

Blood Circulation and the Flows of Heat in an Incubated Egg

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ABSTRACT At the start of incubation, heat flows through the egg by conduction only. During incubation, the embryo's developing circulation should augment conduction in the egg, distributing heat from the brood patch more uniformly through the egg. The augmentation of heat flow through the egg should be very small in small eggs, but should be larger in large eggs.

Many investigators studying the thermal energetics of eggs have focused on heat exchange between the surface of an egg and its environment (e.g. Webb and King, '83; Turner, '85) (see also Ackerman and Seagraves, '87; Sotherland et al., '87; Tazawa and Rahn '87). I will take a slightly different view and explore what happens to heat inside an egg. How does it move? What aids or impedes its flow? How is its flow affected by the very basic property of egg size? To what extent could the incubating parent or the embryo alter the flow of heat inside an egg?

For any organism that has a circulatory system, heat can move about in the body in two ways: by conduction in the tissues and by convection in flowing blood. The actual flow of heat within the body depends on the interaction of these two modes of heat flow. An interesting thing about birds' eggs is that this interaction changes with incubation age. At the beginning of incubation, heat moves solely by conduction, for the simple reason that there is no circulatory system. As incubation proceeds, and the circulatory system develops, heat flow by conduction is gradually augmented by flowing blood. An obvious question is: By how much?

HOW IMPORTANT IS BLOOD FLOW FOR AN EGG'S EXCHANGES OF HEAT?

Blood flow is not uniformly important for heat exchange in eggs of all sizes, and it is not equally important to an egg in all circumstances (Turner, unpublished observations). This assertion follows readily from a simple "core-shell" model for an egg's fluxes of heat. The core-shell model (Fig. 1a) consists of a well-mixed (i.e. isothermal) core, surrounded by a "shell" (not the eggshell),

whose sole function is to contain a temperature gradient between the core and the surface. The choice of the thickness of the shell is somewhat arbitrary. Because a core radius (r_i) of about three-fourths of the outside radius (r_o) closely models the heat fluxes of animals (e.g. Tracy et al., '80), I have chosen this thickness for the model "egg."

I can abstract the egg further, drawing an analogy between the flow of heat in a core-shell model and the flow of current in an electrical circuit (Fig. 1b, c) (Thomas, '80). In this case, heat flows internally across an internal resistance (R_i , units of $K W^{-1}$; Fig. 1b). The internal resistance can be dissected into two resistors in parallel (Fig. 1c): one for conduction (R_k) and one for blood flow (R_b). Outside the egg, heat flows across an external resistance (R_e ; Fig. 1b), and R_e can also be dissected into parallel resistors. I have chosen two: one resistor to represent convection (R_{co}) and one resistor to represent radiation (R_r). There could be more external resistors; I limit them to two because convection and radiation probably are the most important (Webb and King, '83; Turner, '85). Note that the external resistances are in series with the internal resistances.

Once the problem is abstracted in this way, a body of theory becomes available that makes it easy to analyze the question: How important is blood flow for an egg's exchanges of heat? In general, the answer will depend on two factors: the size of the egg and the environment the egg is in (Turner, unpublished observations).

Blood flow should affect the internal flows of heat in a large egg more than it should in a small egg. This is true because conduction is relatively more important for heat flow within small bodies than in large bodies

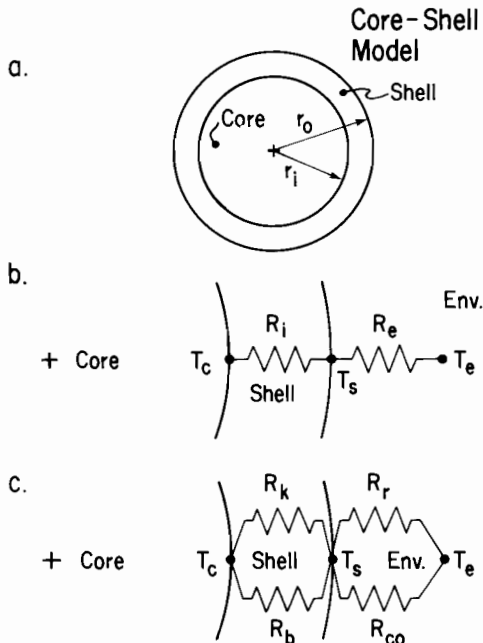


Fig. 1. The core-shell model. **a:** The core-shell model consists of a core of radius r_i , surrounded by a shell of inner radius r_i and outer radius r_o . **b:** Electrical analog of a core-shell model. Heat flows between nodes of different temperatures in the core (T_c), the shell surface (T_s), and the environment (T_e). Between the nodes, heat flow is impeded by resistances, one in the shell (R_i) and one external to the shell (R_e). **c:** Expanded electrical analog. The internal resistance is expanded to a conduction resistance (R_k) and a blood flow resistance (R_b). The external resistance is expanded to a radiation resistance (R_r) and a convection resistance (R_{co}).

(Turner, '86 in press). I illustrate this with some model calculations, summarized in Table 1 (a detailed discussion of the calculations will be published). The quantity ρ in Table 1 is the proportion of heat that moves within the egg by conduction. The quantity $(1-\rho)$ is the proportion of heat that moves by convection in blood. By definition, ρ is unity for eggs of all sizes at the start of incubation. In other

words, at the start of incubation, heat flow in any egg is assumed to be by conduction only. By the end of incubation, ρ is less than unity for eggs of all sizes. This means that blood flow is transporting some heat inside eggs of all sizes. Additionally, at the end of incubation, ρ is smaller for large eggs than it is for small eggs. This means that blood flow carries a larger proportion of the heat in large eggs than it does in small eggs.

If blood flow lowers an egg's internal resistance, the expectation is that the egg's heat loss will increase by some amount. At maximum, the proportional increase of heat loss will be close to the inverse of the proportional decrease of resistance (i.e. the proportional increase of conductance). Usually, the increased heat loss will be much less. This is because the egg's loss of heat depends on the internal resistance *in series* with the external resistance (Fig. 1b). Clearly, if external resistance is very large relative to internal resistance (i.e., the egg is well insulated), the developing circulation may not reduce total resistance appreciably, even if the decrease of internal resistance is large (as might occur in a large egg, Table 1). Only if external resistance is small relative to internal resistance (the egg is poorly insulated) will a change of internal resistance alter the egg's overall exchanges of heat. In fact, blood flow can never increase heat flux by more than the fraction $1/\rho$, and this will be approached only when $R_e \ll R_i$. Depending on the magnitude of R_e relative to R_i , blood flow will increase heat flux by some proportion less than $1/\rho$. I have illustrated these assertions with an experiment (Turner, unpublished results summarized in Table 2).

The cooling rate of an egg depends in part on its total resistance to heat exchange (Turner, '85; also, Turner unpublished results). An egg in still air typically has a very large external resistance, roughly 5 to 10 times larger than the internal resistance. In

TABLE 1. Proportional change of internal resistance as a result of blood flow in eggs of various sizes

Egg mass (gm)	Example	$\rho = R_i/R_k$	
		Start of incubation	End of incubation
2	Blue-gray gnatcatcher	1	0.83
10	Bobwhite	1	0.70
50	Chicken	1	0.55
150	Goose	1	0.43
1,500	Ostrich	1	0.23

TABLE 2. Ratios of time constants at day 18 (τ_{18}) and day 0 (τ_0) for bobwhite and chicken eggs cooling in still air and still water

Cooling in	T_{18}/T_0			
	Bobwhite		Chicken	
	Predicted	Observed	Predicted	Observed
Still air	1.00	0.96	1.00	0.98
Still water	0.70	0.75	0.56	0.58

this circumstance, a change in blood flow should have negligible effects on the total resistance of the egg, even if it significantly lowers the resistance inside the egg. Thus, if one lets living eggs cool in still air, their cooling rates near the end of incubation should be about the same as at the beginning of incubation (Turner, unpublished results). This appears to be the case for both chicken and bobwhite eggs (Table 2).

When an egg is placed in still water, however, external resistance becomes very low, roughly 10 times less than internal resistance. Any reduction of internal resistance brought on by the embryo's circulation should now measurably reduce the total resistance and increase the egg's cooling rate. In fact, the ratio of the time constant near the end of incubation (τ_{end}) and the time constant at the start of incubation (τ_0) should be roughly equivalent to ρ (Turner, unpublished results). Thus, for a bobwhite egg, τ_{end}/τ_0 should be about 0.70 (Table 1). For a chicken egg, this ration should be about 0.55 (Table 1). This is largely borne out experimentally (Table 2).

It is now possible to propose two 'rules' for how important blood flow should be to an egg's exchanges of heat. 1) Blood flow will contribute more to the internal flows of heat if the egg is large than if it is small; 2) If blood flow is important to an egg's internal flow of heat, it will contribute to the egg's overall exchanges of heat only if the egg is poorly insulated (as a rule of thumb, if $R_i > R_e$). If the egg is well insulated (as a rule, if $R_i < R_e$), blood flow will have little consequence for the egg's thermal energetics.

BLOOD FLOW AND TEMPERATURE OF AN INCUBATED EGG

Outside of the laboratory (or away from immersion in water baths), would blood flow in an egg ever be important for the egg's temperature? At first glance, there is good reason to suppose not. For example, many birds' eggs are found in well-insulated nests (Collias and Collias, '84). In light of the second of my proposed rules, one could reason-

ably suppose that the embryo's developing circulation would have little effect on the heat balance of its egg. For many birds' eggs, however, there is often at least one low-resistance connection between it and its external environment, and that is through a brood patch pressed against its surface. Could blood flow in an egg interact significantly with heat flow from the brood patch?

This question cannot be explored using a simple core-shell model. A core-shell model assumes, among other things, a uniform surface temperature (i.e., heat flows in one dimension only). This is obviously not true for an egg warmed at its upper surface by a brood patch (e.g., Rahn et al., '83). Heat transfer models that could accommodate the two and three-dimension fluxes of heat in an egg warmed by a brood patch can be forbiddingly complex (e.g. Carlslaw and Jaeger, '59). Fortunately, there are simpler ways of studying this problem, and one of the simplest is to use an analog computer.

Making an analog computer of an egg warmed by a brood patch is easy if heat flow through the egg is restricted to two dimensions. This can be supposed without appealing too much to credulity. All that is required is that heat flow in the egg be symmetrical about an axis extending from the center of the brood patch through the center of the egg. More precisely, for any pair of spherical coordinates r and ϕ , temperatures must be the same for all values of θ . This is reasonable for a single egg warmed by a brood patch and having a uniform external resistance (R_e is constant for all ϕ). It also may apply if external resistance is not uniform ($R_e = f[\phi]$), but only if the variation of external resistance is symmetrical ($R_e = f[\phi] = f[-\phi]$). If external resistance is not symmetrical, heat flow is no longer two-dimensional. Therefore, a two-dimensional analog computer cannot model two eggs sitting side by side, but it may come close for an egg surrounded on all sides by other eggs.

The analog computer itself is readily made from simple materials (Fig. 2). Electrically conductive paper (PASCO Scientific, Hay-

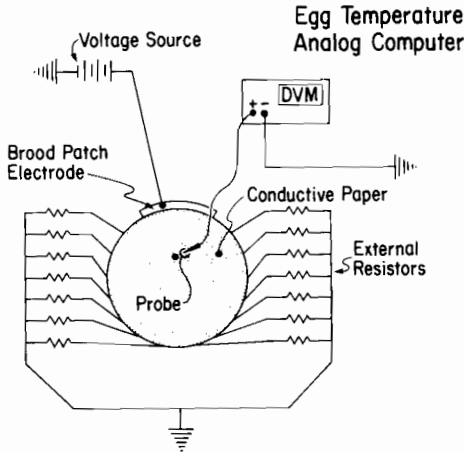


Fig. 2. Schematic diagram of the egg temperature analog computer. DVM, digital voltmeter.

ward, CA) is cut out in the shape of a circle. The "brood patch" is made by painting a circular segment of electrically conductive paint (PASCO Scientific) over a 60° arc on the top of the circle. This ensures that the part of the "egg" covered by the "brood patch" is "isothermal." Current travels from the brood patch through the egg and is lost to earth through 14 connections to external resistors, distributed over the portion of the egg not covered by the brood patch. A voltage is imposed across the egg, from the brood patch to the "environment." The "temperature distribution" is mapped out by sampling voltages from a regular array of points inside the egg. Isothermal lines, which are equivalent to the isopotential lines, can then be calculated and mapped.

The temperature distribution (voltage distribution) will depend not on the absolute resistance inside the egg, but on the ratio of the internal resistance and the external resistance, a quantity known as the Biot number (Thomas, '80). Any two objects of the same shape that have the same Biot number will have identical temperature distributions, irrespective of the absolute values of the resistances. I wish to measure how the

temperature distribution inside the egg is changed as the internal resistance is lowered by blood flow (i.e., as the egg's Biot number is lowered). A strictly analogous egg-temperature computer would mimic the effect of blood flow by lowering the resistance of the conductive paper while leaving the external resistors unchanged. This is technically difficult. Therefore, I mimicked increased blood flow (which lowers the egg's Biot number) not by lowering the conductive paper's resistance, but by increasing the resistance of the external resistors (which lowers the computer's "Biot number").

I have done model calculations of the Biot numbers expected at the beginning and at the end of incubation for eggs of three sizes: 2 gm (e.g., blue gray gnatcatcher), 50 gm (e.g., chicken), and 1,500 gm (e.g., ostrich). The calculated Biot numbers are given in Table 3. I estimated external resistance from basic heat transfer models, described in more detail in Turner ('85) and in Thomas ('80). I estimated conduction resistance for a spherical shell (Thomas, '80), with an internal radius that is three-fourths the external radius and with a thermal conductivity approximately that of water. As a basis for estimating blood flow in the egg, I used Tazawa's measurements ('80) of chorioallantoic blood flow in chickens. To estimate blood flow in eggs smaller or larger than chicken eggs, I have assumed that blood flow scales to the three-fourths exponent of egg mass, calculated for metabolic rate in near-term eggs (Rahn et al., '74; Hoyt and Rahn, '80). The internal temperature distributions are presented in Figure 3. Surface temperatures are presented in Figure 4.

When heat can only move in the egg by conduction, small eggs are less heterothermal than large eggs (i.e., small eggs enclose fewer isotherms than large eggs; Fig. 3). This is expected from Fourier's law of conduction: The temperature difference that develops is proportional to the distance over which heat must be conducted. Heat must move further

TABLE 3. Estimated resistances ($K W^{-1}$) in eggs of three sizes at the beginning (0) and end of incubation

Egg mass (gm)	Example	R_e	$R_{i,0}$	$R_{i,end}$	Bi_0	Bi_{end}
2	Blue-gray gnatcatcher	83.8	6.69	5.52	0.080	0.066
50	Chicken	12.3	2.31	1.27	0.188	0.103
1,500	Ostrich	1.6	0.75	0.08	0.487	0.110

Bi, Biot number.

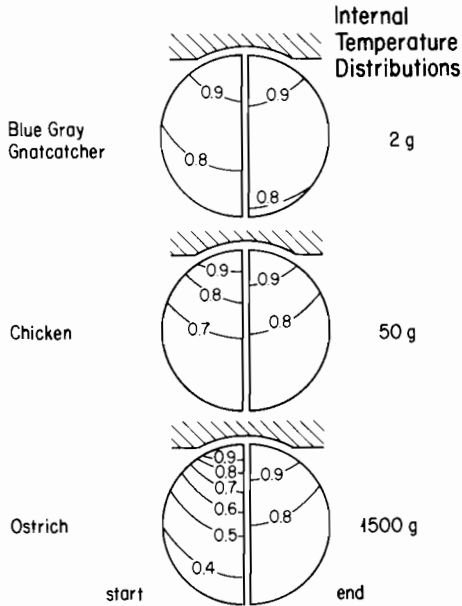


Fig. 3. Predicted temperature distributions inside eggs of different size, warmed by a brood patch (hatched area). Isotherms are the fraction of the temperature difference between the brood patch and the surroundings. Each egg is split in half. The left half-egg shows temperature distribution at the start of incubation. The right half-egg shows temperature distribution at the end of incubation.

in a large egg than in a small egg. Therefore, larger temperature differences are expected in larger eggs.

When blood flow supplements conduction, eggs of all sizes become less heterothermal, evidenced by the isotherms spreading out. The effect is greater in larger eggs. In very small eggs, the isotherms spread out, but only slightly (Fig. 3). In very large eggs, the isotherms spread out so much that most of them disappear from the egg (Fig. 3). It is interesting to observe that blood flow makes eggs of all sizes heterothermal to roughly the same degree; the temperature distributions in chicken eggs and ostrich eggs are virtually indistinguishable by the end of incubation,

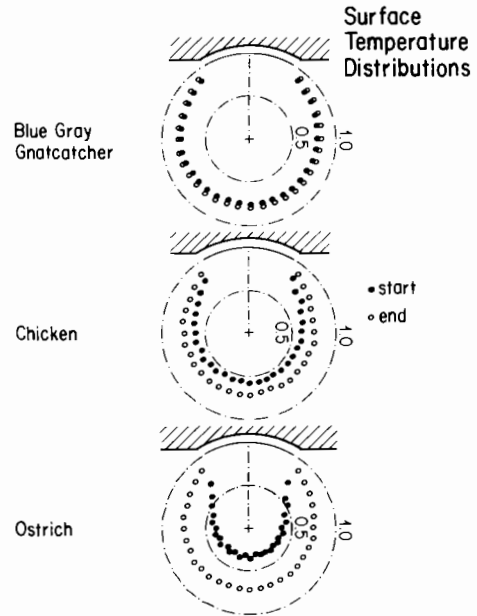


Fig. 4. Predicted surface temperatures of eggs of different size, warmed by a brood patch. The plot is in polar coordinates. The angular coordinate corresponds to the position on the egg surface, relative to 0° at the top of the egg. The radial coordinate is the fraction of the temperature difference between the brood patch and the surroundings. The radial distance for fractional differences of 0.5 and 1.0 are given for reference.

and only slightly different from the blue gray gnatcatcher's, despite the obvious differences between these eggs at the start of incubation (Fig. 3).

Trends in surface temperature roughly parallel those for internal temperatures (Fig. 4). At the beginning of incubation, large eggs have surfaces that are cooler overall (Table 4) and that vary considerably in temperature over the surface of the egg (Fig. 4). Surfaces of smaller eggs are warmer overall (Table 4) and are more uniform in temperature (Fig. 4). At the end of incubation, blood flow makes the surfaces of all eggs warmer (Fig 4; Table 4), and the relative increase in surface temperature is greatest for large eggs (Table 4).

TABLE 4. Weighted average of surface temperature of eggs of three sizes at the beginning and end of incubation

Egg mass (gm)	Example	$T_s - T_e / T_b - T_e$		
		Beginning	End	Proportional increase
2	Blue-gray gnatcatcher	0.771	0.799	1.04
50	Chicken	0.610	0.737	1.21
1,500	Ostrich	0.408	0.732	1.79

T_s , average surface temperature; T_e , environmental temperature; T_b , brood patch temperature.

BLOOD FLOW AND THERMAL ENERGETICS OF
AN INCUBATED EGG

What inferences about the energetics of incubation can be drawn from these theoretical explorations? At this stage, they are few, not least because of the assumption that all the heat flowing through the egg comes from the brood patch. This is not true, of course, especially at the end of incubation, when considerable heat may come from the embryo (Drent, '70; Ricklefs, '74). Nevertheless, at least one interesting thing can be said, not despite this omission, but actually because of it.

It is well known that egg temperature increases through incubation (Drent, '75). Thought on why this occurs has focused on what the parent might do to bring it about, such as altering attentiveness, brood patch vascularity, or nest insulation (Drent, '75). My models suggest that the embryo's circulation also should cause egg temperature to rise through incubation, even in the absence of any adjustment by the parent or of any production of heat by the embryo. Furthermore, the importance of blood flow should vary with egg size in a regular and predictable way. Could the embryo's circulatory system interact with blood flow in the brood patch to facilitate the influx of heat from the parent, especially at the end of incubation? If so, it should be most evident in large eggs, and not at all evident in very small eggs.

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