

## 9 Maintenance of egg temperature

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Contact incubation of eggs is one of the most conspicuous features of avian biology. Its purpose is the maintenance of a warm and steady egg temperature, and during incubation, the parent bird undergoes remarkable changes in its behaviour and physiology, all seemingly directed to meeting this need. For example, the pectoral skin of incubating birds, commonly the female, but in some instances the male as well, develops into a fleshy and well-vascularised brood patch, naked of feathers (White and Kinney 1974; Grant 1982; Tøien *et al.* 1986; Chapter 8). While incubating, the brood patch is pressed against one surface of the egg, warming it, a process known as contact incubation. The transfer of heat into the egg is regulated through adjustments to both blood flow through the brood patch and heat production by the parent, mediated through temperature sensors in the skin of the brood patch (Collias 1964; White and Kinney 1974; Midtgard *et al.* 1985; Chapter 8). Likewise, many birds construct nests constructed to insulate the eggs against losses of heat from their exposed surfaces. In some instances, the nest completely encloses the egg in its protected environment, although many nests are cup-shaped, open at the top to accommodate the parent while it sits on the eggs (Collias 1964; Grant 1982; Skowron and Kern 1984). Many birds are steady incubators, sitting on the eggs without interruption from the completion of the clutch to hatching. However, many are intermittent incubators, leaving the nest periodically during the day to feed or defend the territory around the nest. These absences seem timed to limit the extent to which the eggs cool during the absence: in colder conditions, the absences are shorter, while warmer conditions are correlated with longer absences (Turner 1994a; Chapters 6 and 15).

Incubation involves a transfer of heat between the parent and embryo, which in principle can be understood as a physical process mediated by the physiology of both parent and embryo. The intention of this chapter is to provide a brief overview of the physical and physiological principles underpinning the maintenance of egg temperature. These principles have potentially far-reaching implications for the ecology and life histories of birds. Thus, it is essential that they are properly understood from the outset. Many attempts to make this link rely on erroneous assumptions about the ways heat flows through eggs, usually from a misplaced desire for simplicity. The transfers of heat between parent and egg are marvellously subtle, however, and it is argued that these subtleties are important features in how parent and offspring manage the flows of heat between them. Understanding these subtleties is impossible if they are simplified away from the beginning.

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*Maintenance of egg temperature: steady state*

At its simplest, the maintenance of egg temperature is a straightforward problem of energy balance:

$$Q_{\text{in}} + Q_{\text{out}} + Q_{\text{s}} = 0 \quad (9.1)$$

where  $Q_{\text{in}}$  = rate of heat flow into the egg,  $Q_{\text{out}}$  is rate of heat flow out of the egg and  $Q_{\text{s}}$  = rate of heat storage in the egg; all rate terms in units of watts ( $\text{W}$ ;  $\text{J s}^{-1}$ ). If egg temperature is steady, *i.e.* not varying with respect to time, the storage term  $Q_{\text{s}}$  is zero. In this section, this is assumed to be the case, and the matter of the unsteady state, *i.e.* where  $Q_{\text{s}} \neq 0$ , is described later.

When egg temperature,  $T_{\text{egg}}$ , is steady, equation 9.1 can be rewritten as follows:

$$Q_{\text{emb}} + Q_{\text{bp}} + K (T_{\text{air}} - T_{\text{egg}}) = 0 \quad (9.2a)$$

where  $Q_{\text{emb}}$  = rate of embryonic heat production (always a net addition of heat),  $Q_{\text{bp}}$  = heat transfer rate between the brood patch and egg (commonly an addition of heat, but sometimes a removal of heat if the egg is too warm),  $K$  = thermal conductance of the egg ( $\text{W } ^\circ\text{C}^{-1}$ ), and  $T_{\text{air}}$  = air temperature ( $^\circ\text{C}$ ). Evaporation is a potential avenue of heat loss, but these are generally negligible compared to the other flows of heat (Turner 1985). The conductance term,  $K$ , is a proportionality that relates a rate of heat transfer to the temperature difference driving it. It encompasses a variety of factors, including surface area of contact between brood patch and egg, heat transfer by blood flow and conduction, and so forth. Based on this, the parental cost of incubation can be estimated simply:

$$Q_{\text{bp}} = K (T_{\text{egg}} - T_{\text{air}}) - Q_{\text{emb}} \quad (9.2b)$$

This equation states that the parent's energy cost is determined by the heat lost from the egg to the environment [ $K (T_{\text{egg}} - T_{\text{air}})$ ], offset by the addition of heat to the egg by the embryo [ $Q_{\text{emb}}$ ]. Thus, the energy cost of maintaining an egg's temperature depends upon three things: the environmental temperature, the heat production by the embryo, and the thermal conductance of the egg. A number of simple predictions follow from this. For example, it predicts a linear dependence of parental incubation costs on environmental temperature. Also, it predicts that the parent's incubation costs should decline during the incubation period as the embryo's own production of heat increases.

Simple models are not subtle tools. They are useful mainly when the system to be analysed is itself simple. Unfortunately, much of the important biology that underpins the maintenance of egg temperature is subtle, most of it residing in the conductance term,  $K$ . As written, the conductance term is primarily a physical property of the egg and environment: traditionally there has been little appreciation of the extent to which this term is under physiological control, both by the parent and the embryo. The perils of ignoring these physiological factors are illustrated by the implied reduction of the parent's energy costs during the incubation period. As the embryo develops, its rate of

heat production increases. According to equation 9.2a, this should lessen the subsidy of heat required from the parent. In fact, the opposite is true: as the embryo matures, the parent's heat subsidy required to maintain egg temperature increases (Turner 1991).

The key to understanding this disparity involves understanding the distribution of temperatures in the egg, the so-called temperature field. In any body, heat flow is driven by differences in temperature. Where heat goes and how rapidly it flows there is governed by how the potential energy gradients driving its flow are distributed. In some instances, these temperature distributions are simple, and simple models of heat flow describe them accurately. In other instances, including heat flow through eggs, the temperature fields are more complicated.

### The temperature field

The starting point for any analysis of heat flow is Fourier's Law of conduction, which is generally expressed as a differential equation (Thomas 1980):

$$dQ = -k dA dT / dx \quad (9.3)$$

where  $k$  is the thermal conductivity of the material through which heat flows ( $\text{W m}^{-1} \text{ } ^\circ\text{C}^{-1}$ ). Heat flow through any object will depend not only upon the temperature differential ( $dT$ ,  $^\circ\text{C}$ ), but also upon the object's shape, which is accounted for by the differential terms  $dx$  (m) and  $dA$  ( $\text{m}^2$ ). The simplest such shape is a flat plate of thickness  $x$  and cross-section area  $A$ , for which case Fourier's Law is solved as:

$$Q = A k (T_1 - T_2) / x \quad (9.4)$$

Implicit in this equation is a temperature field which exists between both surfaces of the plate, and which can be expressed graphically as a series of isotherms within the object (Figure 9.1). The temperature field in a flat plate is uniform, its isotherms parallel to the plate surfaces and evenly spaced through the plate. This simply indicates that the temperature gradients driving heat flow are everywhere the same. As such, the vectors for heat flow are likewise uniform and parallel (Figure 9.1).

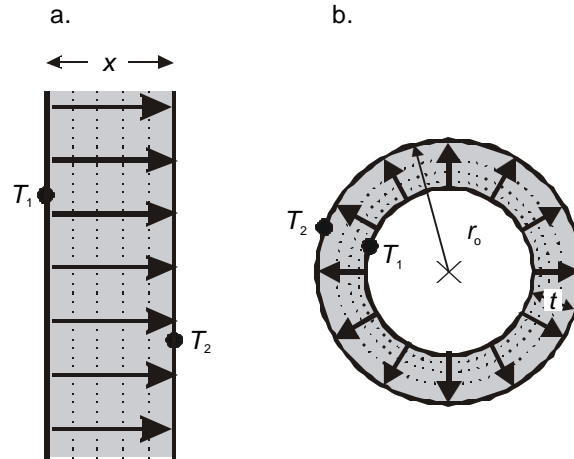
Fourier's Law is easily solved for other shapes (Thomas 1980), such as heat flow through a cylindrical shell of thickness  $t$  and outer radius  $r_o$ :

$$Q = 2 \pi L k (T_1 - T_2) / \ln (r_o / (r_o - t)) \quad (9.5)$$

or, more germane to the problem of eggs, through a spherical shell:

$$Q = 4 \pi r_o (r_o - t) k (T_1 - T_2) / r_o \quad (9.6)$$

The temperature fields and heat flows in such cases are somewhat more complicated than those in a flat plate. In a spherical shell, for example, the isotherms may not be uniformly spaced, and the vectors for heat flow will diverge from the inside surface of the shell to the outer. In both cases, however, the temperature field, and the heat flows associated with it, are functions of only one spatial dimension, specifically the distance  $x$  from one side of a flat plate to the other, or the radial distance  $r$  from the inside surface of a spherical shell to the outer (Figure 9.1). Such temperature fields are said to be one-dimensional.



**Figure 9.1.** Isotherms and heat flow vectors in two one-dimensional heat flow regimes. *a.* One-dimensional heat flow through a flat plate of thickness  $x$  with temperatures  $T_1$  and  $T_2$  on either side of the plate. *b.* One-dimensional heat flow through a circular tube or spherical shell of outer radius  $r_0$  and thickness  $t$ . Heavy arrows represent heat flow vectors. Dotted lines represent isotherms.

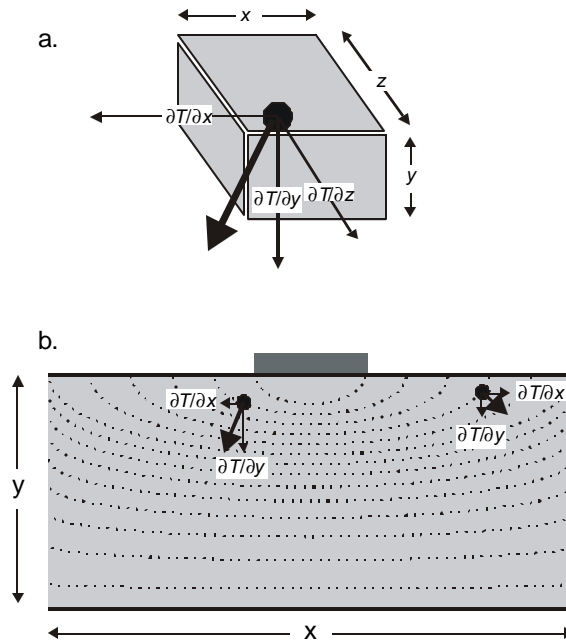
One dimensional temperature fields and heat flows are a special case. More common are circumstances in which heat moves through objects in complex spatial patterns that cannot be reduced to a single dimension. One example of obvious relevance to eggs would be heat applied to a limited surface on a block of material, similar to the way a brood patch might warm an egg. As heat flows through the block, it spreads from its point of origin. The vectors for the heat flow can be resolved into three mutually perpendicular components,  $x$ ,  $y$  and  $z$  (Figure 9.2). For such cases, Fourier's Law resolves the temperature field into three partial differential equations.

$$dQ_x = -k dA_x \partial T / \partial x \quad (9.7a)$$

$$dQ_y = -k dA_y \partial T / \partial y \quad (9.7b)$$

$$dQ_z = -k dA_z \partial T / \partial z \quad (9.7c)$$

The temperature field is now three-dimensional, because the temperature at any locality in the block is a function of the three variables,  $x$ ,  $y$  and  $z$ .

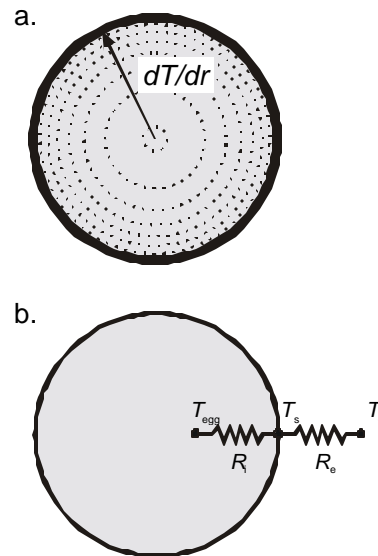


**Figure 9.2.** Multidimensional heat transfer in solid bodies. *a* A heat flow vector (heavy arrow) that results from temperature gradients (light arrows),  $\partial T$ , in three dimensions,  $\partial x$ ,  $\partial y$  and  $\partial z$ . *b* Hypothetical scenario for two-dimensional heat flow through a solid body (light grey) warmed at one locality by a heated strip (dark grey). In this circumstance, temperature gradients in the  $z$  dimension are *nil*, i.e.  $\partial T / \partial z = 0$ . Heat flow is governed by temperature gradients in the  $x$  and  $y$  dimensions,  $\partial T / \partial x$  and  $\partial T / \partial y$ , which varies from place to place in the block.

Treating heat flow through any object as one-dimensional is essentially a statement that only one of the partial differentials, say,  $\partial T / \partial x$ , matters. This, in turn, commits one to the converse assumption that the other partial differentials, in this case  $\partial T / \partial y$  and  $\partial T / \partial z$ , and the heat flows that go with them are negligible. Similarly, two dimensional heat flows are those in which only one of the partial differentials can be safely neglected. Three-dimensional heat flows, of course, are those circumstances in which none of the partial differentials can be ignored. This underscores a general principle of heat exchange theory. One can always approximate multi-dimensional heat flows as one- or two-dimensional. However, the accuracy of such approximations will depend on the extent to which the ignored partial differentials are indeed negligible. If they are not, the simplified estimate will be seriously in error.

### Temperature fields in eggs

It is noteworthy that much of the literature on the energetics of egg incubation presumes that heat flow through eggs is one-dimensional. While this is true in some circumstances, it is not in many (Turner 1991). Of the likely circumstances eggs might be found in, there are four likely, but not exclusive, types, two of which result in a one-dimensional temperature field: one-dimensional radial fields, in which the temperature variation is predominantly in the radial dimension (Figure 9.3); one-dimensional axial



**Figure 9.3.** One-dimensional radial heat flow in a spherical egg. (a) Isotherms (dotted lines) and heat flow vector (arrow) in the radial dimension  $r$ , down a temperature gradient  $dT/dr$ . (b) Electrical analogy for one-dimensional heat flow in a spherical egg, where heat flow is limited by an internal resistance,  $R_i$ , spanning an egg centre temperature  $T_{egg}$  and the egg surface temperature  $T_s$ , in series with an external resistance  $R_e$  spanning egg surface temperatures and the environmental temperature  $T_e$ .

fields, in which the temperature variation is along an axis that runs through the egg (Figure 9.4); two-dimensional fields, in which the temperature variation is differentiable into a combination of two axial or radial components (Figure 9.5); and three-dimensional fields, in which the temperature field is a function of three radial or axial components.

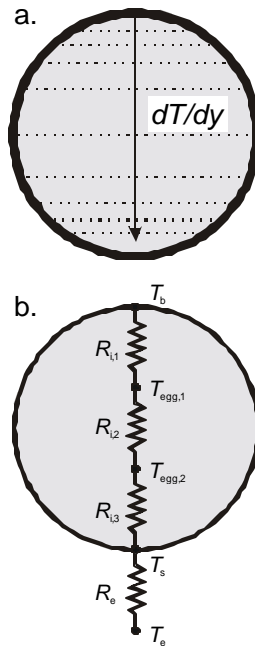
One-dimensional radial temperature fields arise when the egg is surrounded by a uniform fluid medium, or by nest materials which incorporate insulating layers of still air. Such a circumstance could arise for eggs left for a time by an incubating parent. In a one-dimensional radial field, the egg's thermal conductance can be simplified to two conductances in series (Figure 9.3): an internal conductance,  $K_i$ , which governs the flow of heat from the interior of the egg to the eggshell surface; and an external conductance,  $K_e$ , which governs the flow of heat from the surface of the egg to the environment. The egg's thermal conductance,  $K_{egg}$ , is therefore:

$$1 / K_{egg} = 1 / K_e + 1 / K_i \quad (9.8a)$$

or in terms of the inverse of the conductance, the thermal resistance:

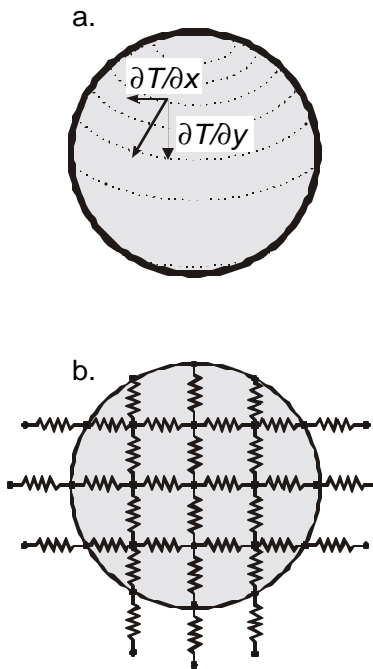
$$R_{\text{egg}} = R_e + R_i \quad (9.8b)$$

In air, the egg's external resistance is generally larger than its internal resistance (Turner 1985), with the result that  $R_{\text{egg}} \approx R_e$ . The extent to which the external resistance dominates the total conductance of the egg depends upon its size and the cardiac output by the embryo (Table 9.1), but it is unlikely that the external resistance will ever be less than 74% of the egg's total resistance. For most eggs, the external resistance accounts for more than 90% of the egg's total resistance (Table 9.1). The disproportionately high external resistance signifies two important features in the



**Figure 9.4.** One-dimensional axial heat flow in a spherical egg warmed at one surface by a brood patch. *a.* Isotherms (dotted lines) and heat flow vector (arrow) in the axial dimension  $y$ , down a temperature gradient  $dT/dy$ . *b.* Electrical analogy for one-dimensional heat flow in a spherical egg, where heat flow is limited by several series internal resistances,  $R_{i1} \dots R_{i3}$ , spanning the brood patch temperature  $T_b$ , several internal egg temperatures  $T_{\text{egg},1} \dots T_{\text{egg},2}$ , and the egg surface temperature  $T_s$ , in series with an external resistance  $R_e$  spanning egg surface temperatures and the environmental temperature  $T_e$ .

maintenance of egg temperature. First, any factor which influences  $R_e$ , such as protection from wind, reflection of solar radiation and so forth, will have a large effect on the egg's thermal resistance. Secondly, because the external resistance is so high, there is little potential for the embryo to have any physiological control of thermal conductance of its egg. The reductions in  $R_i$  which might result from the embryo's burgeoning circulation have relatively little effect on the egg's total thermal resistance, except in very large eggs, several hundred grams or more in mass. (Table 9.1).



**Figure 9.5.** Two-dimensional heat flows in a spherical egg warmed at one surface by a brood patch. *a.* Isotherms (dotted lines) and heat flow vectors (arrow) in the horizontal (x) and vertical (y) dimensions, resolved into the temperature gradients  $\partial T/\partial x$  and  $\partial T/\partial y$ . *b.* Electrical analogy approximation for two-dimensional heat flow in a spherical egg warmed at one surface by a brood patch, where heat flow is limited by an array of internal resistances which feed heat to the egg surface where its flow is further limited by an array of external resistances.

**Table 9.1.** Estimated internal and external resistances of birds' eggs at start and end of incubation (Turner unpublished).

Egg mass (g)	$R_e$ ( $^{\circ}\text{C W}^{-1}$ )	$R_i$ ( $^{\circ}\text{C W}^{-1}$ )		$R_t$ ( $^{\circ}\text{C W}^{-1}$ )		$R_e/R_t$	
		Start	End	Start	End	Start	End
2	100.7	6.0	5.1	106.8	105.8	0.94	0.95
10	38.4	3.5	2.6	41.9	40.9	0.92	0.94
60	13.4	2.0	1.1	15.4	14.5	0.87	0.92
150	7.6	1.4	0.7	9.0	8.2	0.84	0.92
1500	1.9	0.7	0.2	2.6	2.1	0.74	0.92

Where:  $R_e$  = External resistance;  $R_i$  = internal resistance;  $R_t$  = total resistance

One-dimensional axial gradients are probably rare in naturally incubated eggs, but these are often invoked as an approximation of the two-dimensional gradients that commonly would arise in an egg warmed by a brood patch (Ackerman and Seagrave 1984; Turner 1991). In a contact-incubated egg, the normally expected two-dimensional gradient could approach a one-dimensional axial gradient when heat flows

through the egg between a strong source at one surface, and a strong sink at the other. An egg warmed at one surface by a brood patch while its antipodal surface sat in water, on ice or on cold ground could qualify as a sufficiently strong source and sink. A one-dimensional axial gradient could also result when heat loss from the exposed sides of the egg is prevented. The natural situation that comes closest is probably found in the Aptenodytes penguins, where the egg is warmed on one side by a brood patch, cooled on the other by sitting on the penguin's cold feet, and is enveloped in a well insulated pouch (Burger and Williams 1979; Handrich 1989; Rahn 1991).

In most contact-incubated eggs, a two-dimensional temperature field is more likely (Turner 1991). The two dimensional fields in a contact-incubated egg show strong vectors for heat flow to the exposed surfaces of the egg adjacent to the brood patch, while heat flow to the antipodal surface of the egg is fairly weak. This is a crucial distinction: a one-dimensional axial gradient assumes, among other things, that heat from the brood patch (equivalent to an energy cost to the parent) ultimately leaves the egg uniformly over its surface. In a two-dimensional field, this is not the case: of the parent's heat imparted to the egg through the brood patch, more leaves the egg from surfaces near the brood patch, while relatively little leaves the egg from surfaces opposite the brood patch. This has some interesting consequences, both for the total energy cost for incubation, considered below, and for the role the embryo might play in the regulation of its own egg temperature. In the initial stages of incubation, when there is little or no embryonic circulation of blood, heat flows through the egg by conduction only. Consequently, most of the heat imparted to the egg leaves the egg at surfaces near the brood patch. The temperature of the egg's antipodal surface is very close to air temperature and little heat leaves the egg there. As the embryo's circulation develops, this promotes the axial transport of heat, warming the egg's antipodal surfaces, and increasing the loss of heat therefrom. Thus, the embryo's circulation affects the energy cost of incubation in a way that it could not if the egg was surrounded by air. For an egg of the domestic fowl (*Gallus gallus*), Turner (1991) estimated that the increase of embryonic circulation during incubation will roughly double the parent's energy costs of maintaining the egg temperature. This stands in marked contrast to the oft-stated presumption that the parent's energy costs will decline as the embryo's own heat production increases through the incubation period.

Three-dimensional temperature fields arise in circumstances where there are significant asymmetries in the sources or sinks for heat flow. For example, the air cell of the egg is usually located at one end of the egg's major axis, while the major axis, for its part, usually lies approximately parallel to the parent's brood patch. Thus, heat will flow through one of the egg's major poles differently than through the other. Another conceivable circumstance would be in a clutch of eggs where each egg has been warmed differently than its clutch-mates. Temperature fields in eggs in the centre of a clutch surrounded by warm eggs could have temperature fields that are approximately one-dimensional. Eggs at the periphery, for their part, might have within them substantial horizontal temperature gradients, warmed on one side by its clutch-mates and cooled on the other by the outside environment.

*The common fallacies of steady-state incubation energetics*

It would seem, therefore, that the energy cost of incubation depends crucially upon what types of temperature fields exist in the incubated eggs. There can be no presumption that one particular type of field will be common. It follows that any model of energy costs that assumes just the opposite, either explicitly or implicitly, will often be inaccurate. Consider, for example, the famous Kendeigh equation, which purports to estimate the energy cost of incubating a clutch of  $n$  eggs (Kendeigh 1963):

$$Q_{bp} = n M c_p (T_{egg} - T_{air}) (1 - c) / \tau \quad (9.9)$$

where  $M$  = egg mass (kg),  $c_p$  = egg specific heat ( $J \text{ kg}^{-1} \text{ }^\circ\text{C}^{-1}$ ),  $c$  = fraction of egg surface covered by brood patch and  $\tau$  = time constant for cooling (s). In the Kendeigh equation, the term  $(M c_p / \tau)$  is equivalent to the egg's thermal conductance,  $K$  ( $\text{W }^\circ\text{C}^{-1}$ ). In Kendeigh's original formulation, the time constant  $\tau$  was measured from eggs cooling in still air, conditions in which the temperature field in the egg will be one-dimensional in the radial dimension, and surface temperatures will be uniform. Kendeigh also assumes that heat loss from a contact-incubated egg is simply that lost from an egg cooling in air, corrected by the fraction of surface area left uncovered by the brood patch,  $(1 - c)$ . This presumes that the distribution of surface temperatures in a contact-incubated egg is uniform as they are likely to be in an egg cooling in air. This is incorrect because the temperature field in a contact incubated egg is qualitatively different: it is a two-dimensional field, in which different rules for heat transfer apply.

This assumption introduces some significant errors in the estimates of energy cost calculated from Kendeigh's equation (Turner 1991). For an unembryonated fowl egg, Kendeigh's equation estimates an energy cost that is roughly double the measured cost when the egg is incubated by an artificial brood patch. The source of the error is clearly in the presumption that the temperature fields in eggs cooling in air describe the temperature fields in contact incubated eggs. A egg cooling in air has a high external thermal resistance, and uniformly high surface temperatures. A contact incubated egg has high surface temperatures only near the brood patch, and is significantly cooler at the egg's antipodal surfaces. Heat losses from the egg, and the energy costs of keeping the egg warm, are commensurably lower.

Consider also the conflicting roles of embryonic circulation and metabolism (Turner 1991). The thermal conductance of an egg cooling in still air is uninfluenced by the embryos' circulation, but its temperature is significantly influenced by the embryo's metabolism. For example, at the end of the incubation period of a fowl egg, the embryo dissipates heat at a rate sufficient to raise egg temperature 2-3°C above air temperature (e.g. Meir and Ar 1990). At the same time, the egg's thermal conductance in still air remains unchanged throughout the incubation period, despite the substantial increases in internal blood circulation. Equation 9.2a suggests that as the embryo matures, the parent's energy cost should decline as the embryo provides more of the heat required to keep the egg warm. For a fowl egg, Kendeigh's equation predicts the energy costs of maintaining egg temperature should decline by about 30% through the incubation period. However, the energy costs measured by an artificial brood patch actually increase by about 25%. Again, the error results from unrealistic

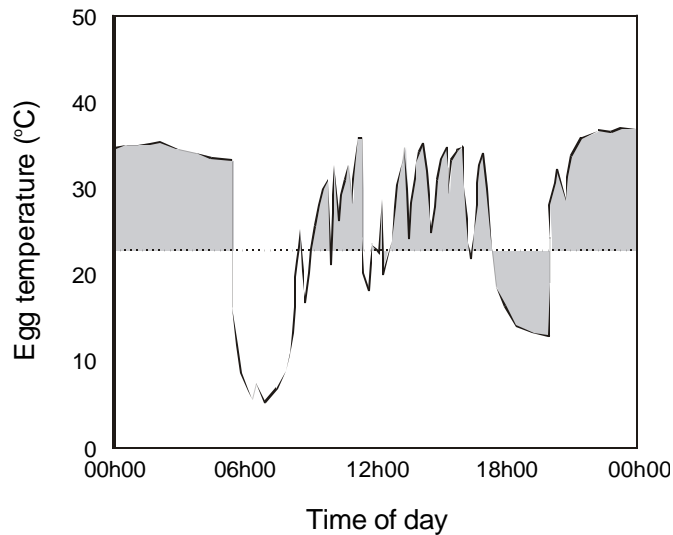
assumptions about the temperature distributions inside contact-incubated eggs. One-dimensional radial fields where the external resistance is large compared to the egg's internal resistance limit the extent to which the embryo's blood circulation can affect the egg's thermal conductance. This leads to the erroneous implication that  $K$  in equation 9.1 is assumed by Kendeigh's equation to be constant, or at least controllable principally through externally-driven factors. However, the situation Kendeigh's equation is intended to simulate results in two-dimensional fields inside the egg. Based upon the evidence that embryonic circulation can influence energy costs so strongly, this signifies that the term  $K$  clearly is not constant. Furthermore, it opens the possibility of active control by the embryo of the parent's energy costs of incubation, particularly near the end of incubation, when the embryo has the neural machinery for temperature regulation, even if it lacks the thermogenic capacity for it.

Finally, consider how incubation energy costs should scale with egg size (Turner 1991). The thermal conductance of an egg cooling in air is a composite conductance for heat flow by convection and radiation from the surface of the egg. This composite resistance scales to roughly the 0.6 power of egg mass. By implication, the energy cost of incubation predicted by Kendeigh's equation should also scale to 0.6 power of egg mass. However, in a two-dimensional temperature field, the axial component of heat flow through the egg is important, and this should scale to the 0.33 power of egg mass. The thermal conductance of a contact-incubated egg is a composite conductance that melds these two, and should therefore scale to a power of egg mass intermediate between 0.6 and 0.33. Turner (1991) estimated the scaling exponent to be 0.45.

Thus, by conflating the temperature fields that characterise two very different thermal regimens, approaches like that adopted by Kendeigh (1963) are prone to serious errors in estimating the energy costs of maintaining egg temperature. Three obvious ones spring to mind. First, the energy cost of incubation is presumed to be more than it really is. Second, the energy cost of incubation is presumed to decrease through the incubation period, when in fact it increases. Third, the effect of egg size on energy cost of incubation is exaggerated.

#### *Maintenance of egg temperature: unsteady state*

In steady conditions, the net heat exchange of the egg with its surroundings (which include the parent) is *nil*, and the temperature of the egg does not change with respect to time. If the net heat flow is no longer nil, egg temperature changes at a rate proportional to the rate of heat storage,  $Q_s$  (equation 9.1). This can be either negative (with a decline of egg temperature) or positive (with an increase of egg temperature). Birds' eggs often experience this so-called unsteady condition. For example, intermittent incubation involves a cycle of visits to, and absences from, the nest by the incubating parent, with the result that egg temperature cycles synchronously through a periodic excursion of temperature (Turner 1994a, 1997). The energy cost of maintaining the egg's temperature includes both the cost of keeping the egg warmer than the surroundings and the costs involved in changing the egg's temperature (Figure 9.6).



**Figure 9.6.** Transient and steady components of egg temperature, illustrated using a representative daily march of temperature (solid line) of the eggs of the dusky flycatcher (*Empidonax oberholseri*; after Morton and Pereyra 1985). The steady component is represented by the average egg temperature over the course of the day (dotted line) of egg temperature. The transient component, those involving a net storage or release of heat from the egg are represented by the shaded regions between the actual and average temperatures of the egg.

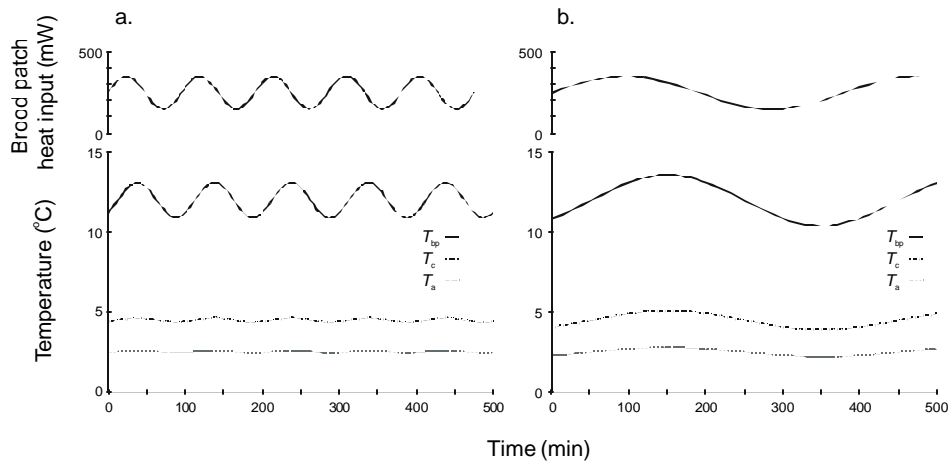
At its simplest, the energy storage term,  $Q_s$ , is proportional to the egg's thermal capacity,  $C$  ( $\text{J } ^\circ\text{C}^{-1}$ ), and the magnitude of the temperature change,  $dT$  ( $^\circ\text{C}$ ):

$$dQ_s = C dT / dt \quad (9.10a)$$

(Turner 1997). The egg's thermal capacity is the product of its specific heat,  $c_p$  ( $\text{J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$ ) and its mass,  $M$  (kg), so equation 10a can also be expressed:

$$dQ_s = M c_p dT / dt \quad (9.10b)$$

This simple description of the energy storage term could be used to estimate the energy costs of re-warming an egg following an absence from the nest. As in the simple application of Fourier's Law to the maintenance of steady temperature, this simple conception is only as good as the assumptions that underlie it. If these assumptions are not met, errors will arise in any estimates of the energy cost of re-warming derived therefrom. Also, the dimension of time is now involved and so these errors will pose a sort of double jeopardy, involving not only energy costs but time costs as well (Turner 1994a, 1997). For example, the time a bird can spend away from its nest, and hence the time that can be spent foraging, patrolling territories and defending the nest, will be influenced by how rapidly the eggs change temperature, both in how fast they cool when the parent is absent from the nest, in how fast they can be re-warmed when the parent returns, and by how many eggs are in the clutch. How differently sized clutches of eggs and eggs of different masses affect nest attentiveness is discussed in Chapter 6.



**Figure 9.7.** Transient heat flows and temperatures in a fowl egg warmed by an artificial brood patch. Egg temperature was forced by a sinusoidal input of heat from the artificial brood patch which had an amplitude of 100 mW around a mean heat input of 250 mW (top panels). Egg temperatures were measured at the shell beneath the brood patch ( $T_{bp}$ , solid lines), the egg centre ( $T_c$ , dotted lines) and the eggshell antipodal to the brood patch ( $T_a$ , dashed lines). *a.* Sinusoidal heat input with a period of 100 min. *b.* Sinusoidal heat input with a period of 400 min. After Turner (1994c).

### The unsteady temperature field

Unsteady flows of heat through eggs are driven by temperature fields, just as are steady flows (Turner 1994b). An unsteady temperature field consists of two components: a steady component, which is equivalent to the temperature fields in steady conditions, and an unsteady component, expressed as a time-dependent change of temperature superimposed on the steady temperature field. The unsteady component is driven by a so-called unsteady forcing, in the case of eggs, a pulse of heat applied intermittently to the egg surface through a brood patch. This method of warming forces a periodic oscillation of temperature in the egg, the so-called unsteady component, about some average,  $T_0$ , the steady component.

The unsteady temperature field is most easily visualised by forcing the egg temperature with a sinusoidal wave of heating from an artificial brood patch (Figure 9.7). This forces a sinusoidal variation of temperature throughout the egg, the amplitude and phase of which varies with locality in the egg. In general, at greater distances from the brood patch, the amplitude of the unsteady temperature diminishes, and becomes increasingly out of phase with the heat wave forcing the temperature (Turner 1994a, 1994b).

### The effective thermal capacity

This distribution of unsteady temperatures indicates that not all parts of a contact-incubated egg participate equally in the unsteady flows of heat through it. In particular, the unsteady heat flows are strongest near the brood patch, and diminish with distance from the brood patch (Turner 1997). Simple formulae (*e.g.* equation 9.10) presume that the temperature change is uniform throughout the egg. It demonstrably is not (Figure 9.7). This means that the actual cost of re-warming must be weighted by the distribution of temperature change within the egg. Those regions of the egg closest to the brood patch will experience large increases of temperature, and the costs of re-warming those parts of the egg will be high. In contrast, those regions of the egg which experience smaller changes of temperature will incur re-warming costs that are commensurably lower. Finally, those regions of the egg which experience no temperature change will incur no re-warming costs at all, as if this portion of the egg's mass was thermally not there. Thus, a contact-incubated egg will have an "effective thermal capacity" which should be considerably less than the more commonly used "gravimetric thermal capacity" implied by an equation like 9.10, *i.e.* the product of the egg's mass and its specific heat (Turner 1997). The effective thermal capacity is smaller and so the re-warming costs will therefore be less than might be predicted from the egg's gravimetric thermal capacity. Time spent re-warming is also a function of thermal capacity, meaning that time costs should also be considerably less. Turner (1997) has estimated the effective thermal capacity of a fowl egg might be as little as 15% of its gravimetric thermal capacity.

### The concept of the thermal impedance

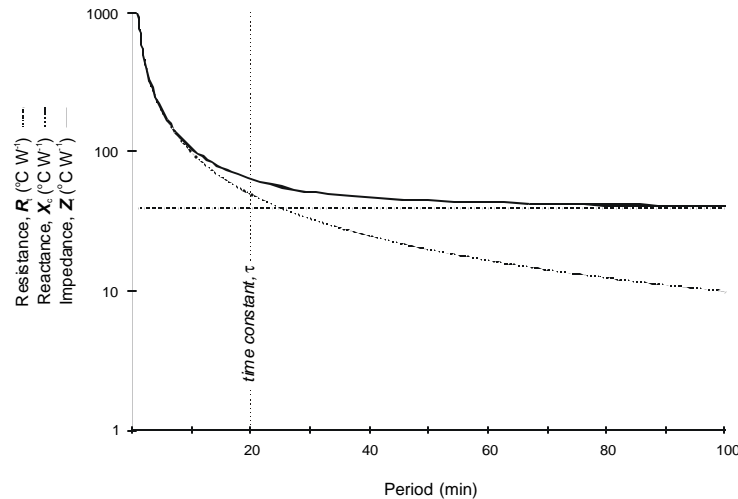
The effective thermal capacity of an egg is less than its gravimetric thermal capacity because the unsteady flows of heat penetrate unevenly into the egg. It follows that the effective thermal capacity will vary depending upon how readily the unsteady component of heat flow penetrates the egg. If the unsteady heat flow penetrates the egg poorly, only a small region of the egg will experience a temperature change, and the effective thermal capacity will be small. On the other hand, if the unsteady heat flow penetrates far into the egg, a larger portion will experience a temperature change, and the effective thermal capacity will be larger.

The temporal component of the unsteady heat flow is very important in determining how effectively it penetrates the egg (Turner 1994c). Again, this is easily demonstrated by forcing egg temperatures using a sinusoidally-varying heat input from an artificial brood patch. When the brood patch's heat input varies at high frequency (short period), the unsteady flows of heat are confined to a small region of the egg close to the brood patch. Temperatures in regions of the egg far from the brood patch oscillate only weakly (Figure 9.7). However, low frequency inputs of heat spread through the egg more broadly (Figure 9.7). As a result, temperatures of the egg far from the brood patch oscillate more strongly than they do under high frequency inputs (Figure 9.7).

These temporal effects further complicate the analysis of egg re-warming. Fortunately, this problem has much in common with unsteady energy flows through a variety of physical systems, such as are found in alternating current flow through an electronic circuit or acoustic energy flow through pipes. There is a substantial body of theory developed to deal with such flows, and this should, in principle, be applicable to the problem of unsteady energy flows through contact-incubated eggs. One of the more useful aspects of this theory is the notion of impedance, a sort of transient-state analogue to the egg's thermal resistance (Turner 1994c). Put simply, the thermal impedance,  $Z_t$ , accounts both for the steady and unsteady components of energy flow through the egg:

$$Z_t = (R_t^2 + X_c^2)^{0.5} \quad (9.11)$$

where  $R_t$  = the steady state resistance through the egg, by definition insensitive to the temporal component of the heat input, and  $X_c$  = the capacitive reactance, which varies with the frequency of the heat input (all terms are expressed in units of  $^{\circ}\text{C W}^{-1}$ ). Contact-warmed eggs behave like a low-pass thermal filter, so that their thermal impedance declines with the period of the unsteady heat flow driving the temperature. At very long periods (low frequencies), *i.e.* where the period approaches infinity, the thermal impedance is equivalent to the thermal resistance (Figure 9.8), and heat supplied from the brood patch penetrates deeply into the egg. For periods shorter than the egg's time constant,  $\tau$  (roughly 20 min for fowl eggs), the impedance increases sharply, rising several orders of magnitude higher than the steady thermal resistance (Figure 9.8). Here, the unsteady component of heat supplied through the brood patch penetrates the egg poorly. Again, the embryo has some significant control over this. As the embryo's circulation develops, it distributes both the steady and unsteady components of heat flow more widely through the egg, resulting in a decline of the egg's thermal impedance over all frequencies.



**Figure 9.8.** The components of the thermal impedance and their variation with period of the transient component of the heat input from the brood patch. Thermal impedance of a chicken egg,  $Z$ , (heavy solid line), is the vector mean of the egg's steady thermal resistance,  $R$ , (dotted line) and the egg's capacitive reactance,  $X_c$  (dashed line), all terms in units of  $^{\circ}\text{C W}^{-1}$ . The time constant  $\tau$  for a contact-warmed fowl egg is indicated by the vertical dotted line. After Turner (1994c).

The thermal impedance of an egg suggests some interesting possibilities for ways birds might manage the unsteady heat flows through their eggs (Turner 1994a). Most of these are unexplored, but could form the basis for future investigation. Imagine, for example, how an intermittently incubating bird might manage its incubation energy budget through the incubation period. Re-warming the egg should involve primarily warming of the embryo: it makes little sense to warm those parts of the egg not occupied by the embryo. If only those parts of the egg occupied by the embryo could be selectively re-warmed, energy savings could accrue to the parent. Early on in incubation, the embryo and yolk are free to rotate within the egg, such that the embryo is automatically positioned near the egg's upper surface. During this time, the incubating parent may need to warm only those regions near the egg's upper surface, i.e. that region occupied by the embryo (Rahn 1991). This the parent could do by adjusting the visitation schedule to favour high impedance warming. High frequency input of heat are now favoured, which are confined to those regions of the egg occupied by the embryo. As the embryo grows, however, it comes to fill more and more of the egg. High impedance warming, which warms only a narrowly circumscribed region of the egg near the brood patch, might no longer warm the whole embryo effectively. The parent might then shift its visitation schedule to one that favours low-impedance warming, which would penetrate further into the egg and warm all parts of the egg occupied by the embryo.

#### Thermal impedance and natural incubation rhythms

Subtle aspects of the maintenance of egg's unsteady temperatures, such as concepts of thermal impedance, or effective thermal capacity, emerge clearly when egg

temperatures are forced by well-behaved sinusoidal heat inputs from an artificial brood patch. Whether such subtleties have any relevance to living eggs under actual brood patches is presently unknown. One obvious problem is whether the actual unsteady heat inputs to eggs by incubating parents bears any resemblance to the well-behaved sinusoidal heating one can impart to an egg using an artificial brood patch. Whatever the unsteady heat inputs to a naturally incubated egg might be, they are unlikely to be well-behaved. Thus, the temptation might be strong to dismiss these biophysical subtleties as laboratory curiosities, with little relevance to the “real world” situation faced by eggs and their parents in nature.

Fortunately, there is a way to evaluate such temptations critically, and these rely crucially on concepts like the thermal impedance. Any periodic phenomenon, whether it be sinusoidal or not, can be resolved into a series of sinusoidal components, each with a particular amplitude and phase (Trimmer 1950). This is the Fourier series:

$$f(t) = \sum_{n=0 \rightarrow k} (a_k \cos kt + b_k \sin kt) \quad (9.12)$$

where  $f(t)$  is some function with respect to time,  $t$ . The function  $f(t)$  can be resolved into a summed series of sinusoidal components of amplitudes  $a_k$  and  $b_k$ . Thus, any periodic forcing of egg temperature, whether it be sinusoidal or not, can, in principle, be resolved into a series of sinusoidal components, each governed by the thermal impedance appropriate to the frequency of that component (Trimmer 1950; Turner 1994b). The response, namely the egg’s unsteady temperature, can be reconstructed from the sum of the unsteady responses to each of the sinusoidal components of the forcing. Consider, for example, a forcing of egg temperature by a square-wave input of heat. A square wave can be resolved into the following infinite series:

$$Q_s = Q_{bp} - Q_{bp,A} P (\sin t + \sin 3t / 3 + \sin 5t / 5 \dots) / 2\pi \quad (9.13)$$

where  $Q_{bp}$  is the average heat input, equivalent to the steady component of heat from the brood patch, and  $Q_{bp,A}$  is the amplitude of the heat input, and  $P$  is the period of the dominant frequency (Figure 9.9). The effect of each of the sinusoidal heat inputs on egg temperature is weighted by the thermal impedance of the egg at that frequency. Thus, the high-frequency components will heat the eggs less than the low-frequency components. The actual change of egg temperature will be the sum of the forcing at each of the sinusoidal frequencies. Thus, the transient heat flow into the egg is derived from the sum of all the sinusoidal heat forcings that go into this series. The result is a damped oscillation of egg temperature that reflects the differential heating effects of the various components of the series.

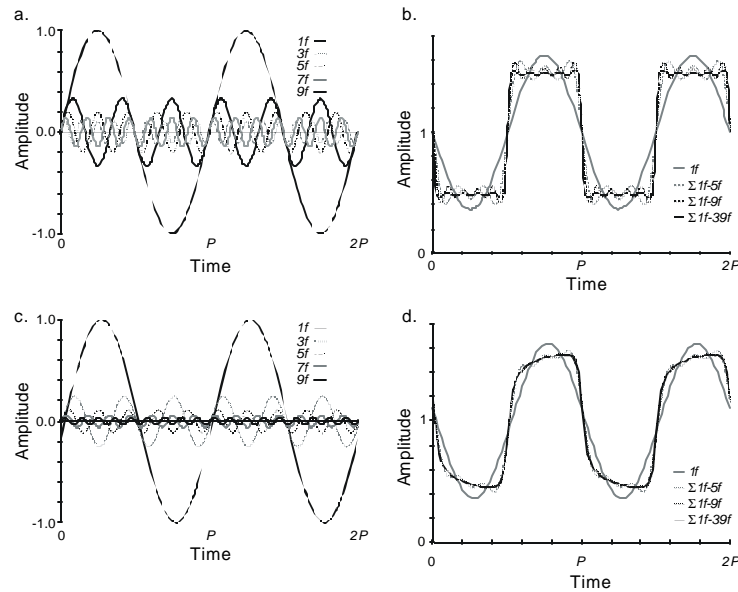
One of the more interesting implications of this approach is the notion that not all joules imparted to the egg during an intermittent bout of incubation will be equal. Some (those in the high frequency components) will penetrate the egg only slightly, while others (those in the low frequency component) will spread more broadly through the egg. In short, to estimate the costs of re-warming accurately, it is not sufficient to simply measure the egg’s temperature excursion. Rather, one must construct a power spectrum that accounts for the differential effects of the different frequency components of the warming.

#### Relaxation of the unsteady temperature field

There is a final complication in eggs driven by unsteady heating that needs to be considered. During visits to the nest, the eggs presumably are warmed by contact with a brood patch, and this will result in the eggs taking on the two-dimensional temperature fields characteristic of contact incubation. When the parent vacates the nest, however, the egg's temperatures will shift toward the one-dimensional radial temperature fields characteristic of eggs surrounded by still air. The process whereby a temperature field shifts from one configuration to another is known as relaxation. In a cooling egg, relaxation is evident as a two-phase pattern of temperature change (Turner 1987; Figure 9.10). Early in the cooling phase, the egg cools at a rate dominated by the redistribution of heat from near the brood patch to the centre. As the egg assumes the one-dimensional temperature field typical of cooling in air, the egg's cooling rate changes because heat now is flowing uniformly out of the egg across its surface (Figure 9.10). Thus, the cooling of the egg is a two-phase process, governed by two time constants, one early in the transient for the relaxation time,  $\tau_1$ , and the other,  $\tau_2$ , later in the transient for normal cooling of the egg:

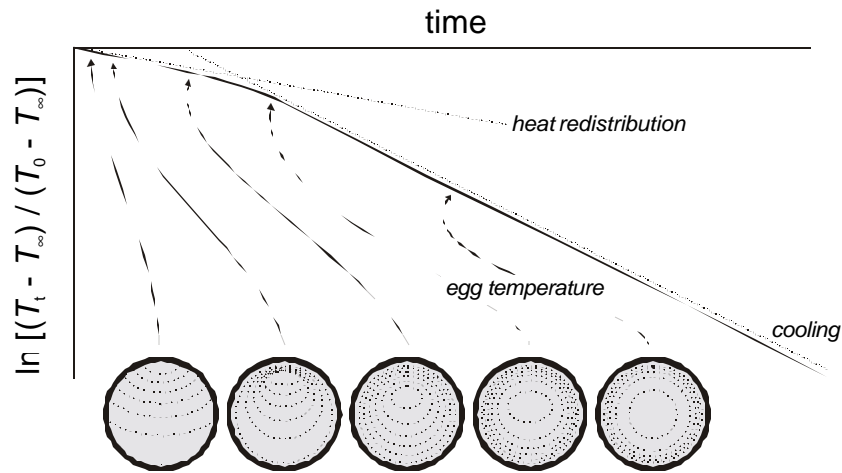
$$T_{\text{egg}} = T_{\infty} + (T_0 - T_{\infty}) (\alpha e^{-t/\tau_1} + \beta e^{-t/\tau_2}) \quad (9.14)$$

where  $\alpha$  and  $\beta$  are coefficients representing the ratios of the time constants (Turner 1987). The reverse should happen when the parent returns to the nest. The returning parent first encounters an egg containing a one-dimensional radial temperature field, and imposes upon it the two-dimensional field characteristic of contact incubation. The egg will similarly change temperature in two phases.



**Figure 9.9.** Partial decomposition and reconstitution of a square-wave forcing of egg temperature and the temperature response of the egg. *a.* The first five sinusoidal components of a square-wave forcing of heat input from a brood patch. *b.* Reconstituted square wave response showing the effects of summing various of the sinusoidal components of the forcing, including the fundamental frequency ( $f$ ), the sum of the components of the first three components ( $\Sigma 1f-5f$ ), the sum of the components of the first five components ( $\Sigma 1f-9f$ ), and the sum of the components of the first twenty components ( $\Sigma 1f-39f$ ). *c.* The first five sinusoidal components of the response of egg temperature to the forcings of egg temperature by a sinusoidal wave of heat input from a brood patch in *a.* *b.* Reconstituted temperature response of the egg forced by the components in *b.* including the response at the fundamental frequency ( $f$ ), the sum of the responses of the first three components ( $\Sigma 1f-5f$ ), the sum of the responses of the first five components ( $\Sigma 1f-9f$ ), and the sum of the responses of the first twenty components ( $\Sigma 1f-39f$ ).

The implications of this type of temperature change are largely unknown, except for the work of Hainsworth and Voss (Chapter 15). However, it may be substantial, particularly in those circumstances where the period of the incubation rhythm is shorter than the egg's time constant for cooling. For example, imagine an intermittently incubating bird which, during its visit to the nest, engages in high-impedance heating of the egg, so that the added heat is confined to a small region close to the brood patch, this region surrounded by a sharply graded temperature field into the egg. This will enable the bird to deposit a load of heat, and leave the nest quickly. Once the bird leaves, this sharply graded temperature field will shift within the egg as the heat deposited there is redistributed (Figure 9.10). The parent's deposit of heat is therefore retained in the egg, rather than being lost, because it migrates preferentially into the egg rather than out through the egg's warmed surface. This could be a useful heat conservation measure, because heat that is retained in the egg is heat that will not have to be replaced on a subsequent visit.



**Figure 9.10.** Hypothetical course of temperature change as egg temperatures relax from a distribution of temperatures characteristic of contact-warming, to the temperature distribution characteristic of an egg cooling in air. Temperatures are expressed as the natural log of a dimensionless ratio of temperature at any time  $t$ ,  $T_t$ , cooling toward an equilibrium temperature of  $T_\infty$ , starting at an initial temperature  $T_0$ . Cartoons show likely temperature distributions, indicated by isotherms (dotted lines) at various times through the transient.

### *Limitations of the biophysical approach to maintenance of egg temperature*

The biophysical approach to egg temperature outlined above assumes that temperature maintenance, *i.e.* incubation, is largely a matter of how incubating birds and embryos manage the flows of heat into and out of the egg. This approach follows ultimately from the notion that natural selection is the result of a sort of cost-benefit analysis. Differential reproduction results when one phenotype is able to mobilise more energy to do reproductive work than another. Phenotypes can be favoured as a result of increases of physiological efficiency, so that a greater proportion of an animal's total energy budget is diverted to reproduction. However, it can also result from seemingly costly behaviours and investments: as long as more reproductive work accrues from a costly investment, it will be favoured. Contained within this energetic definition of selection is a seductive promise: understand the energetics of an organism and you open a window on all features of an animal's biology, such as its behaviour, its physiology, its life history, any aspect that is subject to evolution by natural selection. The biophysical approach to the maintenance of egg temperature embodies this promise: understand the energy flows between parents and eggs and you understand all features of avian biology that follow from it, such as attentive behaviour, parental care, and so forth. Realising this promise was an important motivation for the pioneers of the field such Charles Kendeigh and his contemporaries.

As we have seen, the flows of heat through eggs are far more complex and subtle than these pioneers ever imagined it could be. This rich complexity presents a three-

sided challenge to the promise just outlined. On the one hand, understanding these biophysical subtleties can reveal tremendous possibilities for ways incubating birds might manipulate their incubation energy budgets. For example, applying impedance concepts to the heating of eggs suggests that costs and benefits accrue differently to behaviour patterns that result in “high-impedance” heating of the egg compared to “low-impedance” heating (Turner 1997). On the other hand, the complexity makes a rigorous experimental approach to the problem of incubation energetics more difficult. The difficulty arises for the same reasons economics or sociology are experimentally difficult sciences. The systems under study are themselves adaptable which means that it is sometimes uncertain whether a result is due to the experimental treatment, or due to an adaptive response of the system to the novel and artificial environment posed by the experiment. Finally, these complex and subtle features of egg incubation operate in a natural environment that is itself highly variable and unpredictable. Turbulent winds, for example, can introduce such high variation in heat exchange rates that other, more subtle sources of variation, such as egg colour, nest insulation, time spent away from the nest, etc., are swamped. So, while theoretical tools are available for quantifying the thermal interaction between parent, egg and embryo in great detail, applying them to the “real world” might be problematic.

Given these problems, it may be worthwhile at this stage to step back and ask: what is to be gained by pursuing an ever more sophisticated physical understanding of the maintenance of egg temperature? If we attain a perfect understanding of the biophysics of heat transfer between parent and egg, could we then say that we understand incubation?

The biophysical approach to egg temperature reflects the reductionist faith that a system can be understood through a knowledge of the behaviour of its parts. While very powerful, inherent in reductionism is the tendency to alienate the parts of the system from the system itself. For example, an enzyme can be analysed as an entity in itself, which can illuminate such enzyme-level questions as how the active site operates, or how substrate is turned into product. This approach, however, divorces the enzyme from the biochemical, cellular, organic and organismic milieu in which it normally operates, such that a thorough understanding of active site kinetics may be of only limited value in understanding how the enzyme works in the system of which it is a part.

The initial biophysical studies of incubation energetics, exemplified by Kendeigh (1963), similarly offered a useful reductionist framework for answering the seemingly simple question: how much energy is required from the parent to keep its eggs warm? However, these initial approaches alienated the egg profoundly: from the parent, treated now as a disembodied regulated heat source; from the embryo it contained, denying the embryo any physiological control over its own temperature; and even from the environment in which it lived. As we have come to understand the biophysics of incubation more fully, the alienation between parent and embryo has eased to a degree. For example, we now know that the embryo can, in some contexts, affect its own temperature through physiological distribution of heat from the parent. The important question now is not whether or not the embryo can control its own temperature, but whether, and how often the embryo is found in contexts that enable it to control its own temperature. Such questions might be more profitably approached

by examining how the egg, embryo, parent, and environment function together as a system, identifying and studying the mutually interacting feedbacks and physiological systems which govern the behaviour of the whole.

### The egg as part of a thermal mutualism

Treating the egg, embryo, parent and environment as a unified system (*i.e.* the bird-nest incubation unit described in Chapter 1) is tantamount to describing egg temperature as the outcome of a type of symbiosis, which includes the components (*i.e.* the embryo, the parent and so on) and the feedbacks which regulate the flows of energy between them (Figure 9.11). Symbiosis can take the form of a mutualism, a physiological phenomenon whereby two disparate organisms associate in some mutually beneficial way. A mutualism usually involves partners that have complementary physiologies, mechanisms for one partner adjusting the physiology of the other, and some means of controlling the common environment shared by the partners. Consider, for example, the quintessential mutualism, the lichen (Ahmadjian 1993). The heterotrophic and autotrophic physiologies of the fungal and algal partners complement one another, each partner providing nutrients that the other partner could not synthesise on their own. At the same time, the physiology of the autotroph is regulated by a feedback from the heterotroph: *e.g.* the algae's rate of photosynthetic carbon fixation is regulated by the production rate of urea in the fungus. Finally, the intimate association between the alga and fungus ensures that environmental perturbations do not disrupt the orderly exchange of matter and energy between the partners.

An incubated egg meets some of the criteria for being a mutualism. For example, there is complementarity of metabolisms: the embryo requires a high temperature to grow, but is not itself capable of providing the heat required to elevate the egg temperature more than a degree or so. The heat required by the embryo must come mostly from the parents, supplied through the brood patch. There is also an intimate association between parent and egg: the egg is usually contained within a nest of some sort, and the transfer of heat is usually through the intimate contact between the brood patch and the egg. Finally, there are feedbacks whereby this transfer of heat is

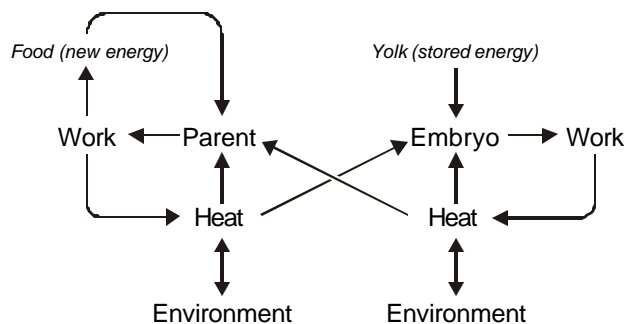


Figure 9.11. Sketch of the elements of a thermal mutualism between parent and embryo. The control of this mutualism resides in the control of the crossed arrows representing heat transfers between parent and embryo.

governed. For example, heat flow between the brood patch and egg appears to be regulated by adjustments to blood flow through the brood patch and heat production by the parent (White and Kinney 1974; Vleck 1981a, 1981b; Tøien et al. 1986). The insulation of nests is adjusted to some degree to the local conditions (Ponomareva 1971; Schaefer 1976; Webb and King 1983a, 1983b; Kern 1984; Kern and van Riper 1984; Skowron and Kern 1984). Still largely unknown, though, is the extent or mechanisms of feedbacks within the embryo, or between the embryo to the parent, but there is tantalising evidence these exist. For example, fowl embryos appear to have the neural regulatory machinery to regulate egg temperature several days prior to hatching, although the ability to actually do so is limited by the resistance of the eggshell to exchange of respiratory gases, which in turn limits the thermogenic capabilities of the embryo in ovo (Tazawa et al. 1988). Also, the embryo might, through some pheromonal or other mechanism, signal to the parent that it requires more heat. Indeed, recent work has shown that nitric oxide appears to play a role in embryo-parent interactions during incubation (Ar *et al.* 2000). It is even conceivable that the embryo, through altering the building behaviour of its parents, could actually control the structure of its own nest.

#### What is “egg temperature?”

If the egg is part of a thermal mutualism, this puts the question “what is egg temperature?” in a particularly critical light. Consider, for example, the title of this chapter. A contribution on the “maintenance of egg temperature” implies some knowledge of just what egg temperature is. Biophysically, though, the question is nonsensical. Eggs do not have a temperature, they have temperature fields (Table 9.2). which can behave in some complicated ways. In this light, the term “egg temperature” has to be qualified somehow. Is it temperature of the embryo? Is it temperature of the egg’s exposed surface? Is it temperature of the shell underneath the brood patch? All these temperatures co-vary (Rahn 1991), and simple measurements of either egg temperature, brood patch temperature offer little insight into which is the important temperature that is maintained.

**Table 9.2.** Body, brood patch and egg temperatures in various bird species, based on the compilation by Rahn (1991).

	Average	SD	N
Body	39.53	1.36	23
Brood patch	38.39	1.61	27
Egg center	35.85	1.80	103

Certainly, a case can be made for designating any of the temperatures in an egg as the most important temperature. For example, one could credibly argue that the embryo’s temperature is the most critical, on the grounds that it must be kept within the limits of the embryo’s thermal tolerance. When the egg is treated as an autonomous individual, separate from the parent that incubates it, such embryo-

centred biases colour the types of questions asked. For example, what is the nature of the “physiological zero”, the low temperature at which embryonic development suspends? Similarly, what is the nature of the embryo’s tolerance to either high or low temperatures? These are clearly important questions, but coming as they do from an essentially reductionist perspective, they imply that the embryo is essentially a “physiological problem” presented to the parent, which the parent then “solves” through behaviour and adaptation, similar in kind to other “physiological problems” posed to the parent by cold temperatures, high insolation, water scarcity and so forth.

If the embryo is thought of as an active partner of a thermal mutualism, however, the focus shifts to the critical feedbacks and regulators that drive the behaviour of the system as a whole. This poses a whole new set of criteria for deciding which, of all the temperatures in the egg, is the important one. For example, an important component of a thermal mutualism are temperatures which are sensed by both partners, and which form crucial control points for the system itself. In this perspective, the embryo’s temperature is of little relevance, because only one of the partners in the mutualism can be aware of it. The other partner, namely the parent, cannot directly sense the temperature of an embryo deep within the egg. A more relevant temperature might be one that both partners can sense, and perhaps control. The best candidate for the regulated temperature in an egg-parent mutualism would be the egg surface contacting the brood patch. Incubation behaviour, life history, thermal tolerance and so forth will centre around and adapt to the maintenance of the egg’s surface temperature, rather than the maintenance of the embryo’s temperature per se.

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