  $T_{\text{emb}}$  when  $T_{\text{inc}}$  declines. Indeed, the opposite occurs and as  $T_{\text{inc}}$  decreases so does oxygen consumption. Tazawa *et al.* (1989) showed that at about 18 d of incubation the chick embryo could maintain oxygen consumption when temperature fell from 38 to 35 C but as temperature decreased further, oxygen consumption then declined. After pipping, an increase in oxygen consumption in response to a decrease in  $T_{\text{inc}}$  has been observed in both chickens (Tazawa *et al.*, 1989) and Japanese quail (Nair *et al.*, 1983), but full thermoregulatory response in Galliformes only develops after hatching (Dietz and van Kampen, 1994).

Although metabolic responses to short-term changes in incubation temperature have been studied, only

limited data are available on responses to long term or continuous alterations to normal incubation temperature. Chicken eggs incubated continuously at 38 or 35.5 C had different growth rates but oxygen consumption at comparable embryo mass was the same (Tazawa, 1973). Decuyper *et al.* (1979) incubated chicken eggs at 35.8, 36.8, 37.8, and 38.8 C for the first 10 d and then at 37.6 C for the rest of incubation. Although the temperature treatments altered rate of development, embryo heat production remained the same at equivalent developmental stages. Similar results were obtained with turkey embryos incubated at 37.5, 38.5, 39.5, and 40.5 C for the first 6 d of incubation (Meir and Ar, 1992, Tel-Aviv University, Tel-Aviv, 69978 Israel, personal communication). These workers also investigated the effect on oxygen consumption by varying temperature either during the second and last third of incubation or by using a lowering temperature regimen. Although temperature changed growth rate, oxygen consumption per unit of dry embryo mass remained the same.

Contrary to the above observation, a study by Geers *et al.* (1983) showed that temperature could affect oxygen consumption per unit of dry embryo mass. These workers incubated chicken eggs for the first 10 d at either 35.8 or 37.8 C and then subsequently at 37.8 C. Although the cool incubator temperature reduced early embryo growth rate, once the cool embryos were returned to normal temperature at 11 d they grew faster than the controls, confirming observations in an earlier study (Geers *et al.*, 1982) that embryos can exhibit compensatory growth. The faster growth in the cool treated embryos resulted in a higher metabolic heat production per unit dry embryo mass than that of the control group.

Hoyt (1987) developed a model that separated embryo metabolism between growth and maintenance and used this model to predict that the pre-internal pipping rate of oxygen consumption would be greater in embryos that grow faster to achieve a given final embryo weight. The model would suggest that altering embryo growth rate by manipulating incubation temperature would affect the rate of oxygen consumption per gram of embryo mass; however, studies to critically test this prediction have not been undertaken and the available evidence is ambiguous.

## EGG SIZE

Equation 4 shows that thermal conductance,  $K$ , scales with egg mass to the power of 0.53. The result is that as egg mass increases, thermal conductance does not increase proportionally, so that larger eggs should have greater difficulty losing metabolic heat produced by the embryo. Meijerhof and van Beek (1993) predicted the rise in  $T_{\text{emb}}$  over  $T_{\text{inc}}$  for eggs of different sizes for two hypotheses:  $H_{\text{emb}}$  is 1) constant per gram of egg, or 2) constant per egg regardless of size. If  $H_{\text{emb}}$  per egg is constant, then  $T_{\text{emb}} - T_{\text{inc}}$  should decline with egg size

TABLE 4. Effect of fresh egg weight on the hatchability of turkey eggs incubated at three temperatures (French, 1994b)

Incubator temperature (C)		Fresh egg weight				
		70 to 79 g	80 to 84 g	85 to 89 g	90 to 94 g	95 to 104 g
36.5	HOF, <sup>1</sup> %	53.6 <sup>a,x</sup>	73.5 <sup>a,x</sup>	77.5 <sup>a,x</sup>	77.4 <sup>a,x</sup>	67.6 <sup>a,x</sup>
	n	28	102	147	93	37
37.5	HOF, %	69.7 <sup>ab,x</sup>	78.9 <sup>ab,x</sup>	80.6 <sup>a,x</sup>	68.1 <sup>ab,x</sup>	56.2 <sup>b,x</sup>
	n	33	109	139	91	32
38.5	HOF, %	54.8 <sup>ab,x</sup>	48.3 <sup>abc,y</sup>	47.0 <sup>abc,y</sup>	34.7 <sup>ac,y</sup>	25.0 <sup>bc,y</sup>
	n	31	118	134	95	32

<sup>1</sup>Hatch of fertile eggs.

<sup>a-c</sup>Hatchabilities within rows with no common superscript differ significantly ( $P < 0.05$ ) using the G-Test (Sokal and Rohlf, 1981).

<sup>x,y</sup>Hatchabilities within columns with no common superscript differ significantly ( $P < 0.05$ ) using the G-Test (Sokal and Rohlf, 1981).

because of the increase in  $K$ . Alternatively, if  $H_{emb}$  per gram is constant,  $T_{emb} - T_{inc}$  increases with egg size because  $K$  does not increase proportionally.

The estimates of Meijerhof and van Beek (1993) are, of course, artificial, as  $H_{emb}$  does not remain constant per egg nor per gram of egg regardless of egg size. Interspecific allometric relationships between egg mass ( $M$ ) and the rate of oxygen consumption before internal pipping (PIP  $VO_2$ , milliliters per day) have been investigated in several studies (Rahn *et al.*, 1974; Hoyt *et al.*, 1978; Vleck *et al.*, 1980; Vleck and Vleck, 1987), and the following relationship was derived:

$$\log \text{PIP } VO_2 = 1.36 + 0.73 \log M \quad [6]$$

Poultry species do not deviate significantly from this relationship (Vleck, 1991). However, Hoyt (1980) has observed that the above relationship does include an independent relationship between PIP  $VO_2$  and the length of incubation, because larger eggs tend to have longer incubation times. PIP  $VO_2$  was related to  $M$  and incubation period ( $I$ , days),

$$\text{PIP } VO_2 = 139 M^{0.848} / I^{0.654} \quad [7]$$

Using Equation 7 to estimate  $H_{emb}$  just before pipping and Equation 4 to estimate  $K$ , Figure 5 shows the predicted relationship between egg size and  $T_{emb} - T_{inc}$  for eggs with an incubation period of 28 d. Although the temperature gradient does increase with egg mass, the rate of increase is low, with temperature increasing by 0.1 C over a 30-g egg mass range. Based on Figure 5, it is possible to predict that eggs of different mass should not have significantly different incubation temperature requirements.

This prediction is not in accordance with the data presented in Table 4, taken from French (1994b). At high incubation temperatures (38.5 C), turkey hatchability progressively decreased with increasing egg size and large eggs had the best hatchability when incubated at a

reduced incubation temperature (36.5 C). The decline in hatchability at high temperature with increased egg size occurred mainly due to an increase in embryo mortality between 24 to 26 d of incubation (French, unpublished observations), coinciding with the stage before internal pipping. Other data presented in French (1994b) showed that large eggs hatched better when incubation temperature was reduced from 37.5 to 36.5 C during the second half of incubation; however, similar improvements were not observed in small eggs. As far as the author is aware, no other studies have investigated the possible relationship between egg size and incubation temperature, and this relationship warrants further investigation.

The hypothesis that large eggs are more sensitive to high temperatures than small eggs is supported by many studies that have shown large eggs do not hatch

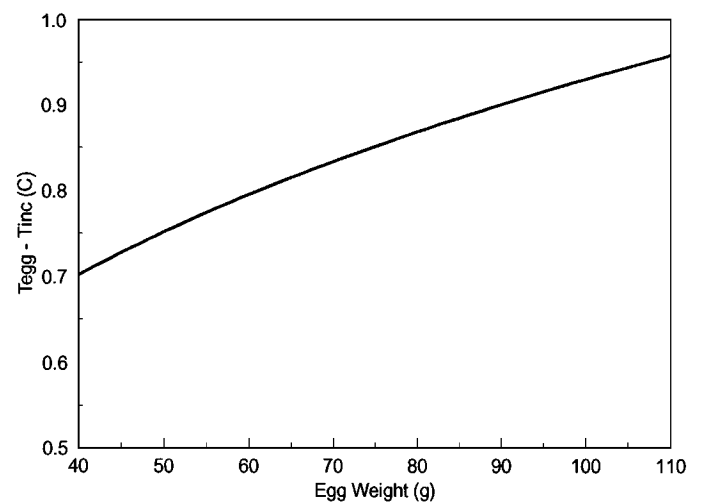


FIGURE 5. The predicted relationship between egg size and the temperature gradient between the inside of the egg ( $T_{egg}$ ) and the incubator air ( $T_{inc}$ ) just before internal pipping. The prediction is based on an egg with a 28-d incubation period and has a pre-internal pipping oxygen consumption estimated using Equation 7 in the text.

TABLE 5. Metabolic heat production of turkey embryos

Egg weight	Pre internal pipping metabolic heat production	Reference
(g)	(mW)	
79	134 <sup>2</sup>	Rahn (1981)
88	174	Dietz (1995)
88	194 <sup>2</sup>	Tullett <sup>1</sup>
100	217 <sup>2</sup>	Tullett <sup>1</sup>

<sup>1</sup>Tullett (1983, AFRC Poultry Research Centre, Roslin, Midlothian EH25 9PS, UK, personal communication).

<sup>2</sup>Estimated from oxygen consumption.

as well as small eggs (Landauer, 1961). More recently, Ogunshile and Sparks (1995) have shown that broiler hatchability decreases with increasing egg size when eggs are incubated at normal temperatures.

Figure 5 does not show a large increase in  $T_{emb} - T_{inc}$  with increasing egg size because PIP  $VO_2$ , and therefore  $H_{emb}$ , only scale with egg mass to the power of 0.848 (Equation 7). The limited data available on either PIP  $VO_2$  or  $H_{emb}$  of turkey eggs of different sizes are shown in Table 5 and plotted with the estimate of  $H_{emb}$  derived from Equation 7 in Figure 6. It would appear that  $H_{emb}$  of turkey eggs increases with egg mass at a greater rate than that predicted by Equation 7. Hoyt and Roberts (1985) showed that the scaling of embryo mass and PIP  $VO_2$  differed between interspecific comparisons and intraspecific comparisons derived from five poultry species. However, it is unlikely that the disparity between predicted and actual  $H_{emb}$  observed in Figure 5 can be accounted for by the use of intraspecific scaling of PIP  $VO_2$ , as the scaling component is still close to  $\frac{3}{4}$  as used in Equations 6 and 7 (Hoyt, 1987).

Understanding the relationship between egg size and incubation temperature requirements has important

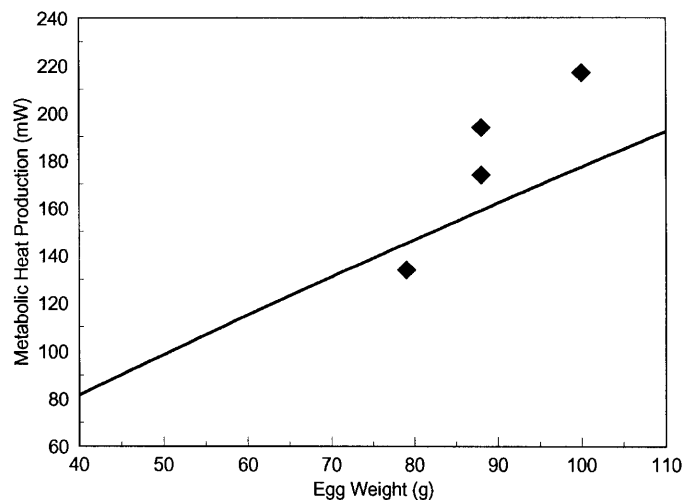


FIGURE 6. Predicted and actual embryo metabolic heat production of turkey embryos as affected by egg size. The predicted heat production derived from Equation 7 in text. Sources of actual heat production data are given in Table 5.

implications for the hatching industry and further investigation is needed. Monitoring internal or surface temperatures of eggs of different sizes would be of interest to determine whether large eggs do have a greater difficulty losing heat at the end of incubation. Problems may also arise in commercial incubators that do not have sufficient heating, cooling, and air exchange capacity for a total egg mass larger than the machine was originally designed. It is not uncommon to see a decrease in hatchability when the egg capacity of an incubator is increased above its original specification or when an incubator is adapted from chicken to turkey eggs without proper adjustment for the change in total egg mass within the machine. Today, incubator manufacturers are moving towards designing incubators for individual poultry species, which is a positive step for the whole industry.

## CONCLUSIONS

The temperature experienced by the developing embryo is dependent on the incubator temperature, the metabolic heat production of the embryo, and the thermal conductance of the egg and surrounding air. Studies investigating the effects of temperature on the development and hatchability of poultry embryos have concentrated mainly on the effects of incubator temperature and have ignored the other two factors. Equation 1 provides a simple model that provides a more accurate description of egg temperature than can be achieved by simply equating egg and incubator temperature. The model can also be used to predict the effects of incubator design on egg temperature and highlights the importance of air flow within the machine. Further studies are required to determine the effects of incubation temperature and egg mass on the metabolic heat production of poultry embryos.

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