Journal of Thermal Biology 55 (2016) 7–13

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

The cooling time of fertile chicken eggs at different stages of incubation

Jacopo P. Mortola*, Vanda Gaonac'h-Lovejoy

McGill University, Department of Physiology, McIntyre Medical Sciences Bldg, Room 1121, 3655 Sir William Osler promenade, Montreal, Quebec, Canada H3G 1Y6

ARTICLE INFO

Article history:
Received 9 June 2015
Received in revised form
24 October 2015
Accepted 25 October 2015
Available online 28 November 2015

Keywords:
Avian embryo
Bird
Heat loss
Thermal adaptation
Thermoregulation

ABSTRACT

We asked whether or not the thermal characteristics of fertile avian eggs changed throughout incubation. The cooling and warming times, expressed by the time constant τ of the egg temperature response to a rapid change in ambient temperature, were measured in fertile chicken eggs at early (E7), intermediate (E11) and late (E20) stages of embryonic development. Same measurements were conducted on eggs emptied of their content and refilled with water by various amounts. The results indicated that (1) the τ of a freshly laid egg was ~50 min; (2) τ decreased linearly with the drop in egg water volume; (3) the dry eggshell had almost no thermal resistance but its wet inner membrane contributed about one-third to the stability of egg temperature; (4) the egg constituents (yolk, albumen and embryonic tissues) and the chorioallantoic circulation had no measurable effect on τ; (5) the presence of an air pocket equivalent in volume to the air cell of fertile eggs reduced τ by about 3 min (E7), 5 min (E11) and 11 min (E20). Hence, in response to warming the egg τ at E20 was slightly shorter than at E7. In response to cooling, the egg τ at E20 was similar to, or longer than, E7 because embryonic thermogenesis (evaluated by measurements of oxygen consumption during cold) offset the reduction in τ introduced by the air cell. In conclusion, until the onset of thermogenesis the thermal behavior of a fertile egg is closely approximated by that of a water-filled egg with an air volume equivalent to the air cell. It is possible to estimate the cooling τ of avian eggs of different species from their weight and incubation time.

1. Introduction

The development of an embryo inside the egg depends on ambient temperature (Ta). An incubation temperature 3 °C below normal delays growth of chicken embryos by almost 3 days; a further drop by 1° halts hatching of most eggs (Mortola, 2006). Despite the risks of leaving the eggs unattended, most birds during incubation abandon the nest periodically for flight, foraging and territorial defense (Drent, 1975). These absences cause some cooling of the eggs because the optimal incubation temperature usually exceeds Ta. The rate of cooling and the parental energetic cost in re-warming the egg influence the behavior of the incubating parent and ultimately the ecology and evolution of the species (Drent, 1975).

Several studies have examined, both theoretically and experimentally, the cooling time and the modes of heat loss in eggs (e.g., Kaplan et al., 1978; Van Brecht et al., 2005; Björn et al., 2012). In most cases the temperature of an egg (Tegg) exposed to Ta lower than Tegg decreased according to an exponential time-trajectory expressed by the time constant τ (the time to 63% of the total change in Tegg) (Kaplan et al., 1978; Tazawa and Rahn, 1987; Tazawa et al., 1988). However, several structural and functional changes occur during incubation that could modify the egg thermal characteristics.

At the onset of incubation an egg is filled by yolk and albumen. Hence, the response time to a change in Ta should correspond to that of water, as long as the thermodynamic properties of egg constituents do not deviate from those of water and the eggshell does not offer any thermal protection. With the progression of incubation the egg content changes into embryonic tissues, the eggshell gets thinner because of calcium absorbance and the egg loses 5–15% of the initial liquid volume by evaporation (Mortola, 2009). The drop in water content, responsible for the formation of the air cell, should shorten the egg τ because air has a much lower thermal capacitance than water. At about half incubation (E12 in chicken eggs) the chorioallantoic membrane (CAM) is fully formed and envelops the inside of the eggshell (Ackerman and Rahn, 1980); whether or not this may facilitate the transfer of heat from the egg core to the periphery is controversial (Sotherland et al., 1987). At the end of incubation some thermogenic response to cold begins to appear (Szdzuy et al., 2008) while the internal pipping into the air cell coincides with the onset of pulmonary ventilation (Mortola, 2009); the former should delay egg cooling while the latter is a potential source of heat loss by evaporation. Of all the variables influencing the egg thermal properties it seems

* Corresponding author.

http://dx.doi.org/10.1016/j.jtherbio.2015.10.009
0306-4565/

likely that the liquid volume represents the primary factor, but it is difficult to anticipate the net result of the changes occurring throughout incubation. The only previous observations refer to the role of blood flow on the egg's response to cold. Turner (1987), on theoretical grounds, suggested that the embryo's blood flow could lower the egg's cooling time if the total internal resistance of the egg was high by comparison to the external resistance. This is usually the case only for eggs cooling in water, because the boundary layer of still air offers high external resistance to heat dissipation (Sotherland et al., 1987).

The primary goal of this study on chicken eggs was to evaluate to what extent different stages of development could influence the egg's thermal characteristics. First, we have measured the thermal τ of eggs water-filled by various amounts; these data provided a set of reference values which fertile eggs could be compared to. Then, measurements were conducted on fertile eggs at three stages of embryonic development, E7, E11 and E20. At E7 the embryo is still very small, ~2% of egg weight, with a metabolic rate of ~5% of the final value, and only about one-fourth of the CAM is formed (Mortola and Al Awam, 2010). At E11 the CAM is virtually complete and at E20 the embryo enters into the hatching phase, with internal pipping and initiation of thermogenesis and pulmonary ventilation (Mortola, 2009).

2. Methods

Experiments were performed on fertile fresh Chicken (*Gallus gallus*) eggs of the White Leghorn variety obtained by a local supplier. They were stored at 15 °C and used within one week after have been laid. A first group of eggs was used to construct reference data for comparison with the fertile eggs (Table 1). They consisted of eggs completely depleted of their original liquid content (yolk and albumen) and refilled with known quantities of distilled water to cover a range in weight between 5.8 g (empty and dry) and 62 g (full). For all other eggs, the fresh egg weight was noted and at midday (embryonic day E0) the eggs were placed in incubators (Hova-Bator 1602N, Savanah, GA, USA) set at 38 °C and 60% relative humidity, with 90° rotation eight times a day. Measurements were performed on separate sets of eggs at embryonic day E7, E11 and E20 (out of the average 20.5 days of complete incubation).

Table 1
Eggs characteristics.

Measurements	Embryonic age (day)	*N*	Fresh egg weight (g)
τ in water-filled eggs: cooling		42	5.8–61.4
τ in water-filled eggs: warming		20	31–55.9
τ in fertile eggs: cooling	7	22	58.6 ± 0.4
	11	14	58.3 ± 0.9
	20	22	59.6 ± 0.5
τ in fertile eggs: warming	7	9	58.3 ± 0.5
	11	5	54.5 ± 0.5
	20	7	59.1 ± 0.9
V_{O_2} (gradual cooling)	7	13	59.9 ± 0.9
	11	5	57.5 ± 1.1
	20	10	60.0 ± 1.3

For fertile eggs, weight refers to fresh conditions at the onset of incubation. *N*, number of eggs used for that measurement. Values are means ± 1SEM.

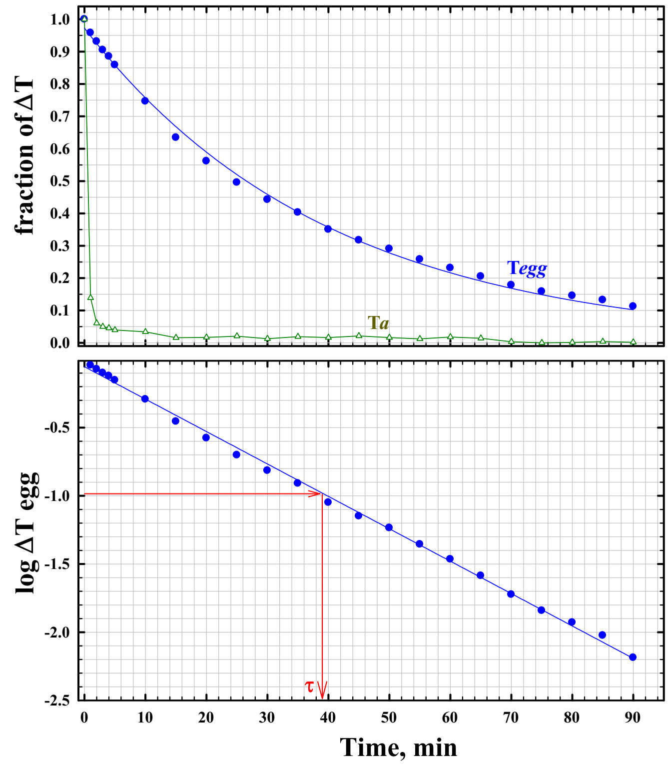

Fig. 1. Top: Time profile of the temperature of a representative egg (Tegg, filled circles) during cooling when ambient temperature (Ta, open triangles) was switched from 38 °C to 23 °C. Tegg and Ta values are expressed as fraction of the total variation, ΔT. The Tegg trajectory was adequately described by an exponential curve. Bottom: The same Tegg data of the top panel are represented in semi-log format; from the linear regression, the time constant τ was computed at ln(1/2.718) = −1(arrows). In this example, τ was 39.5 min.

2.1. Time constant of cooling or warming

A 1-mm^2 hole was drilled at the blunted end of the egg and an ultra-fine tungsten–constantan thermocouple (~0.2 mm O.D.) was threaded through it until its tip was positioned approximately at middle height of the egg vertical axes (checked by transillumination). If the process damaged the embryo, as assessed at the end of the measurements by opening the egg, the data were disregarded. Thermocouples were positioned similarly into the water-filled and fertile eggs. Then, the eggs were returned to the incubator until their temperature was stable in the 37–38 °C range ("warm" conditions). Data of egg temperature (Tegg) were taken in warm conditions every 2 min for 15 min to check for thermal stability, together with ambient temperature (Ta), which was measured by a thermocouple positioned in proximity of the egg. Then, the lid of the incubator was removed to rapidly decrease Ta to room temperature (~23.5 °C); data of Ta and Tegg were recorded for 90 min, every minute for the first 5 min and every 5 min thereafter.

The time trajectory of the values of Tegg, expressed as fraction *R* of the total Ta change (ΔT), followed very closely the exponential function $R(t) = 1 - e^{-(t/\tau)}$ in both water-filled and fertile eggs (Fig. 1, top); the square of the correlation coefficient (r^2) of these functions averaged, respectively, 0.994 ± 0.002 (N=38) and 0.996 ± 0.0004 (N=90). Hence, the representation of ln(R) as function of time was linear and the time constant of cooling τ was the time at $R = 1 - e^{-1} = 1 - 0.3679 = 0.632$ (Fig. 1, bottom).

Separate groups of water-filled and fertile eggs were subjected to sudden warming, to measure the τ of temperature equilibration