

Mathematical Modelling of Temperature and Moisture Loss of Hatching Eggs

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Analytical equations are formulated to describe the influence of climatic conditions on moisture loss and temperature of hatching eggs. The equations are based on physical properties and are used to calculate moisture loss and temperature of eggs in different situations. Temperature development during cooling of eggs, moisture loss of eggs during cooling or heating and at constant temperature, and temperature in the egg during development of the embryo is described. For every characteristic, analytical equations are formulated and practical impacts are discussed.

1. Introduction

Hatching eggs are exposed to various climatic conditions during production, storage, incubation and hatching. The climatic condition in the respective stages affect embryo development and hatching results. Little is known about the influence of the climate in the nest on hatchability. Kirk *et al.* (1980) reported a slightly reduced hatchability when collecting eggs hourly instead of every 5 hr. North (1984: 72) recommended that eggs should be collected at least four times daily to obtain maximum embryo viability and hatchability. Environmental temperature after oviposition influences the rate of embryonic development (Kaplan *et al.*, 1978), especially during early stages (Romanoff, 1939). This early embryonic development will depend on collection pattern, which may affect viability and hatchability of the embryo.

After collection, eggs are often stored for several days prior to setting. Hatchability decreases when eggs are stored for 7 days or more (Funk *et al.*, 1950). Tandon *et al.* (1983) reported a decrease in hatchability after 2–3 days of storage. To obtain maximum hatchability, optimum storage temperature is reported to decrease with increasing storage time (Kaltofen & El-Jack, 1972; Kirk *et al.*, 1980). Proudfoot (1976) reported that relative humidity during storage should be high to prevent moisture loss. Kauffman (1939) concluded that dehydration caused by extended moisture loss during storage is not the main cause for decrease in hatchability after prolonged storage.

Temperature and moisture loss during incubation have a major impact on hatching results. In practise, incubator temperature is fixed at 37.5–37.8°C. Hatchability and chick quality decreases, hatching time changes and more anomalies occur when incubator temperature is too high or too low (Romanoff, 1960). During

incubation, egg temperature increases to a level above the temperature of the surrounding air, due to metabolic activity of the embryo (Tazawa & Rahn, 1987).

A certain amount of moisture evaporates through the shell during incubation. This amount can vary within a batch of eggs. The coefficient of variation of moisture loss during incubation is reported to be as high as 22% for chicken eggs (Visschedijk *et al.*, 1985). Although several experiments (Hoyt, 1979; Simkiss, 1980) have shown that chicken embryos are able to compensate at least partly for suboptimal moisture loss, it is well accepted that there is an optimal range. Ar & Rahn (1980) suggested that 15% of the initial egg weight should be lost as metabolic water. Others (Tullett, 1981; Meir *et al.*, 1984; Hulet *et al.*, 1987) reported an optimum moisture loss of 12%. Meir & Ar (1987) and Hulet *et al.* (1987) showed that regulating incubator humidity to obtain a specified moisture loss can improve hatchability of turkey eggs.

In the period from oviposition to hatching, eggs are exposed to various environmental conditions. To determine the effects of climatic conditions on the development of the embryo, it is necessary to estimate the effects of macro-climate on micro-climate and therefore on egg content and embryo. In order to estimate these effects, it is necessary to formulate the physical properties of eggs and the physical laws involved with temperature changes and moisture loss of eggs by means of analytical modelling.

In this article, physical aspects of temperature and moisture loss are described. Analytical equations are formulated to calculate temperature development and moisture loss of eggs, as well as temperature in the egg during development of the embryo.

2. Cooling and Heating of Eggs

2.1. THEORETICAL ASPECTS

Basically three different factors influence the cooling process of eggs, namely the temperature difference between egg and surrounding air, heatflow through the egg content and heat transfer between egg shell and surrounding air.

The basic shape (plate, cylinder, sphere) that approximates the shape of a hatching egg is the sphere. The governing equations for conducting heat transfer through a homogeneous sphere, initially at a uniform temperature T_i and surrounded by air of constant temperature T_a , are (Luikov, 1968: 119):

$$\frac{\partial T}{\partial t} = a \left(\frac{\partial^2 T}{\partial r^2} + \frac{2}{r} \frac{\partial T}{\partial r} \right) \quad (1)$$

with boundary condition:

$$\lambda \left(\frac{\partial T}{\partial r} \right)_{r=R} = \alpha (T_{\text{surrounding}} - T_{\text{ambient}}) \quad (2)$$

and starting condition (initial temperature of the egg constant):

$$T(r, 0) = T_{\text{initial}} \quad (3)$$

This set of equations results in the following solution:

$$\theta = \sum_{n=1}^{\infty} A_n \frac{R \sin \mu_n(r/R)}{r \cdot \mu_n} \exp(-\mu_n^2 Fo). \quad (4)$$

The constant A_n in eqn (4) is defined as:

$$A_n = \frac{2(\sin \mu_n - \mu_n \cos \mu_n)}{\mu_n - \sin \mu_n \cos \mu_n} \quad (5)$$

while μ_n are the roots of the transcendental equation:

$$\tan(\mu_n) = \frac{-\mu_n}{Bi - 1}. \quad (6)$$

The dimensionless numbers used in these equations are defined as:

$$\begin{aligned} Fo &= \text{Fourier} = a \cdot t / R^2 \\ Bi &= \text{Biot} = \alpha \cdot R / \lambda \\ \theta &= \text{theta} = (T - T_{\text{ambient}}) / (T_{\text{initial}} - T_{\text{ambient}}). \end{aligned}$$

With eqn (4) it is possible to calculate the temperature as a function of time for every spot in a spherical egg. However, the shape of an egg is more elliptic than spheric. Analytical solutions to estimate the temperature in an ellipsoid are not known by the authors. Preliminary research (unpublished data) indicated that cooling time at the germ position is about 10% longer for a sphere when compared with an egg of identical volume. The difference is about 15% when surface area is identical.

2.2. THERMAL PROPERTIES

In order to compare the calculation of the temperature of hatching eggs during cooling with experimental data, the thermal properties of the egg and the convective heat transfer must be estimated. The thermal properties of eggs can be calculated from the chemical composition (Miles *et al.*, 1983). The calculated thermal properties of yolk and albumen as a function of temperature, based on the chemical composition of the egg (Romanoff & Romanoff, 1949: 311) are given in Table 1.

TABLE 1
Calculated thermal properties of yolk and albumen based on the chemical composition

Temp. °C	Conductivity W/(m K ⁻¹)		Spec. heat J/kg K ⁻¹		Density kg m ⁻³		Diffusivity m ² sec ⁻¹	
	Y	A	Y	A	Y	A	Y	A
0	0.37	0.52	3048	3929	1026	1037	1.20E-7	1.28E-7
10	0.38	0.54	3048	3929	1026	1037	1.23	1.32
20	0.39	0.55	3048	3929	1024	1035	1.26	1.36
30	0.40	0.57	3048	3929	1023	1032	1.28	1.40
40	0.41	0.58	3048	3929	1021	1031	1.31	1.44

Y = yolk, A = albumen.

A method to calculate the cooling rate of an egg is given by Luikov (1968: 417), using the analytical solution for cooling of a system of two spherical bodies with different thermal properties. However, the drawback of this method is that the Biot number (the ratio between convection and conduction) is infinite. While the difference in thermal diffusivity of yolk and albumen is relatively small, a more simplified method would be to use the mean value of yolk and albumen and calculate the cooling rate with eqn (4). To compare both methods, the dimensionless temperature θ of a cooling egg with mean and real thermal properties of yolk and albumen is calculated as a function of time. To be able to compare the results of both methods, convective heat transfer α in the calculations with mean thermal properties is set at infinite level. The results of this comparison are shown in Table 2.

TABLE 2
Dimensionless temperature of a cooling egg with mean and real thermal properties of yolk and albumen

Time (min)	Dimensionless temperature	
	Mean	Real
15	0.537	0.561
30	0.224	0.267
31		0.258
32		0.234
33		0.231
34		0.220

This table shows that the difference in time required to reach the dimensionless temperature 0.22 between both analytical solutions is about 10%. Because of this relative small difference and the mentioned drawback, we prefer to calculate cooling rates with eqn (4).

2.3. HEAT TRANSFER COEFFICIENT

The heat transfer coefficient is the most difficult variable to estimate. The relation between the Nusselt number (dimensionless heat transfer) and the Reynolds-number (dimensionless air velocity) is:

$$Nu = 2 + 1.3 Pr^{0.15} + 0.66 Re^{0.5} Pr^{0.33} \quad (7)$$

The dimensionless numbers are defined as:

$$Nu = \frac{\alpha \cdot 2R}{\lambda_{air}} \quad (8)$$

$$Pr = \frac{v}{a_{air}} \quad (9)$$

$$Re = \frac{V \cdot 2R}{v} \quad (10)$$

Figure 1 shows the increase of the heat transfer coefficient of different-sized spheres (comparable with large, medium and small-sized eggs) with increasing air velocity. Although eqn (7) is often used to predict the heat transfer coefficient, the measured

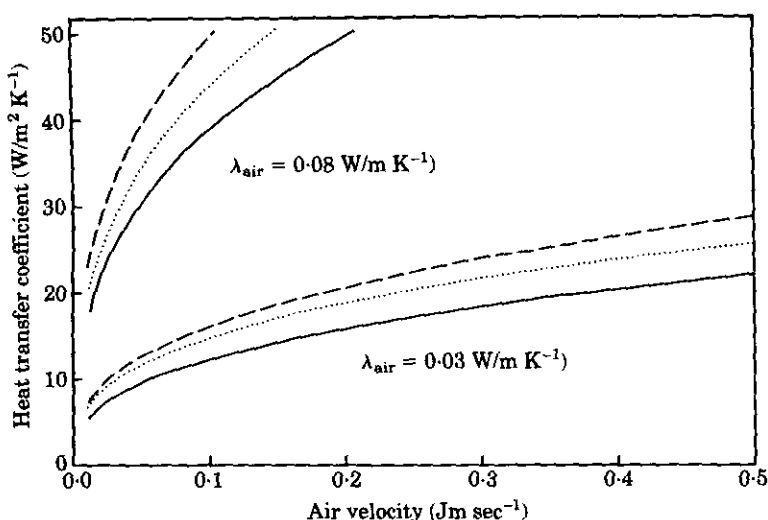


FIG. 1. Relation between heat transfer coefficient of different-sized spheres and air velocity at two levels of thermal conductivity of air. (—), $R = 3.0$ cm; (....), $R = 2.5$ cm; (---), $R = 2.0$ cm.

value can be higher because of buoyancy motion of air in the stagnant air layer around the sphere. The result of the calculations depends largely on the thermal conductivity of air, as is shown in Fig. 1.

2.4. HALF-COOLING TIME

The half-cooling time, defined as the time needed to cool a body through half of the possible temperature range, is a practical property to compare cooling rates. The first half-cooling time of a spherical body can be calculated with eqn (4). The first half-cooling time is longer for the centre of the sphere than for the surface. The difference depends on the thermal characteristics of the sphere. Figure 2 shows the calculated temperature development of the centre, surface and germ-position of a spherical egg with a radius of 2.5 cm, being a characteristic dimension for an egg of 55 g. The contribution of the trailing roots in eqn (4) is neglectable after the first half-cooling time, as can be shown with the solution of eqn (6). This means that the second and following half-cooling times are equal for all co-ordinates in the sphere because eqn (4) can be transformed to:

$$\ln t = \ln \left(\frac{A_1 \cdot R \cdot \sin(\mu_1 \cdot r/R)}{r \cdot \mu_1} \right) - \mu_1^2 \cdot Fo. \quad (11)$$

Equation (11) shows a linear relation between logarithmic temperature and time. The half-cooling time, after the lag period, can be calculated with:

$$t_1 = \frac{R^2 \ln 2}{\alpha \cdot \mu_1^2}. \quad (12)$$

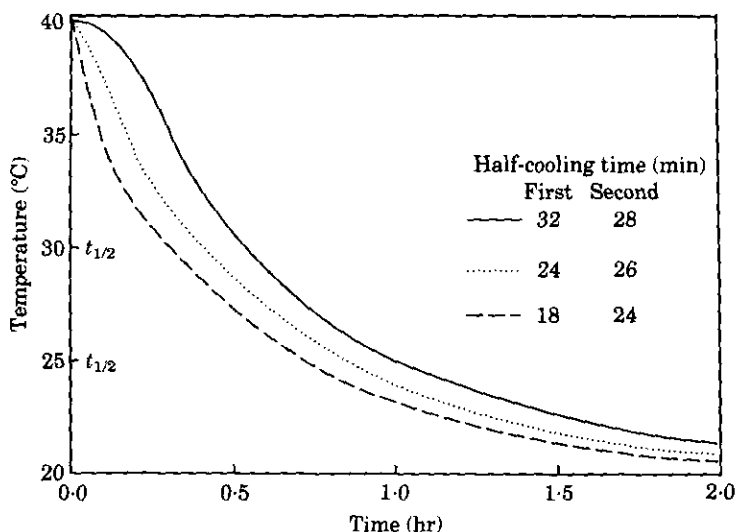


FIG. 2. Calculated temperature development at three places in a spherical egg (radius 2.5 cm) with initial temperature of 40°C and ambient temperature of 20°C. (—), in centre ($r = 0$ cm). (....), at germ ($r = 2$ cm); (---), at surface ($r = 2.5$ cm).

The intercept values in eqn (11) for centre, surface and germ-position of an egg are $\ln t = 1.29$, 0.81 and 1, respectively, as Fig. 3 shows. To be able to calculate cooling rate with eqn (11) or (12) the first roots μ_1 and A_1 as a function of the Biot-number are given in Fig. 4. The Biot-number of a single egg is about $Bi = \alpha \cdot R/\lambda = 15 \cdot 0.25/0.4 = 1$, indicating a half-cooling time of 30 min at the germ position.

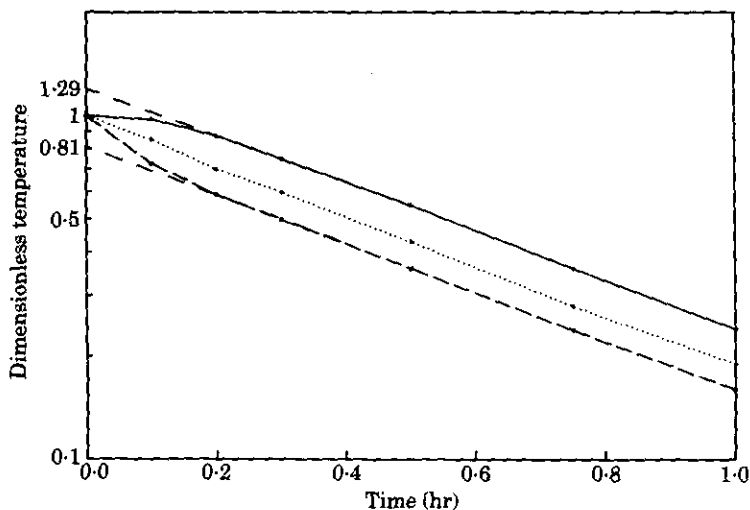


FIG. 3. Calculated logarithmic temperature development at three places in a spherical egg during cooling. (—), in centre; (....), at germ; (---), at surface.

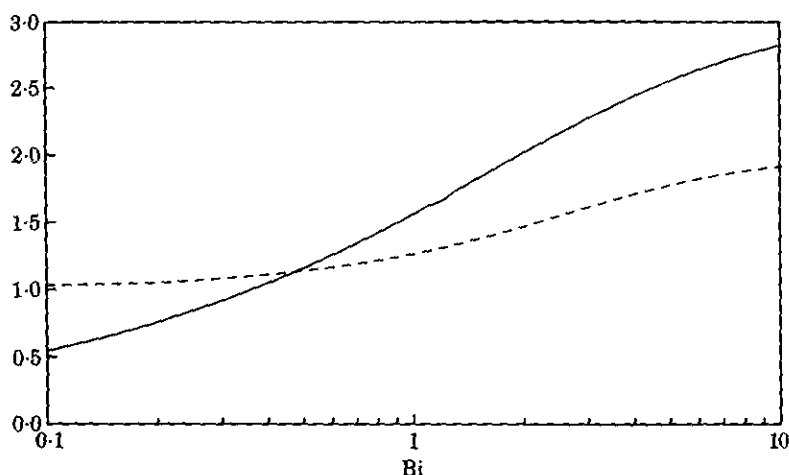


FIG. 4. Relation between the Biot-number and the first roots of u_1 and A_1 (based on Luikov, 1968). (—), u_1 ; (---) A_1 .

2.5. COOLING THROUGH EVAPORATION

Moisture loss accelerates the cooling of an egg and retards the heating process while the heat loss through evaporation acts as a cooling source (van Beek & Meffert, 1981). This means that the actual cooling rate of an egg will be higher than the cooling rate calculated with eqn (4), if moisture loss appears. To be able to calculate the cooling rate of a sphere with internal heat production, eqn (4) can be transformed to:

$$\theta = \frac{Po}{6} \left(1 - \frac{r^2}{R^2} + \frac{2}{Bi} \right) + \sum_{n=1}^{\infty} \left(1 - \frac{Po}{\mu_n^2} \right) \cdot \frac{An \cdot R \cdot \sin(\mu_n \cdot r/R)}{r \cdot \mu_n} \cdot \exp(-\mu_n^2 \cdot Fo). \quad (13)$$

TABLE 3

Temperature of a cooling egg (from 40°C to 20°C) of 60 g with heat production of 0 W m⁻³, -70 W m⁻³ and -700 W m⁻³ after 20 min and after infinite time

Time (min)	Surface		Centre	
	20	∞	20	∞
Heat production				
0 W m ⁻³	29.74	20.00	35.17	20.00
-70 W m ⁻³	29.73	19.97	35.16	19.96
-700 W m ⁻³	29.62	19.71	35.01	19.56

The Pomerantsev-number (dimensionless heat production) used in eqn (13) is defined as:

$$Po = \frac{q \cdot R^2}{\lambda \cdot (T_{\text{initial}} - T_{\text{ambient}})} \quad (14)$$

Moisture loss of eggs is accompanied by heat loss. To estimate the effect of moisture loss on temperature with eqn (11), a homogeneous heat generation in the egg must be introduced. This is allowed if the Biot-number is less than 1, which means that temperature distribution in the egg is rather homogeneous. In Table 3 calculated temperatures after 20 min and at infinitive time (five half-times or more) in the centre and at the surface are given for a cooling egg (40–20°C) of 60 g with moisture loss of 0%/hr, 0.01%/hr and 0.1%/hr and therefore a heat production of 0 W/m³, –70 W/m³ and –700 W/m³, respectively. This table shows that moisture loss of the egg during cooling has a relative small influence on temperature at the surface and in the centre of the egg. This means that moisture loss during cooling and heating can be calculated rather accurately from surface temperature without correction for heat production caused by moisture.

3. Moisture Loss of Eggs During Cooling, Heating and at Constant Temperature

3.1. THEORETICAL ASPECTS

Moisture loss of an egg is related to the driving force for moisture loss and the porosity or conductance of the shell. Several properties can be used as driving force: water potential (Pa), water vapour concentration (kg/m³), water vapour pressure (Pa) and mol fraction (mol/mol). Theoretically, the best property to use is the mol fraction because the related coefficient of diffusion of water vapour only depends on temperature to the power 0.8 and is independent of pressure (Nobel, 1983). However, water vapour pressure is more commonly used. Moisture loss of eggs can be described based on surface area, which is theoretically the best, or based on mass, which is more practical, with:

$$J = k_a \cdot A \cdot dp \quad \text{or} \quad J = k_m \cdot m \cdot dp. \quad (15)$$

3.2. WATER VAPOUR PRESSURE

Evaporation of water is forced by a difference in water vapour pressure between egg and surrounding air. The water vapour pressure of air can be determined using the Mollier diagram. Because of the high water content the water vapour pressure in the egg is nearly saturated. Absolute humidity is related to water vapour concentration by:

$$x = 0.622 \cdot p / (p_{\text{atm}} - p). \quad (16)$$

The saturated water vapour pressure only depends on temperature and can be predicted with the equation of Magnus:

$$p_s = \exp \left(6.414 + \frac{17.26 \cdot T}{(237.2 + T)} \right). \quad (17)$$

3.3. TRANSPIRATION COEFFICIENT

The transpiration coefficient of eggs can be calculated by determining the weight loss of eggs as a function of time, temperature and relative humidity when sufficient

ventilation around the eggs is allowed. When the climatic conditions are known, water vapour pressure deficit can be calculated and transpiration coefficient based on mass can be calculated with:

$$km = \frac{dm}{m \cdot dp \cdot dt} \quad (18)$$

The influence of the mass of the egg on the measured transpiration coefficient is theoretically to the power -0.33 , if thickness of the shell is constant for every mass of the egg, or $+0.33$, if mass of the shell is constant for every mass of the egg. The results of Scriba (1987) indicate that shell thickness is relatively independent of egg mass, which means that the relationship should be to the power -0.33 . This is in agreement with results obtained in our experiments (unpublished data).

To be able to calculate ka from km , or reversed, we use the equation of Bonnet & Mongin (1965) to calculate the surface area of an egg from its mass:

$$A = c \cdot (m \cdot 1000)^{0.66} \quad (19)$$

$c = 4.68$ – constant for eggs of 60–70 g

$c = 4.69$ – constant for eggs > 70 g

$c = 4.67$ – constant for eggs < 60 g.

3.4. MOISTURE LOSS OF EGGS DURING COOLING

Figure 5 shows the development of water vapour pressure deficit during cooling for an egg with initial temperature of 30°C in air of 10°C and 60% relative humidity. According to the Magnus eqn (17) the water vapour pressure in the egg is 4244 Pa.

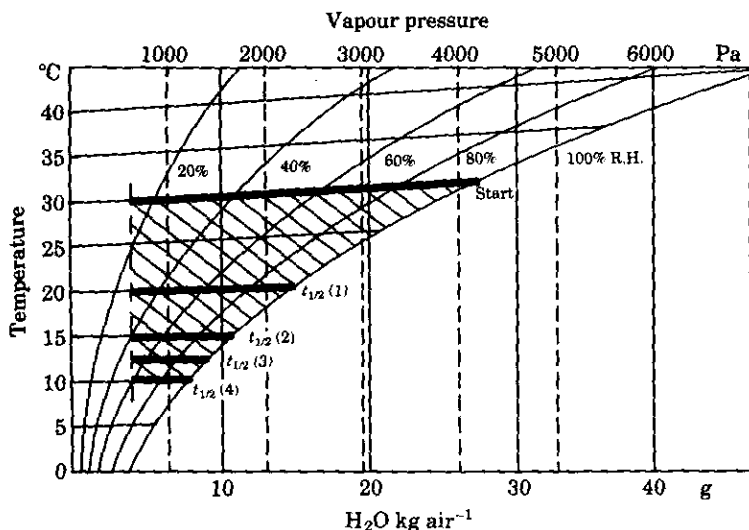


FIG. 5. Development of water vapour pressure deficit of an egg during cooling from 30°C to 10°C in air with 60% relative humidity.

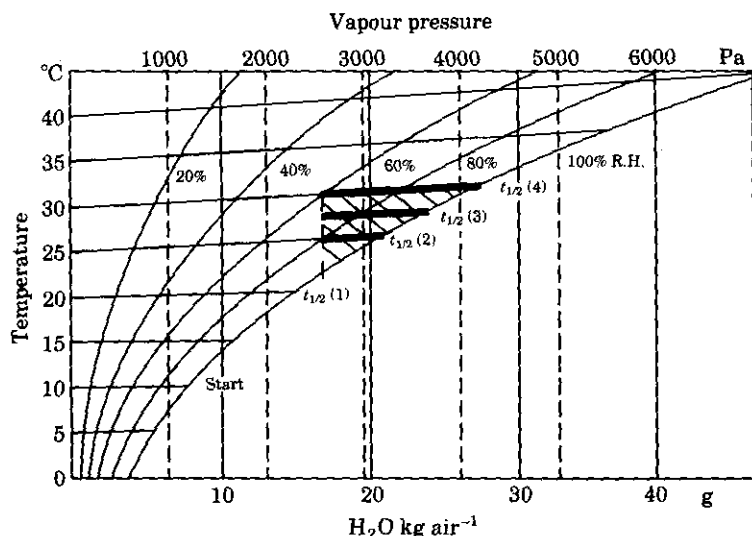


FIG. 6. Development of water vapour pressure deficit of an egg during heating from 10°C to 30°C in air with 60% relative humidity.

The water vapour pressure of the cold air is a fraction, defined by the relative humidity, of the saturated water vapour pressure at 10°C: $0.6 \cdot 1228 = 736$ Pa. At the start of the cooling process, the water vapour pressure deficit is $4244 - 736 = 3508$ Pa. After one-half cooling time, the temperature of the egg is 20°C and the deficit is $2338 - 736 = 1602$ Pa. The water vapour pressure deficit reduces during the cooling process to 492 Pa at 10°C after five or more half-times.

3.5. MOISTURE LOSS OF EGGS DURING HEATING

When an egg is heated from 10°C to 30°C, with air of 60% r.h. and 30°C, the total moisture loss is considerably less compared to cooling over the same temperature interval. The water vapour pressure deficit as a function of temperature during heating is shown in Fig. 6. In the beginning water will condensate on the cold surface of the egg, because the water vapour pressure of the warm air, $0.6 \cdot 4244 = 2546$ Pa, is more than the saturated water vapour pressure of the cold air layer around the egg (at 10°C the saturated water vapour pressure is 1228 Pa). If the temperature of the egg exceeds the dewpoint (21°C) of the surrounding air the condensed water will start to evaporate and moisture loss of the egg will begin. The water vapour pressure deficit will increase during the heating process. At the end of the process, after five half-times, the resulting deficit is $4244 - 2546 = 1698$ Pa.

3.6. MOISTURE LOSS OF EGGS AT CONSTANT TEMPERATURE

Moisture loss of eggs at constant temperature can be calculated directly with eqn (15). Results of our experiments (unpublished data) show good relation with calculations if the transpiration coefficients of the eggs are known.

Knowing by calculation the temperature just under the shell of a hatching egg as a function of time and knowing the development of the water vapour pressure of the air, it is possible to calculate the water vapour pressure deficit as a function of time. Using eqn (15), moisture loss can be calculated as a function of time if the transpiration coefficient or conductance is known.

4. Temperature in the Egg During Development of the Embryo

During incubation, mean temperature of the embryo is a function of ambient temperature, metabolic heat production and heat loss.

Under stationary conditions with high metabolic heat production compared to the latent heat loss, temperature difference between a certain spot in the egg and the surrounding air is described by the first part of eqn (13):

$$\theta = \frac{Po}{6} \left(1 - \frac{r^2}{R^2} + \frac{2}{Bi} \right) \quad (20)$$

or for the centre of the egg:

$$T_{\text{centre}} - T_{\text{air}} = \frac{qR^2}{6\lambda} - \left(1 + \frac{2\lambda}{\alpha R} \right). \quad (21)$$

The latent heat loss caused by moisture loss can not be incorporated in eqn (21). The influence of the evaporation on the centre temperature of the egg can be described using the heat balance: latent heat = heat of convection by eqn (21). This will be a negative difference.

$$T_{\text{centre}} - T_{\text{air}} = \frac{-k_a \cdot dp \cdot h}{\alpha}. \quad (22)$$

The theoretical relationship between size of the egg, heat production and temperature difference between egg and surrounding air at two different levels of air velocity is shown in Figs 7 and 8. The calculations are based on the situation in an incubator, with air temperature of 37.5°C. In the calculations it is assumed that thermal conductivity of the egg increases from 0.5 W/(m · K) with increasing heat production, because of the increasing blood flow in a developing embryo. The figures show that the relationship between egg size and temperature difference between developing embryo and surrounding air depends on the property of the heat production q . If heat production per gram egg is independent of egg size, as is suggested by Ar & Rahn (1978), temperature difference will increase with increasing egg mass. If heat production per egg is independent of egg size, temperature difference will decrease with increasing egg mass.

Because of the relationship between heat transfer coefficient and air velocity, as described in 2.3, the influence of air velocity on temperature differences is relatively high. This means that differences in air velocity in the incubator can cause differences in embryonic temperature and therefore in embryonic development within batches of eggs.

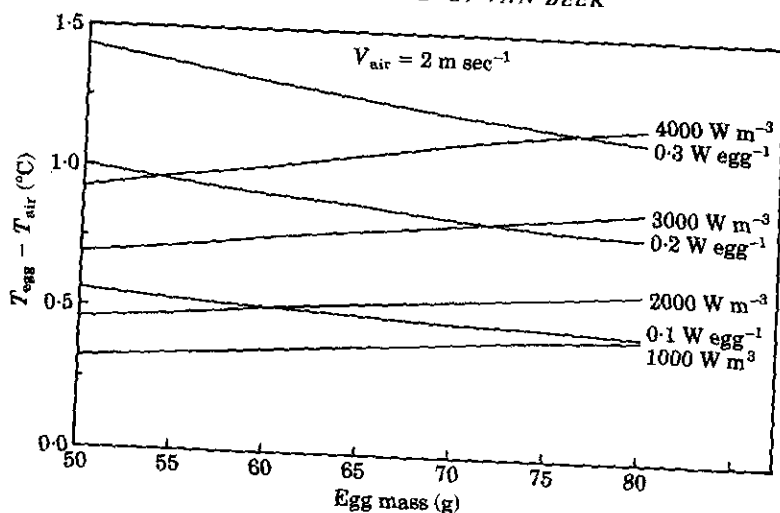


FIG. 7. Calculated temperature difference between egg (germ position) and surrounding air at different levels of heat production and air velocity of 2 m sec^{-1} .

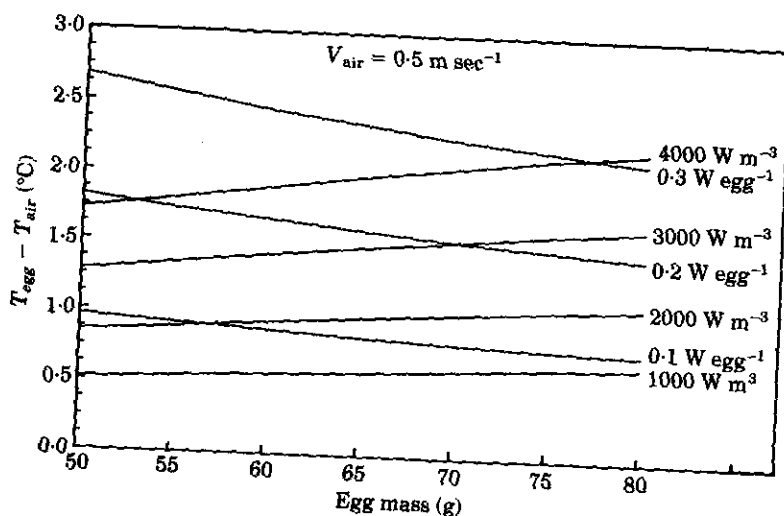


FIG. 8. Calculated temperature difference between egg (germ position) and surrounding air at different levels of heat production and air velocity of 0.5 m sec^{-1} .

5. Discussion

5.1. TEMPERATURE

Sotherland *et al.* (1987) showed that the temperature of an egg can be calculated rather accurately based on its thermal properties. These authors also showed that the heat transfer calculated for spheres and measured at eggs match well. However, the

method presented by Sotherland *et al.* (1987) does not account for heat convection in the egg. With the method presented here, the temperature at every spot in the egg can be calculated as a function of time during cooling and heating. The results of this method showed that the influence of the heat convection through the egg on the cooling process is rather small, because the radius of hens' eggs is rather small and the Biot number of eggs is close to 1. Only at the beginning of the cooling process, a difference in cooling rate can be expected at different spots in the egg. After a small time lag, the cooling rate at every spot will be identical.

The influence of the air velocity on the cooling rate of eggs is high because the heat transfer coefficient depends on air velocity. The influence of the air velocity depends on the size of the egg. This is in agreement with the calculations and measurements of Sotherland *et al.* (1987).

The influence of moisture loss on the cooling rate is small. Even a high rate of moisture loss of 0.1%/hr will cause a temperature difference of less than 0.5°C when compared with a situation without moisture loss.

5.2. MOISTURE LOSS

Moisture loss of eggs is often predicted with Fick's first law of diffusion (Ar *et al.*, 1974). This method is based on egg shell conductance and water vapour pressure deficit across the shell. The method presented here is based on the same principle but calculations are made with different properties. Instead of egg shell conductance, expressed as milligrams of water per torr per day, we prefer to use a transpiration coefficient, based on SI units, which allows to use the Mollier diagram to determine water vapour pressure deficits under different circumstances. This facilitates calculation of moisture loss during cooling and heating.

5.3. INTERNAL HEAT PRODUCTION

It is well known that embryo development causes heat production in the latter part of the incubation process (Tullett, 1990). Due to this metabolic heat production, embryo temperature rises above air temperature (Sotherland *et al.*, 1987). Because of the susceptibility of the embryo development for temperature, it can be questioned if the setter temperature should be lowered during the latter part of the incubation process to retain the embryo temperature at a constant level (Tullett, 1990).

However, because of the dependency of the cooling rate of eggs on air velocity, it can be questioned if embryo temperature is relatively constant between eggs at different places in an incubator. Experiments concerning air velocity in incubators in relation to embryo temperature are not at the authors' knowledge. The design of modern incubators, however, will probably cause a great variety in air velocity over eggs at different spots in the incubator, as is confirmed by our own measurements (unpublished data) and by Owen (1991). Based on the calculations presented, it can be assumed that unidirectional flow of air through the incubator is beneficial for uniformity in development and hatching.

REFERENCES

- AR, A., PAGANELLI, C. V., REEVES, R. B., GREEN, D. G. & RAHN, H. (1974). The avian egg: water vapor conductance, shell thickness and functional pore area. *Condor* **76**, 153-158.
- AR, A. & RAHN, H. (1978). Interdependence of gas conductance, incubation length, and weight of the avian egg. In: *Respiratory Function in Birds, Adult and Embryonic* (Piper, J., ed.). Berlin: Springer Verlag.
- AR, A. & RAHN, H. (1980). Water in the avian egg: overall budget of incubation. *Am. Zoologist* **20**, 373-384.
- BEEK, G. VAN & MEFFERT, H. F. TH. (1981). Cooling of horticultural products with heat and mass transfer by diffusion. In: *Developments in Food Preservation-1* (Thorne, S., ed.) pp. 39-92. London: Applied Science Publishers.
- BONNET, Y. & MONGIN, P. (1965). Mesure de la surface de l'oeuf. *Ann. Zootechnie* **14**, 311-317.
- FUNK, E. M., FORWARD, J. & KEMPSTER, H. L. (1950). Effect of holding temperature on hatchability of eggs. *Missouri Agricultural Experimental Station Bulletin* 539.
- HOYT, D. F. (1979). Osmoregulation by avian embryos: the allantois functions like a toad's bladder. *Physiol. Zoo.* **52**, 354-362.
- HULET, R. M., CHRISTENSEN, R. L. & BAGLEY, L. G. (1987). Controlled egg weight loss during incubation of turkey eggs. *Poultry Sci.* **66**, 428-432.
- KALTOFEN, R. S. & EL-JACK, M. H. (1972). Optimum temperatures for short-term storage of 1 to 7 day-old hatching eggs. *Archiv fur Geflugelkunde* **36**, 116-120.
- KAPLAN, S., KOLESARI, G. L. & BAHR, J. P. (1978). Temperature dynamics of the fertile chicken egg. *Am. J. Physiol.* **234**, 183-187.
- KAUFFMAN, L. (1939). An experimental study of the effects of storage on embryonal development of hens' eggs. In: *Seventh World's Poultry Congress and Exposition Proceedings* (World's Poultry Science Association, ed.) pp. 186-187. Baltimore, MD: Waverly Press.
- KIRK, S., EMMANS, G. C., McDONALD, R. & ARNOT, D. (1980). Factors affecting the hatchability of eggs from broiler breeders. *Br. Poultry Sci.* **21**, 37-53.
- LUIKOV, A. V. (1968). *Analytical Heat Diffusion Theory* (Hartnett, J. P., ed.). New York: Academic Press.
- MEIR, M. & AR, R. (1987). Improving turkey poultry quality by correcting incubator humidity to match eggshell conductance. *Br. Poultry Sci.* **28**, 337-342.
- MEIR, M., NIR, A. & AR, A. (1984). Increasing hatchability of turkey eggs by matching incubator humidity to shell conductance of individual eggs. *Poultry Sci.* **63**, 1489-1496.
- MILES, C. A., VAN BEEK, G. & VEERKAMP, C. H. (1983). Calculation of thermophysical properties of foods. In: *Physical properties of foods* (Jowitt, R., Escher, F., Hallstrom, B., Meffert, H. F. Th., Spiess, W. E. L. & Vos, G., eds) pp. 269-312. London: Applied Science Publishers.
- NOBEL, S. (1983). *Biophysical Plant Physiology and Ecology*. pp. 401-403. New York: Freeman.
- NORTH, M. O. (1984). *Commercial Chicken Production Manual*, 3rd edn. Westport, CT: AVI Publishing Company.
- OWEN, J. (1991). Principles and problems of incubator design. In: *Avian Incubation* (Tullett, S. G., ed.) pp. 205-224. London: Butterworth-Heinemann.
- PROUDFOOT, F. G. (1976). Care of hatching eggs before incubation. *Canadian Department of Agriculture Publication no. 1573*.
- ROMANOFF, A. L. (1939). Effect of temperature shock on development of chick embryo. In: *Seventh World's Poultry Congress and Exposition Proceedings* (World's Poultry Science Association, ed.). Baltimore, MD: Waverly Press.
- ROMANOFF, A. L. (1960). *The Avian Embryo*. New York: Macmillan.
- ROMANOFF, A. L. & ROMANOFF, A. J. (1949). *The Avian Egg*. New York: Wiley.
- SCRIBA, I. (1987). Einfluss der Luftfeuchtigkeit auf das Bruteiergewicht im Vorbruter. *Deutsche Geflugelwirtschaft und Schweineproduktion* **3**, 67-68.
- SIMKISS, K. (1980). Eggshell porosity and the water metabolism of the chick embryo. *J. Zool.* **192**, 1-8.
- SOTHERLAND, P. R., SPOTILA, R. R. & PAGANELLI, C. V. (1987). Avian eggs: barriers to the exchange of heat and mass. *J. exp. Zool.* **1**, 81-86.
- TANDRON, E., GARCIA, M., TABOADA, P. & QUINONES, Y. R. (1983). Influencia del tiempo, temperatura de almacenamiento y perdida de peso de los huevos sobre la incubacion. *Revista Avicultura* **27**, 123-129.
- TAZAWA, H. & RAHN, H. (1987). Temperature and metabolism of chick embryos and hatchlings after prolonged cooling. *J. exp. Zool.* **1**, 105-109.
- TULLETT, S. G. (1981). Theoretical and practical aspects of eggshell porosity. *Turkeys* **29**, 24-28.
- TULLETT, S. G. (1990). Science and the art of incubation. *Poultry Sci.* **69**, 1-15.
- VISSCHEDIK, A. H. J., TAZAWA, H. & PIPER, J. (1985). Variability of shell conductance and gas exchange of chicken eggs. *Resp. Physiol.* **59**, 339-345.

APPENDIX

Symbol	Unit	Property
T	$^{\circ}\text{C}$	Temperature
t	sec	Time
a	$\text{m}^2 \text{sec}^{-1}$	Thermal diffusivity
λ	$\text{W} (\text{m} \cdot \text{K})^{-1}$	Thermal conductivity
ρ	kg m^{-3}	Density
c	$\text{J} (\text{kg} \cdot \text{K})^{-1}$	Specific heat
α	$\text{W} (\text{m}^2 \cdot \text{K})^{-1}$	Convective heat transfer coefficient
V	m sec^{-1}	Air velocity
ν	$\text{m}^2 \text{sec}^{-1}$	Kinematic viscosity of air
x	kg kg^{-1}	Absolute humidity of air
p	Pa	Partial water vapour pressure
dp	Pa	Vapour pressure deficit
p_{atm}	Pa	Total pressure of air
p_s	Pa	Saturation water vapour pressure
k_m	$\text{Kg} (\text{kg} \cdot \text{Pa} \cdot \text{sec})^{-1}$	Transpiration coefficient based on mass
k_s	$\text{kg} (\text{m}^2 \cdot \text{Pa} \cdot \text{sec})^{-1}$	Transpiration coefficient based on surface
m	kg	Mass of egg
A	cm^2	Surface of egg
R	m	Radius of sphere
r	m	Radial distance from centre
q	W m^{-2}	Heat production
h	J kg^{-1}	Latent heat of evaporation
J	kg sec^{-1}	Moisture loss