

The thermal energetics of incubated bird eggs

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Introduction

A bird embryo can generate only a limited amount of heat (Romijn & Lokhorst, 1960; Tazawa *et al.*, 1988). The ability of the egg to dissipate heat is also limited (Spotila, Weinheimer & Paganelli, 1981; Turner, 1985; Sotherland, Spotila & Paganelli, 1987). Consequently, the temperature of an egg can be controlled only slightly by the embryo and deviate from ambient temperature by roughly -0.5°C to $+3^{\circ}\text{C}$ at most (Turner, 1985; Sotherland *et al.*, 1987). Most bird embryos must develop within fairly narrow temperature limits (Barott, 1937; Drent, 1970, 1973, 1975; Deeming & Ferguson, Chapter 10), and environments that provide these temperatures are rare. It follows that an egg will rarely be at an ideal temperature for development unless fluxes of heat into and out of it are somehow supplemented and controlled. The management of heat flux into and out of the egg, effected by the brooding parent, is incubation: all other attributes of incubation (gas and water exchange and turning) are, at root, secondary to this one function.

In this chapter, I wish to address the fundamental problem of how incubation 'works', i.e. how heat flow between an egg and incubating parent is managed. Although the thermal interaction of the embryo and the incubating parent has been extensively studied, it remains poorly understood. The physics and physiology of temperature of incubated bird eggs are examined, and the energy cost to the incubating parent of keeping the egg at that temperature, is determined. The various ways this problem has been studied in the past, and what these approaches have implied and predicted about

the way incubation works will be discussed. A more informative approach to the problem will be introduced which is able to predict many important features of incubation energetics that previous approaches have missed. My goal is to put the thermal energetics of avian incubation onto a sound physiological and physical foundation; a foundation that, in my opinion, has heretofore been missing.

Approaches to incubation energetics

Some definitions

Bird eggs may be incubated in one of two ways. One way is to place the egg in air that is warm enough to bring it to a suitable temperature. This type of incubation, which is typical of a commercial incubator, is termed *convective incubation*. The other way is to warm, and regulate the temperature of, part of the egg's surface. Here, the air surrounding the rest of the egg can be any temperature. Any variation of heat loss to the air is compensated by a similar variation of heat flow into the egg across the warmed surface: egg temperature will then stay more or less constant. This type of incubation, which is what an incubating bird does with its brood patch, is termed *contact incubation*.

Contact incubation is a thermal interaction between the parent and the egg and although it has been studied in many ways (Grant, 1984) conceptually, these approaches can be reduced to just two. The first method, the 'analogical approach', regards the thermal behavior of convectively incubated eggs and contact incubated eggs to be sufficiently similar that an analogy may be drawn between them: what is known

about one type of incubation can inform the other. The second method, the 'lumped conductance approach', regards the thermal behavior of a contact incubated egg to be sufficiently unique to make an analogical approach inappropriate. Further, it presumes that the analysis of the flows of heat in a contact incubated egg can be greatly simplified yet still yield robust answers.

The analogical approach

The most influential analogy between convectively incubated and contact incubated eggs is an equation, derived by Kendeigh (1963), which predicts the heat input required to keep a clutch of eggs at an appropriate temperature for development. Kendeigh's formula (slightly rewritten from the original) is:

$$Q_i = nMc_p (T_c - T_a) (1-c)/\tau \quad (9.1)$$

where: Q_i = instantaneous power requirement for incubation (W), n = number of eggs in a clutch, M = egg mass (kg), c_p = egg specific heat ($\text{J kg}^{-1} \text{ }^\circ\text{C}^{-1}$), τ = time constant for cooling (s), T_c = egg temperature ($^\circ\text{C}$), T_a = ambient temperature ($^\circ\text{C}$), and c = fraction of the egg surface covered by the brood patch. The quantity ($M c_p / \tau$) is equivalent to the egg's thermal conductance, K ($\text{W }^\circ\text{C}^{-1}$).

Equation 9.1 is an analogy due to its reliance on the time constant for cooling, τ , which Kendeigh measured for eggs cooling in still air. Such eggs, of course, are completely surrounded by air, which is characteristic of convective incubation (Fig. 9.1). Therefore, the heat an incubating parent must apply to a contact incubated egg is simply: the heat normally lost from a convectively incubated egg, minus whatever heat would be lost from an exposed surface equivalent in area to that covered by the brood patch (Fig. 9.1).

The lumped conductance approach

This approach starts with the presumption that an analogical approach to incubation cannot work. Put simply, the analogical approach cannot predict a very fundamental attribute, namely the temperature distribution inside a contact incubated egg. A convectively incubated egg is a well-mixed body (Turner, 1987): interior temperatures differ only slightly from surface temperatures (Sotherland *et al.*, 1987). The analogical approach suggests the temperature dis-

tribution in contact incubated eggs should be similar. Yet, contact incubated eggs have marked temperature gradients between the top (near the brood patch) and bottom (Rahn, Krog & Mehlum, 1983; Vleck *et al.*, 1983; Turner, 1987). The energy flows within an egg and cannot reliably be assessed without realistic temperature distributions (nor can temperatures be predicted from energy flows). The analogical approach cannot provide this and therefore must fail.

Analysing the actual temperature distribution (and hence energy flow) in a contact incubated egg is a difficult problem. The lumped conductance approach attempts to simplify the problem by lumping the flows of heat into one or a few discrete elements, or *nodes*. The aim in doing this is to make the problem tractable without simplifying away what is interesting.

There have been three principal applications of the lumped conductance approach: 1) the clutch-mass method regards each egg as an extension of the parent's body: the heat required to incubate the eggs is simply that required to keep an equal mass of parent warm (West, 1960). 2) The egg is treated as a single node interposed between the brood patch and nest environment (Walsberg & King, 1978*a,b*; Webb & King, 1983). 3) The most important model, developed by Ackerman & Seagrave (1984), is the one I shall consider in detail through this paper. Ackerman & Seagrave (1984) distribute the conductance of a 60 g egg into three adjacent nodes (Fig. 9.1). One node is that portion of the egg which contacts the brood patch, a second node is that portion of the egg contacting the substratum and sandwiched between the two, and comprising the third node, is the remainder of the egg. The three-node egg lets heat flow in two dimensions (Fig. 9.1): the middle node can exchange heat with both of the adjacent egg nodes (one dimension) and with the nest air (the other dimension). Additionally, the egg has physiology: the 'embryo' produces heat and circulates blood (Ackerman & Seagrave, 1984).

A third way: the numerical model approach

In a contact incubated egg, heat flow vectors emanate from the egg surface warmed by the brood patch, and spread symmetrically about the egg's vertical axis (Fig. 9.1; Turner, 1987). Both the analogical approach and the lumped con-

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Three approaches to the energetics of contact incubated eggs

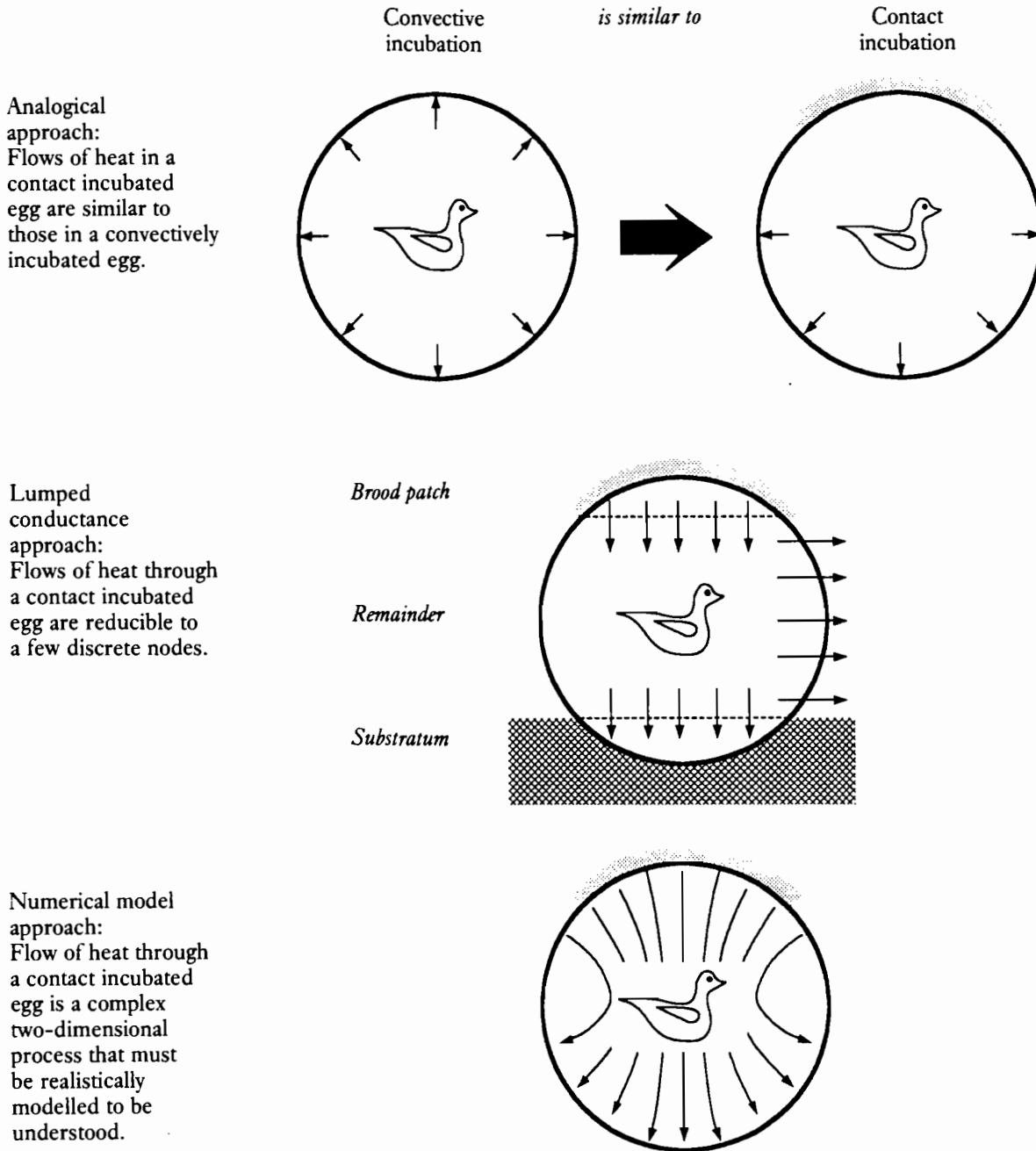


Fig. 9.1. Three approaches to the energetics of contact incubated eggs. Light shading indicates the area of egg covered by the brood patch. Arrows indicate the flows of heat. *Top panel:* the alleged similarity between radial heat flow in convectively incubated eggs and contact incubated eggs. *Middle panel:* heat flows in the lumped conductance approach, where the egg is divided into three nodes. *Bottom panel:* detailed heat flows in the numerical model approach.

ductance approach attempt to simplify this temperature distribution, albeit in different ways. The analogical approach assumes it does not exist and the lumped conductance approach

assumes it can be reduced to three discrete temperatures. A third approach is to model the temperatures and flows of heat in the egg in as much detail as practicable.

This is the approach introduced here: a numerical finite-difference model of temperatures and flows of heat through a contact incubated egg has been developed, which divides the egg into not a few, but many hundreds of nodes. This makes it possible to estimate the temperature distribution in the egg in great detail, which in turn makes possible realistic estimates of energy flows through the egg. This model is designed to be flexible and general. For example, it allows an examination of how the temperatures and flows of heat in contact incubated eggs are affected by various environmental conditions, incubation stages, developmental types, egg size and embryonic physiology. To honour the man who first tried to make physical sense out of the thermal energetics of incubation, I have named this model KENDEIGH and hereafter it is referred to as the numerical model.

Description of KENDEIGH

A brief description of the numerical model KENDEIGH is presented here and a fuller mathematical description is the subject of another paper (Turner, in preparation). KENDEIGH is a computer package, written in Turbo PASCAL, designed to be a general exploratory and predictive tool for the thermal energetics of contact incubated eggs. It is compatible with any IBM personal computer, although best performance requires an AT type machine, preferably with an EGA colour graphics adapter. The package is the property of the University of Cape Town and free use of the program is granted to any researcher, as long as its source is acknowledged and it is not used for monetary gain. Copies of the PASCAL source code and compiled programs are available on request to the author, and upon provision either of a 5.25 inch floppy disc or a 3.5 inch microdiscette.

The basic purpose of KENDEIGH is to estimate the temperatures and flows of heat in a contact incubated egg. It is a numerical finite-difference model. The model egg is divided into 401 interior nodes and 20 surface nodes which are laid out according to a system of spherical coordinates. The model is two-dimensional and temperature is presumed to vary only in the r and ζ dimensions. Consequently, with the exceptions of the centre node and two of the surface nodes, the nodes are toroidal in shape.

Temperatures are calculated by performing a simultaneous heat balance on all nodes. Through various iterative numerical methods, the temperatures required to balance the energy budgets of all nodes simultaneously can be calculated. Heat flows in the egg may be estimated from the solved temperature distribution.

KENDEIGH allows heat to flow into, and out of, each node by conduction from adjacent nodes, circulation of blood between certain adjacent and non-adjacent nodes, and by heat generation within a node. Each node is differentiated according to whether it is embryo, albumen, yolk, chorio-allantois or shell. Depending upon its classification, the node is assigned a certain thermal conductivity. If it is an embryo node, a heat generation term and a circulation term is included in its heat balance. If it is a chorio-allantoic node, a circulation term only is included. Additionally, there are special terms for the circulation between the chorio-allantoic nodes and embryo nodes.

The package KENDEIGH is comprised of three separate programs: The first program, EGGINIT, 'builds' an egg for later simulation. EGGINIT allows the user to specify one of 21 incubation ages, egg size, whether the egg is precocial or altricial, and it allows one to 'switch' on or off metabolism and/or circulation within the egg. The latter feature enables one to build eggs that have either metabolism but no circulation, circulation but no metabolism, or neither circulation nor metabolism. With the specified inputs, EGGINIT maps out the distribution of the embryo, albumen, yolk and chorio-allantoic nodes and assigns the heat flux terms to each node. EGGINIT then writes an information text file, which contains basic descriptive information about the egg, and an initialisation file, to be used by the second program in the package, which identifies the type of node and contains the variable heat balance terms for each node in the model egg.

The second program, EGGHEAT, takes the information about the egg 'built' by EGGINIT, and performs the actual energy balance calculations. EGGHEAT further allows the user to specify how much of the egg is covered by the brood patch, what the temperature is of the surroundings, and allows one to set a 'gain' for the circulation and metabolism terms, so that metabolism can be varied continuously and independently of circulation and vice versa. The program solves the energy balance equations

using standard iterative methods, and solves them to between-iteration error of 0.00001. Upon completion of the simulation, the program writes a data file containing the temperatures of all 421 nodes. It also writes a simulation report, which may be printed out, and which contains descriptive information on the simulation, the energy balance for the incubated egg, and weighted average temperatures for the entire interior of the egg, the surface of the egg not covered by the brood patch and for the nodes identified as embryo.

The third program, EGGDRAW, requires an EGA colour monitor. EGGDRAW reads the temperature data file created by EGGHEAT and draws a colour map of the temperature distribution inside the egg and on the surface of the egg.

Evaluating the three approaches: an artificial brood patch system

To evaluate the three ways of approaching incubation energetics, five 'case studies', which consider different aspects of the problem of incubation energetics, are investigated and the respective predictions of the analogical, lumped conductance and numerical approaches are compared. Experimental data, obtained from an artificial brood patch system which measures the incubation energy budget for contact incubated eggs are presented. These data will allow us to evaluate the predictions of the three approaches.

The artificial brood patch system is based upon a device originally described by Drent (1970) and is fully described in Turner (1990). It consists of two parts. First, the artificial brood patch itself, a custom-built Dewar flask that sits over the upper surface of the egg (Fig. 9.2). The flask contains a heating coil in its cup, and the heating coil and egg are thermally coupled by dental alginate which also serves to secure the artificial brood patch to the egg. This arrangement ensures that the major share of the heat dissipated by the heating coil must exit through the egg although there are minor extraneous fluxes resulting from conduction through the glass walls of the flask. If the temperature of the brood patch thermocouple is regulated, the heat dissipated by the heating coil is a close approximation to the heat an incubating parent must pass into the egg *via* its brood patch.

The second part of the system is the machinery, which has three major elements, that

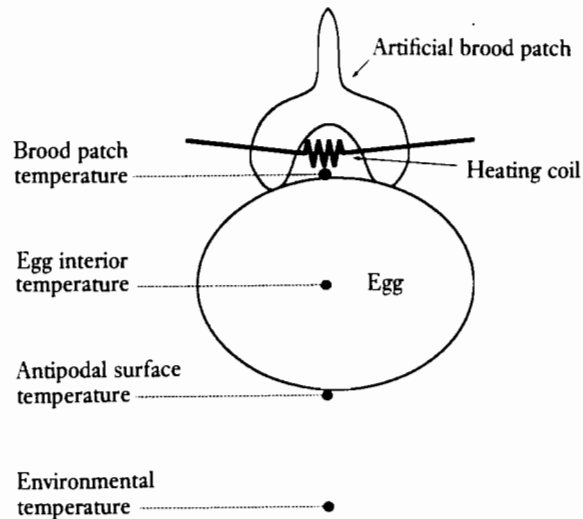


Fig. 9.2. Detail of an egg incubated with an artificial brood patch, showing location of various thermocouples.

estimates the incubation energy budget for the egg under the artificial brood patch (Fig. 9.3). This is comprised of three major elements. First, there is machinery to regulate the temperature of the brood patch thermocouple. The output of the thermocouple is fed to a time-proportional on-off temperature controller, which operates a relay that feeds current through the heating coil (Fig. 9.3). Second, there is a system for estimating the heat production of the embryo based on standard methods of flow-through respirometry. Third, a micro-computer controls the operation of the machinery, senses the signals for the relevant variables, and when the experiment is complete, writes a report detailing the results of the experiment.

Some case studies in the energetics of contact incubated eggs

Case 1: The energy cost of incubating an unembryonated egg

The most obvious test of any model is to ask whether it gives the correct answer to what it is meant to predict. For example, in the case of the analogical approach, does equation 9.1 correctly predict the energy cost of keeping a contact incubated egg at a certain temperature? As an initial test, let us consider the simplest case: a single unembryonated egg, comprised of albumen and yolk, with neither internal generation of heat nor circulation of blood. This is

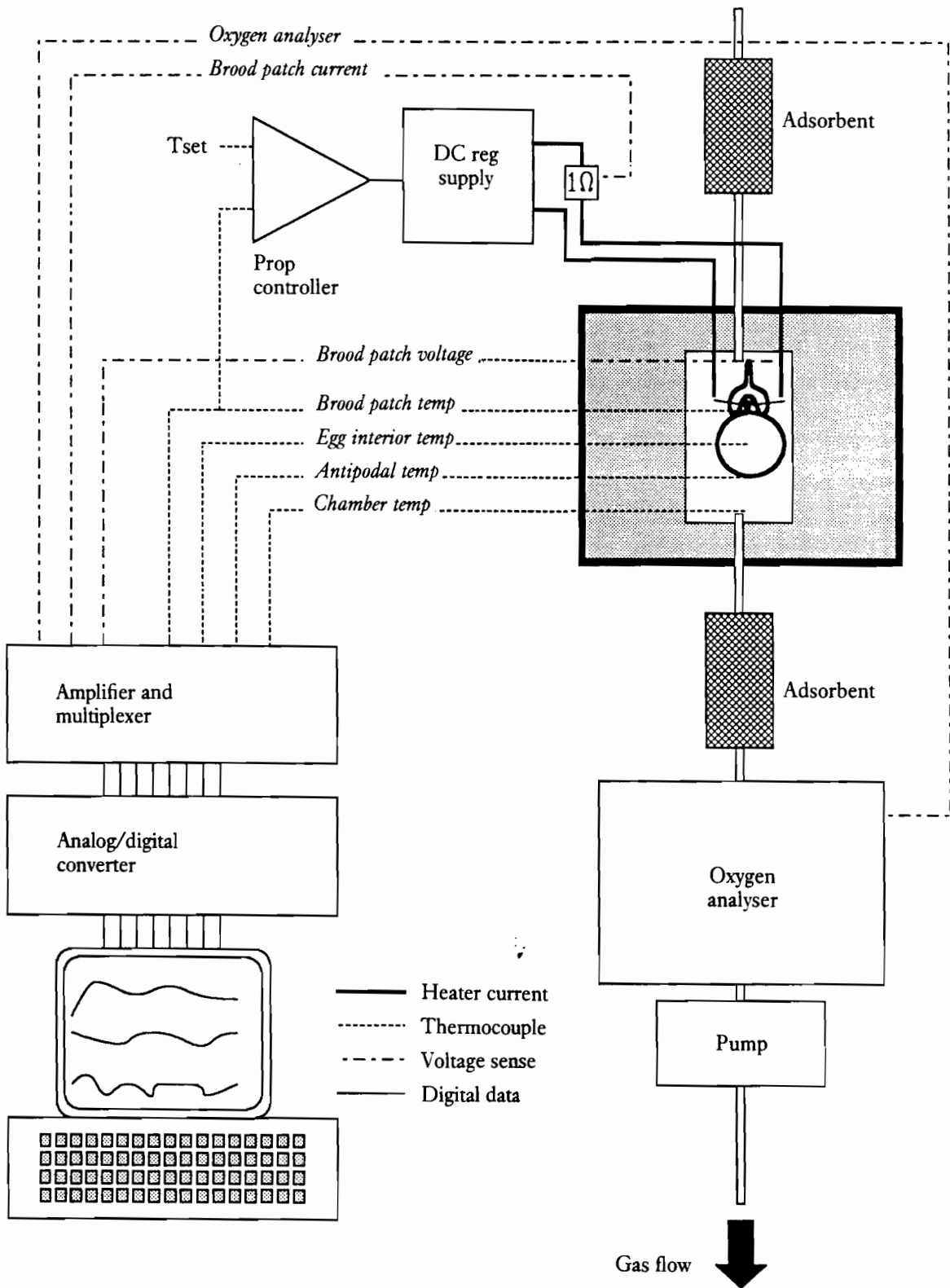


Fig. 9.3. Schematic diagram showing the components of the artificial brood patch system.

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characteristic of an egg at the start of incubation.

Application of equation 9.1 is straightforward: A 55 g fowl (*Gallus gallus*) egg cooling in still air has a time constant of 2492 s, which gives a thermal conductance (K) of 72.9 mW °C⁻¹ (Turner, 1985). For egg temperature in a single egg the most reasonable temperature is that actually regulated by an incubating parent, namely brood patch temperature (White & Kinney, 1974; Tøien, Aulie & Steen, 1986; Swart, Rahn & de Kock, 1987). Let us assume the bird keeps the brood patch at 40 °C in an environment of 30 °C, and that the brood patch covers 20% of the egg's surface. Equation 9.1 estimates that the parent must pass heat into the egg through its brood patch at a rate of 583 mW. By comparison, the numerical model predicts that for the same egg under the same conditions, the parental heat input is 244 mW. How much power actually is required? The actual heat requirement determined for unembryonated fowl eggs using the artificial brood patch system is 253 mW (Turner, 1990).

The reason the analogical approach overestimates energy costs is simple: it implies that the surface temperatures of a contact incubated egg are uniform (Fig. 9.4). However, the surface

temperature of a contact incubated egg declines as one goes from the brood patch to the surface antipodal to the brood patch (Fig. 9.4). Thus, the analogical approach predicts that the average surface temperature of a contact incubated egg is higher than it really is. Consequently, it will always overestimate the heat loss from the egg surface, and by inference, the parent's energy requirements for keeping the egg warm.

What about eggs that are larger or smaller than a 55 g fowl egg? The analogical approach suggests that the incubation conductance for contact incubation has the same scaling exponent as the thermal conductance of eggs cooling in air (Kendeigh, 1963), which is roughly 0.60 (Turner, 1985). The surface temperatures of eggs cooling in air are nearly independent of egg size (Turner, 1987), and the analogical approach predicts the same for contact incubated eggs. On the other hand, the numerical model predicts that larger eggs will have cooler surfaces than smaller eggs. The consequence is a smaller scaling exponent for the incubation conductance of contact incubated eggs (Fig. 9.5). This prediction applies only to unembryonated eggs: the problem of egg size and incubation energetics for eggs containing living embryos is discussed later.

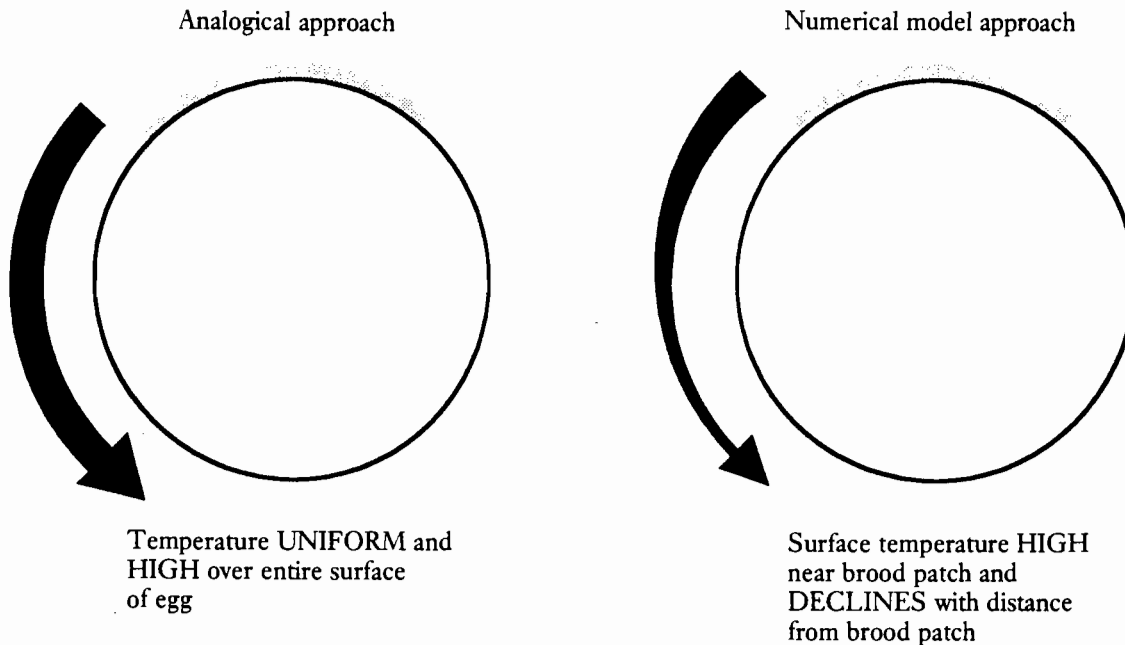


Fig. 9.4. How surface temperature is distributed in a contact incubated egg, as predicted by the analogical approach and by the numerical model approach.

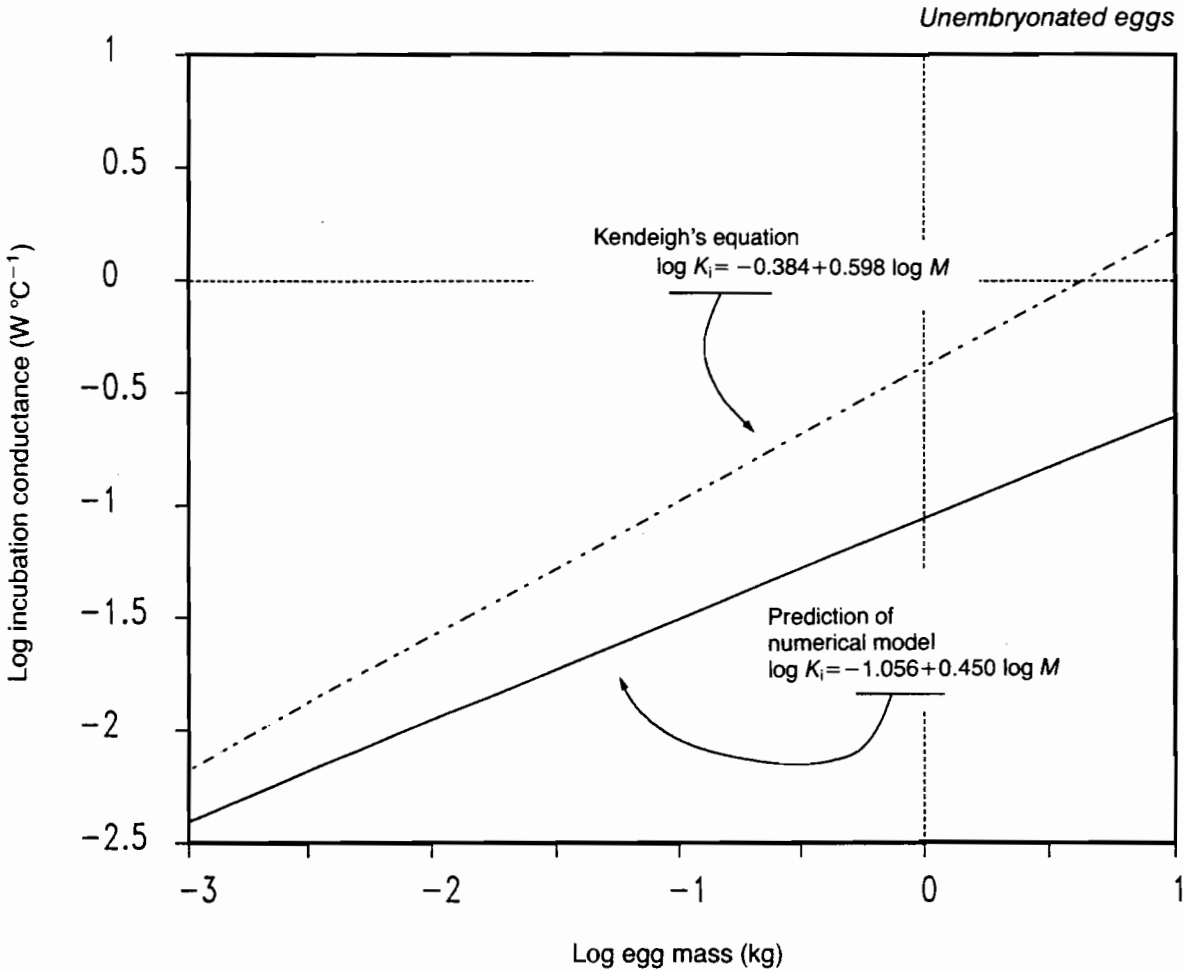


Fig. 9.5. The scaling of incubation conductance, K_i , defined as the heat input from the brood patch (W) required to keep brood patch temperature 1°C warmer than environmental temperature. Both scaling relationships assume the brood patch covers 15% of the egg's surface. *Solid line*: Scaling relationship predicted by the numerical model. *Dashed and dotted line*: Scaling relationship predicted by equation 9.1.

Case 2: Coverage of the egg by the brood patch

The factor $(1-c)$ in equation 9.1 predicts what effect brood patch coverage will have on the energy cost for contact incubating eggs. It is an intuitively sensible prediction. When the brood patch covers a small area of the egg, and there is much surface for the egg to lose heat from, the compensatory heat input from the brood patch must be large (Fig. 9.6). Conversely, at large coverages, when there is little surface area for the egg to lose heat from, the compensatory heat input from the brood patch is smaller (Fig. 9.6).

The numerical model makes a very different prediction (Fig. 9.6). At very small brood patch coverage, the heat input to the egg should be small and it should increase as brood patch

coverage increases. Once brood patch coverage passes a critical value (roughly 18% of the egg's surface area), energy expenditure should decline slowly as brood patch coverage increases further and for brood patch coverages of 10–25%, energy cost of incubation varies only slightly (Fig. 9.6). The effects of differing brood patch coverage on the energy cost for contact incubating unembryonated fowl eggs have been determined (Fig. 9.6). For brood patch coverages of 9%, 19% and 29%, the brood patch heat inputs are indistinguishable. This is consistent with the prediction of the numerical model.

The analogical approach has failed again because (as in case 1) it imposes inappropriate temperatures on the egg. The analogical approach presumes the egg surface to be of high and uniform temperature, and to be unaffected

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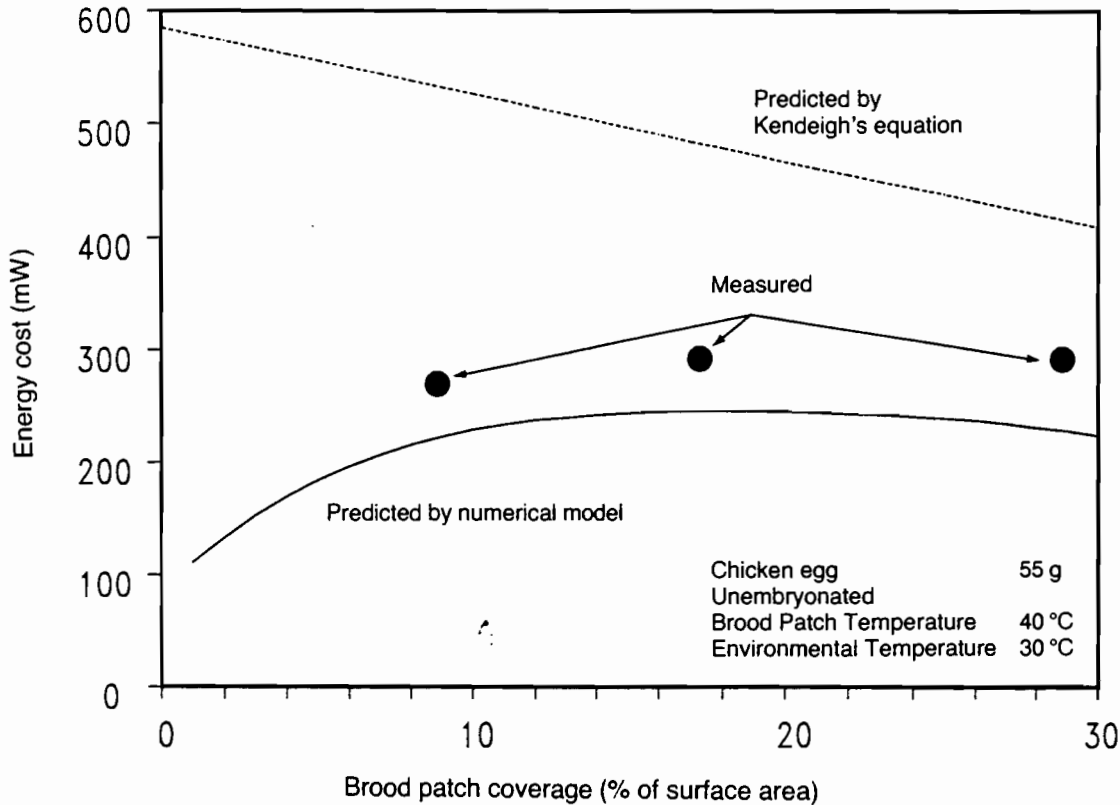


Fig. 9.6. The effect of brood patch coverage on the brood patch heat input for an infertile fowl egg. The brood patch temperature is kept 10 °C warmer than the surroundings. *Solid curve*: Relationship predicted by the numerical model. *Broken line*: Relationship predicted by equation 9.1. *Solid circles*: Mean measured values for 6 infertile fowl eggs at 9%, 19% and 29% coverage by an artificial brood patch. There is no significant difference between the three groups at $p = 0.05$.

by brood patch coverage. Heat loss from the egg (and hence parental energy cost) is determined solely by the reduction of exposed surface area that results from greater brood patch coverage. On the other hand, the numerical model shows that increased brood patch coverage warms the egg and its surface (Fig. 9.7). If, as brood patch coverage increases, surface temperature increases faster than surface area is reduced, the total loss of heat from the egg will increase. This appears to be the case for brood patch coverages smaller than 18% of the egg's surface. At brood patch coverages larger than 18%, temperature does not increase rapidly enough to offset the effect of the reduced surface area. Consequently, heat loss from the egg (and hence heat requirement from the parent) declines.

Case 3: The thermal interaction between incubating parent and living egg

A living embryo generates heat and circulates blood and these have the potential to influence

both the temperature of the egg and the energy costs to the incubating parent. The temperature of a contact incubated egg should be elevated by both the embryo's metabolism and its circulation (Fig. 9.8). Metabolism raises egg temperature by direct generation of heat. Circulation raises egg temperature by distributing heat from the brood patch more readily through the egg. With respect to the energy cost of incubation, metabolism opposes the flow of heat from the brood patch into the egg (Fig. 9.8). As metabolism of the embryo increases, this should drive the energy cost of incubation down. Circulation, on the other hand, facilitates the flow of heat from the brood patch into the egg (Fig. 9.8). As circulation increases, this should drive the energy cost of incubation up.

The net effect of metabolism and circulation will depend upon their relative importances to the egg's thermal energetics. For example, metabolism's effect may so dominate the egg's thermal energetics that circulation's effects are negligible. The analogical approach implicitly

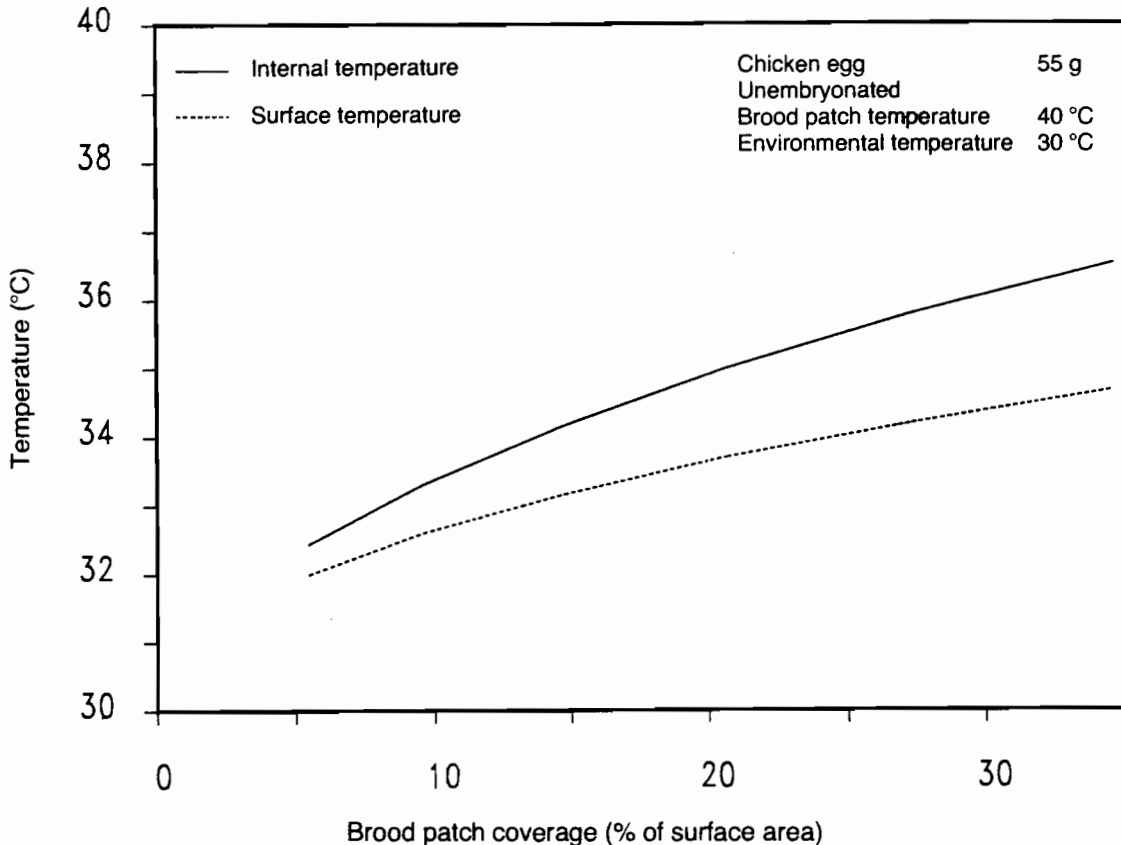


Fig. 9.7. The effect of brood patch coverage on internal temperature and surface temperature as predicted by the numerical model for a 55 g infertile fowl egg. Brood patch temperature is 40 °C. Environmental temperature is 30 °C. Temperatures are weighted averages for all interior nodes (weighted by node volume) and all surface nodes (weighted by surface area) not covered by the brood patch.

denies circulation any role in the energetics of contact incubated eggs. The embryo's circulation has little influence on the cooling rates, and hence the thermal conductances, of eggs cooling in air (Turner, 1987). By extension of the analogy implied in equation 9.1, circulation should then have little influence on the energetics of contact incubated eggs. The lumped conductance approach deals with embryonic metabolism and circulation more explicitly. Nevertheless, Ackerman & Seagrave (1984) conclude that temperature of a contact incubated egg is determined mainly by the embryo's metabolism, and that circulation has only a small effect. By contrast, the numerical model predicts that the influence of the embryo's circulation, not its metabolism, is the most important factor in the thermal energetics of contact incubated eggs.

It is worthwhile outlining how this conclusion is reached. The numerical model allows us to

'construct' eggs that have either circulation only, or metabolism only, or both metabolism and circulation, or neither. This enables one to evaluate how much influence either circulation or metabolism has. If embryonic metabolism dominates the egg's thermal energetics, and circulation is negligible, then a simulated egg with both metabolism and circulation, or a living egg (which also has both), should behave similarly to a simulated egg with *metabolism only* and *no circulation*. Conversely, if circulation is most important and metabolism is negligible, then a simulated egg with both metabolism and circulation, or a living egg, should behave similarly to an egg with *circulation only* and *no metabolism*.

Let us first consider temperatures of a simulated fowl egg, with the embryo just prior to internal pipping. The average internal temperature of the simulated egg with both metabolism and circulation should be roughly

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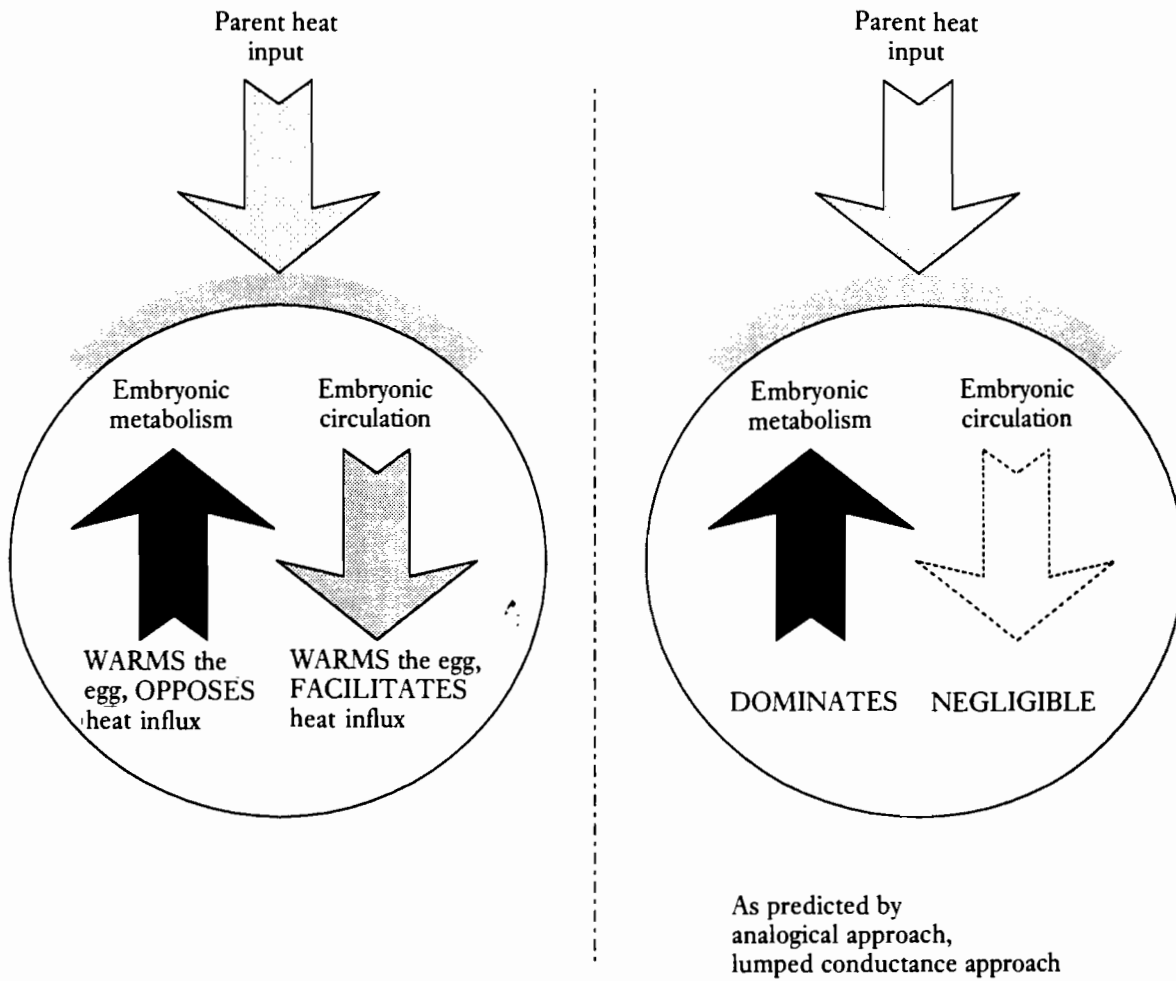


Fig. 9.8. How embryonic metabolism and circulation interact to influence egg temperature and brood patch heat inputs. Arrows represent heat flow vectors. *Left panel:* the effect of embryonic metabolism and circulation on temperature and parental heat input. *Right panel:* The analogical and lumped conductance approaches predict the effect of circulation to be negligible.

37 °C (Fig. 9.9). The temperature of the egg with circulation alone is similar to this, while the temperature of the egg with metabolism alone is not at all similar (Fig. 9.9). By the logic outlined above, the embryo's circulation, not its metabolism, appears to be the most important influence on the temperature of the contact incubated egg.

Turning now to the energy cost of incubation, a simulated egg with both metabolism and circulation should require heat from the parent at a rate of roughly 400 mW (Fig. 9.9). The parental contribution for a simulated egg with metabolism alone and no circulation is roughly 180 mW (Fig. 9.9). If the egg has only circulation and no metabolism, the parent's contribution is roughly 440 mW (Fig. 9.9). Again, the egg with circulation and metabolism is similar to

the egg with circulation alone, and is quite different from the egg with metabolism alone (Fig. 9.9). Again, we may infer that circulation's influence is stronger than that of metabolism.

The predictions just outlined may be tested experimentally by comparing living eggs (which have both metabolism and circulation) with killed eggs (which have neither). When a contact incubated egg is killed, it should cool, irrespective of whether circulation or metabolism dominates (Fig. 9.9). However, if circulation dominates, killing the egg should *reduce* the energy cost to the parent and if metabolism dominates, killing the egg should *increase* the energy cost (Fig. 9.9).

Using the artificial brood patch system, the brood patch heat inputs for chicken eggs containing living embryos with those containing kil-

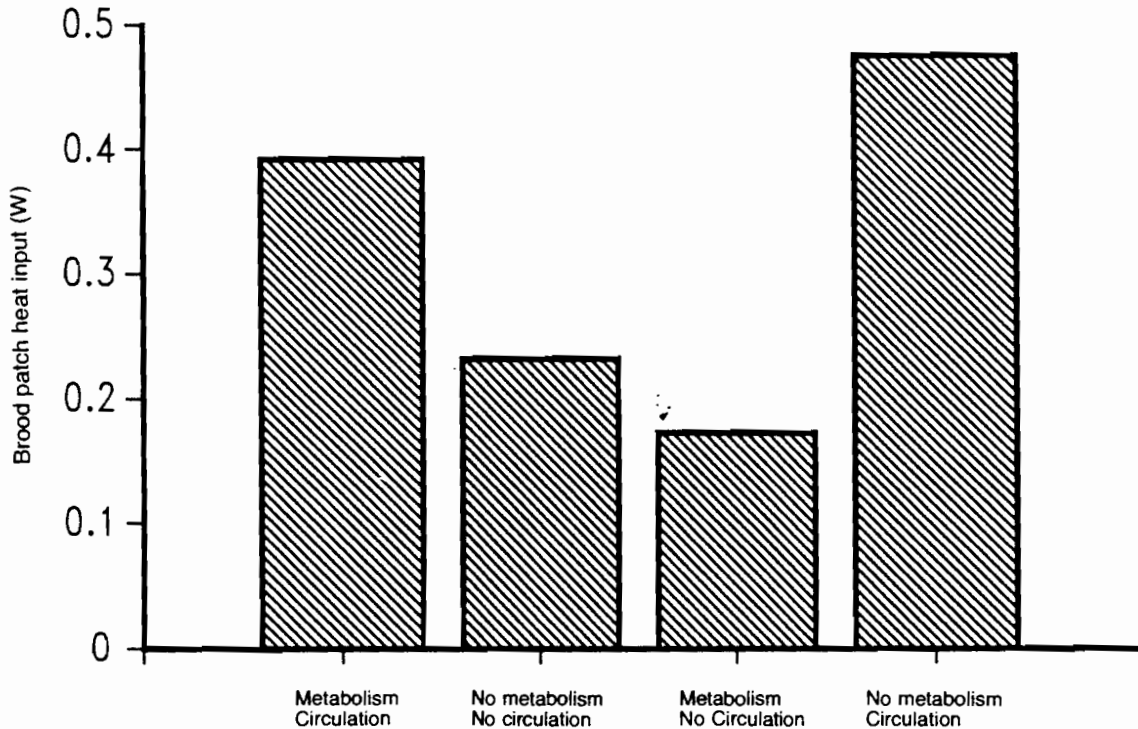
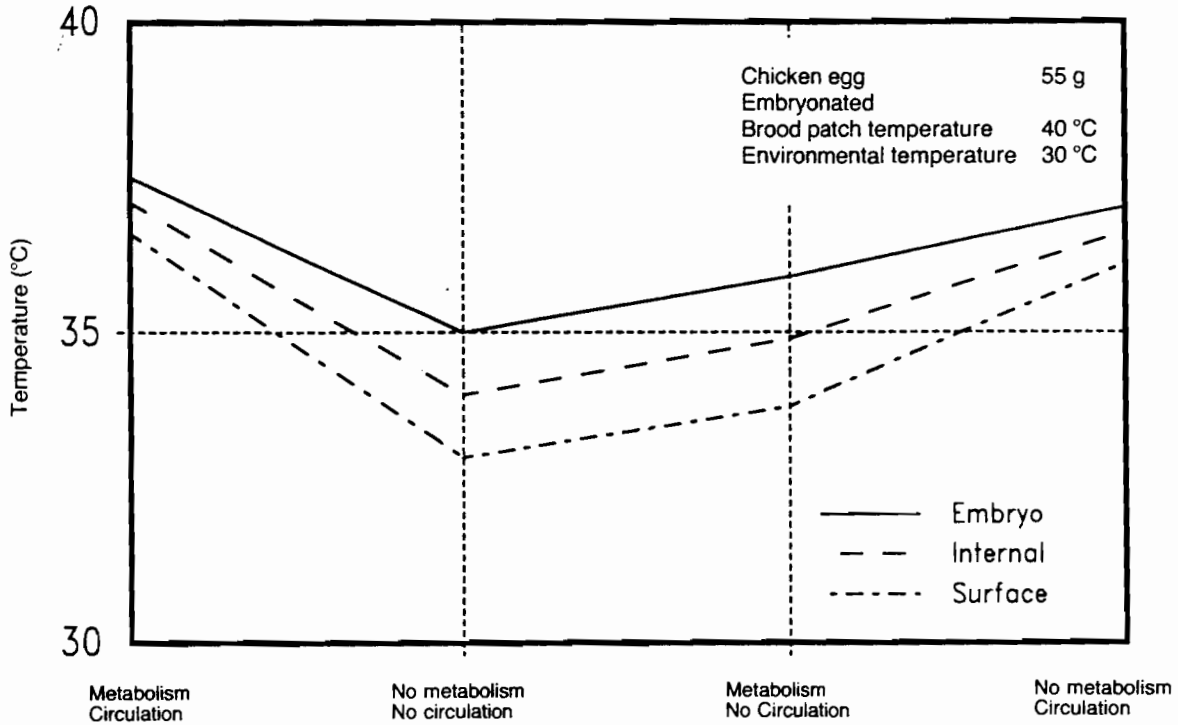


Fig. 9.9. The effects of embryonic metabolism and circulation on egg temperature and brood patch heat input as predicted by the numerical model. The egg is a 55 g fowl egg. The incubation age is just prior to internal pipping. The brood patch covers 15% of the egg's surface area. The brood patch temperature is 40 °C. The environmental temperature is 30 °C. The model considers four conditions: (1) Simulated egg, with metabolism and circulation; (2) Simulated egg, with metabolism and no circulation; (3) Simulated egg, with circulation and no metabolism; (4)

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Table 9.1. *Measured brood patch heat inputs, Q_i required to contact incubate embryonated fowl eggs, embryo heat inputs, Q_e and egg temperatures. Embryos are 1–4 days pre-pipping. Data from Turner (1990). Numbers are mean values for at least ten replicates.*

Type	Heat inputs		Temperatures (°C)		
	Q_e (mW)	Q_i (mW)	Brood patch	Embryo	Ambient
Living	138	403	39.3	35.8	29.9
Killed	0	322	39.6	33.8	30.1

led embryos have been compared (Turner, 1990; Table 9.1). The results are clear: killing the egg reduces the brood patch heat input (Table 9.1). A living egg requires roughly 400 mW from the parent to keep warm, almost exactly as predicted (Fig. 9.9). This is about 25% more than the brood patch heat required to keep a killed egg warm (Table 9.1). Compared to an unembryonated egg, a living egg requires about 40% more energy from the parent (Table 9.1). Clearly, it is circulation, not metabolism that is most influential in the thermal energetics of a contact incubated egg. This important finding cannot have been predicted by either the analogical approach or the lumped conductance approach.

One additional matter concerns the consequences of egg size. In case 1, equation 9.1 predicts a scaling exponent of 0.60 for incubation conductance (Fig. 9.5), while the numerical model predicts a smaller scaling exponent (0.44). The reason for the discrepancy lies in different predictions about egg size and surface temperature (Figs 9.4 & 9.10). Circulation, which distributes heat effectively through the egg, has the interesting effect of making temperatures of contact incubated eggs roughly uniform, irrespective of egg size (Fig. 9.10). Thus, the assumption that proved fatal for applying equation 9.1 to unembryonated eggs, i.e. size independent egg temperatures, is vindicated for mature embryonated eggs! The result is a scaling exponent for incubation conductance that is very close to that predicted by Kendeigh's analogical equation (equation 9.1; Fig. 9.11).

The intercepts of the respective equations still differ considerably, however (Fig. 9.11).

It is important to emphasise that this similarity of scaling exponents in no way vindicates Kendeigh's analogical equation. The similar scaling exponent applies only to eggs at the end of incubation (Fig. 9.11), and does not apply to earlier stages (Fig. 9.5). Second, the reason for the coincidence, high net transport of heat through the egg by circulation, is denied by the analogical approach. Third, equation 9.1 still overestimates the actual costs of incubation by nearly two-fold (Fig. 9.11).

Case 4: Incubation stage

During development of an avian embryo, both circulation and metabolic heat production inside the egg increase. The yolk sac membrane and the chorio-allantois have substantial amounts of blood circulating through them after the first third and half of incubation, respectively (Romanoff, 1960; Tazawa, 1980; Ar, Girard & DeJours, 1987). The embryo's major period of growth occurs in the second half of the incubation period (Hoyt, 1987), and during this time there are concomitant increases in heat production and circulation (Tazawa, 1980; Hoyt, 1987; Vleck & Vleck, 1987). Circulation, and secondarily, metabolism both influence the thermal energetics of mature contact incubated eggs (Case 3; Fig. 9.9; Table 9.1). Is this true throughout the embryo's incubation period, with its complicated variations of both metabolism and circulation?

Fig. 9.9 *contd*

Simulated egg, with neither circulation nor metabolism. *Top panel:* Average egg temperatures. *Solid line:* average embryo temperature. *Dashed line:* internal temperature. *Dashed and dotted line:* exposed surface temperature. *Bottom panel:* Brood patch heat inputs.

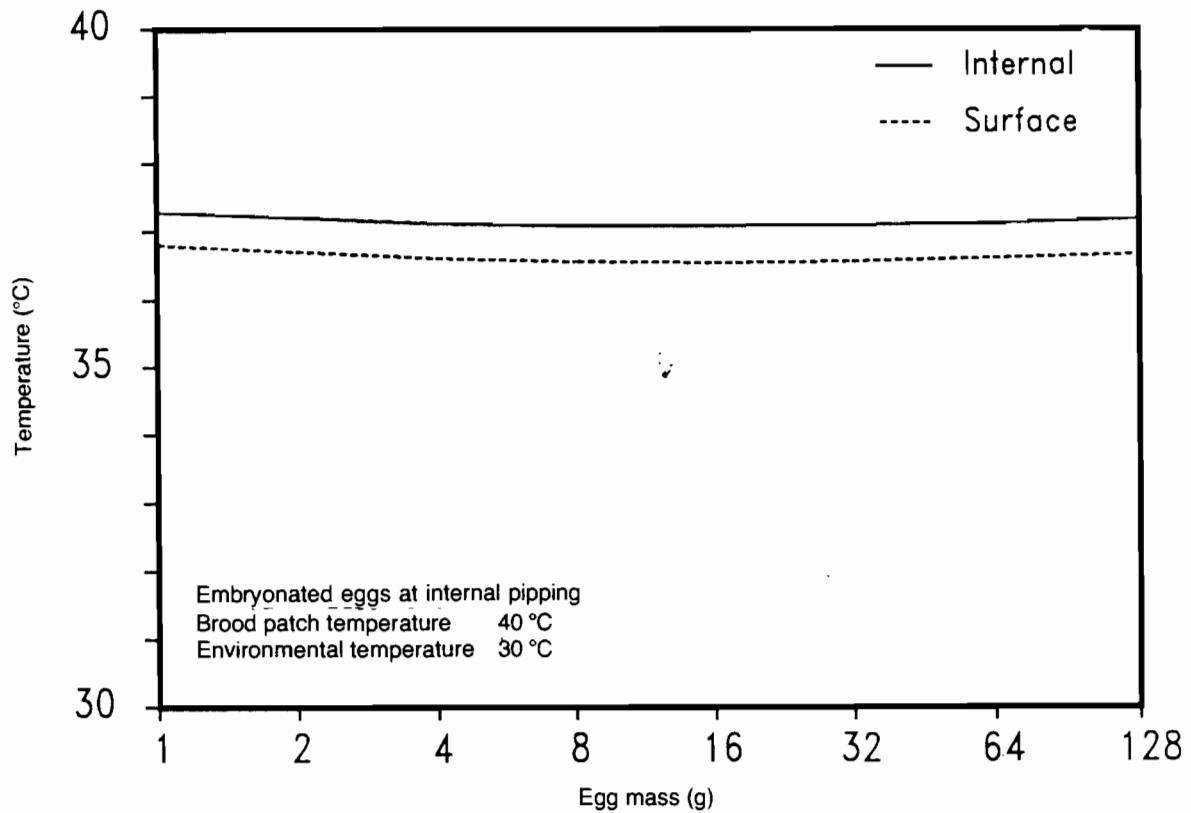
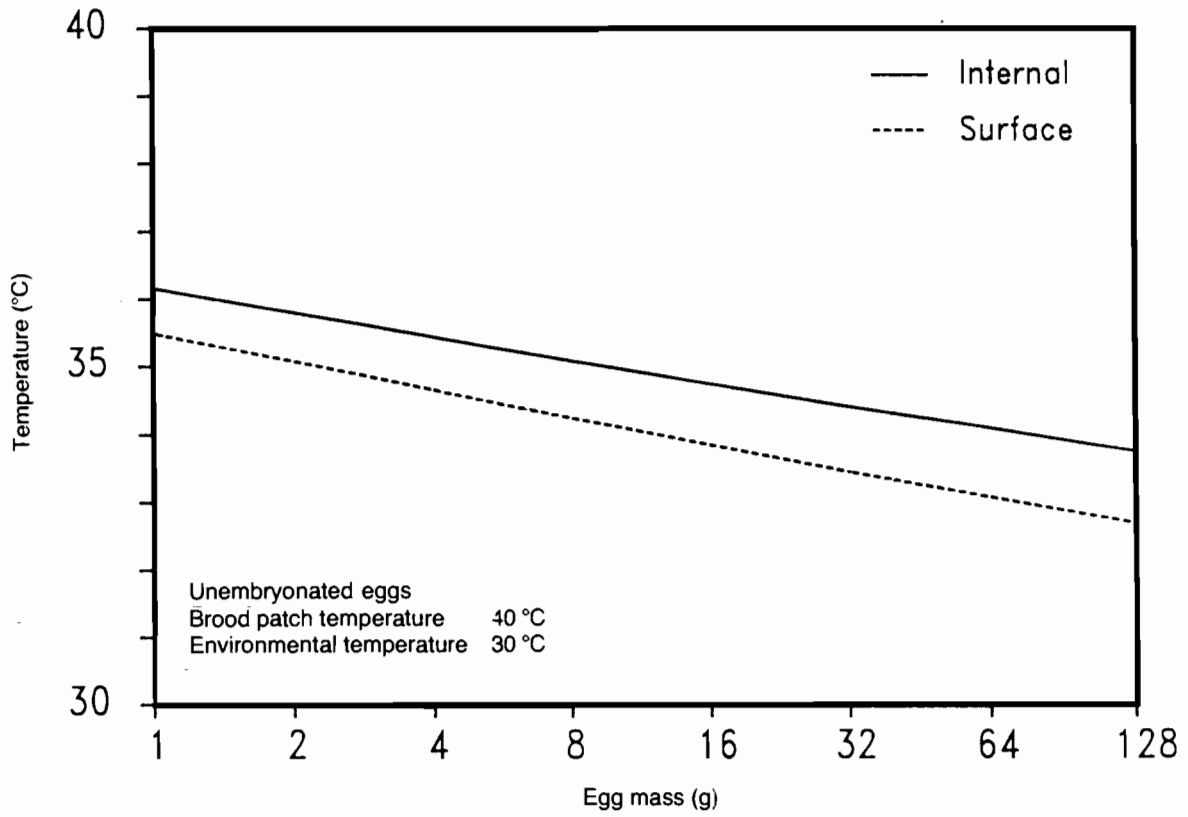


Fig. 9.10. The effect of egg size on temperatures of eggs as predicted by the numerical model. *Solid lines*: average internal temperature. *Broken lines*: average exposed surface temperature. The

THERMAL ENERGETICS OF AVIAN EGGS

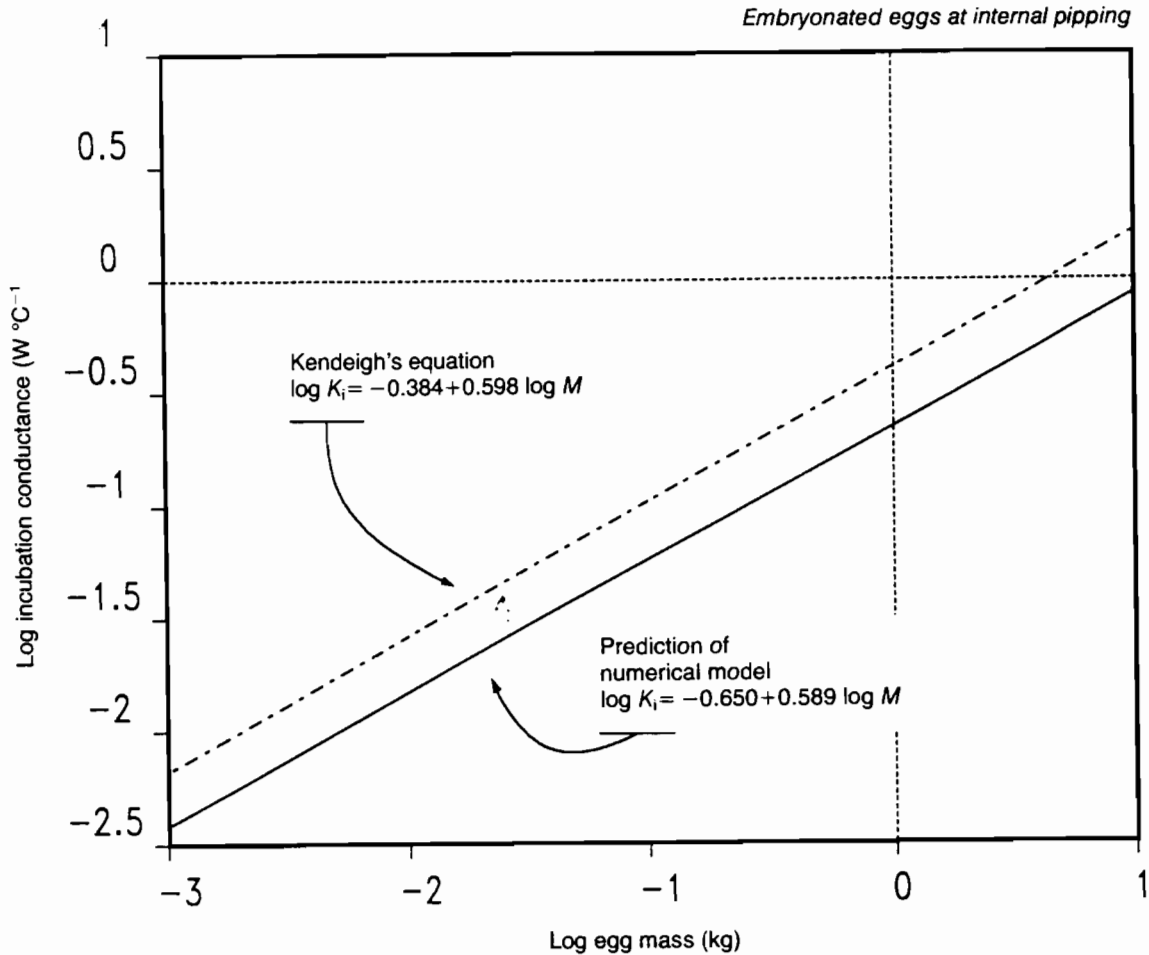


Fig. 9.11. The scaling of incubation conductance, K_i , as defined for Fig. 9.5, for fertile eggs just prior to internal pipping. The brood patch covers 15% of the egg's surface area. *Solid line:* Scaling relationship predicted by the numerical model. *Dashed and dotted line:* Scaling relationship predicted by equation 9.1.

The analogical approach makes no prediction of the course of temperature of a contact incubated egg during incubation. Equation 9.1 contains no term for incubation age and it implicitly assumes that the energy cost for contact incubation is constant through the incubation period. As it develops, the embryo generates more and more heat and presumably this will be heat the parent does not have to contribute. Consequently, the analogical approach implicitly predicts that energy demand on the parent should decline as incubation proceeds. The lumped conductance approach predicts that the egg warms during the incubation period (Ackerman & Seagrave, 1984). Furthermore, it

attributes this warming mostly to the embryo's increasing production of heat and has little explicit to say about fluxes of heat into the egg through the incubation period (Ackerman & Seagrave, 1984).

The numerical model predicts internal and surface temperatures of the egg (Fig. 9.12) that are similar to those predicted by Ackerman & Seagrave (1984). Average egg temperature is roughly steady for the first third of incubation, and increases sigmoidally thereafter (Fig. 9.12). However, the numerical model predicts an interesting course of embryo temperature during incubation. At the start of incubation, embryo temperature is very close to brood patch

Fig. 9.10 *contd*

brood patch covers 15% of the egg's surface area. The brood patch temperature is 40 °C. The environmental temperature is 30 °C. *Top panel:* temperatures of infertile eggs. *Bottom panel:* temperatures of fertile eggs just prior to internal pipping.

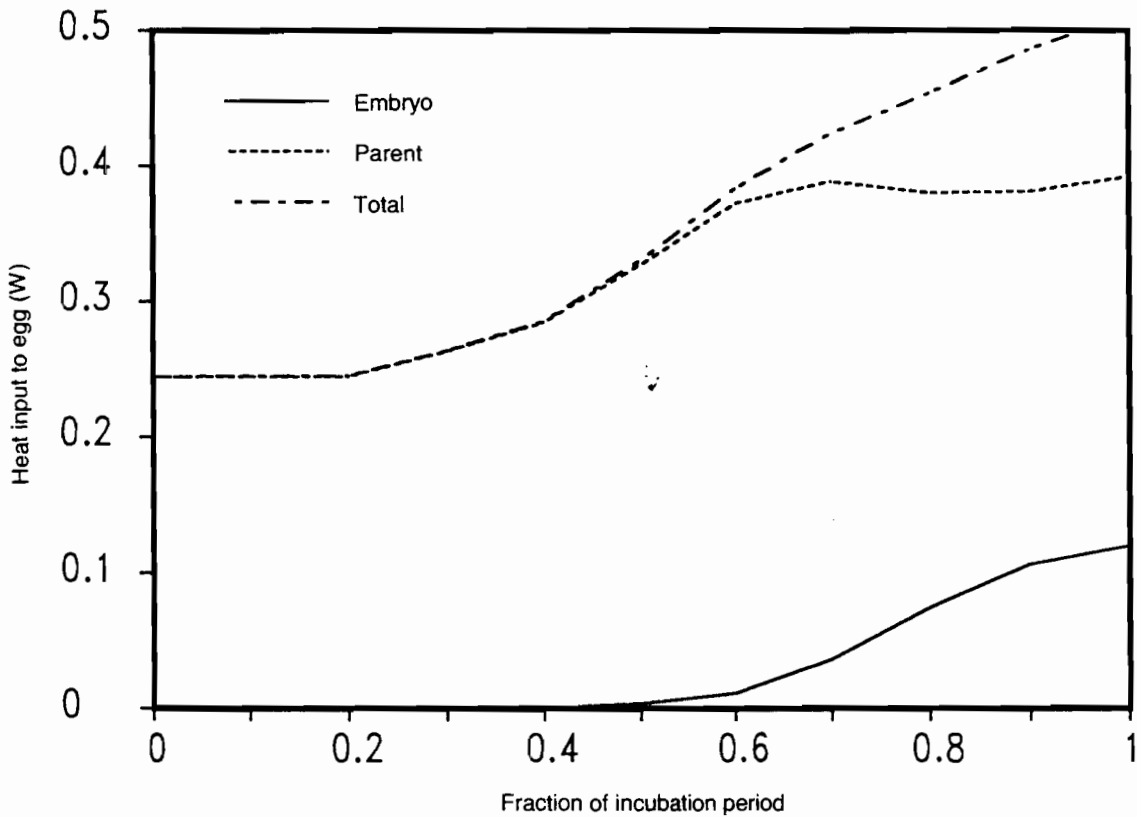
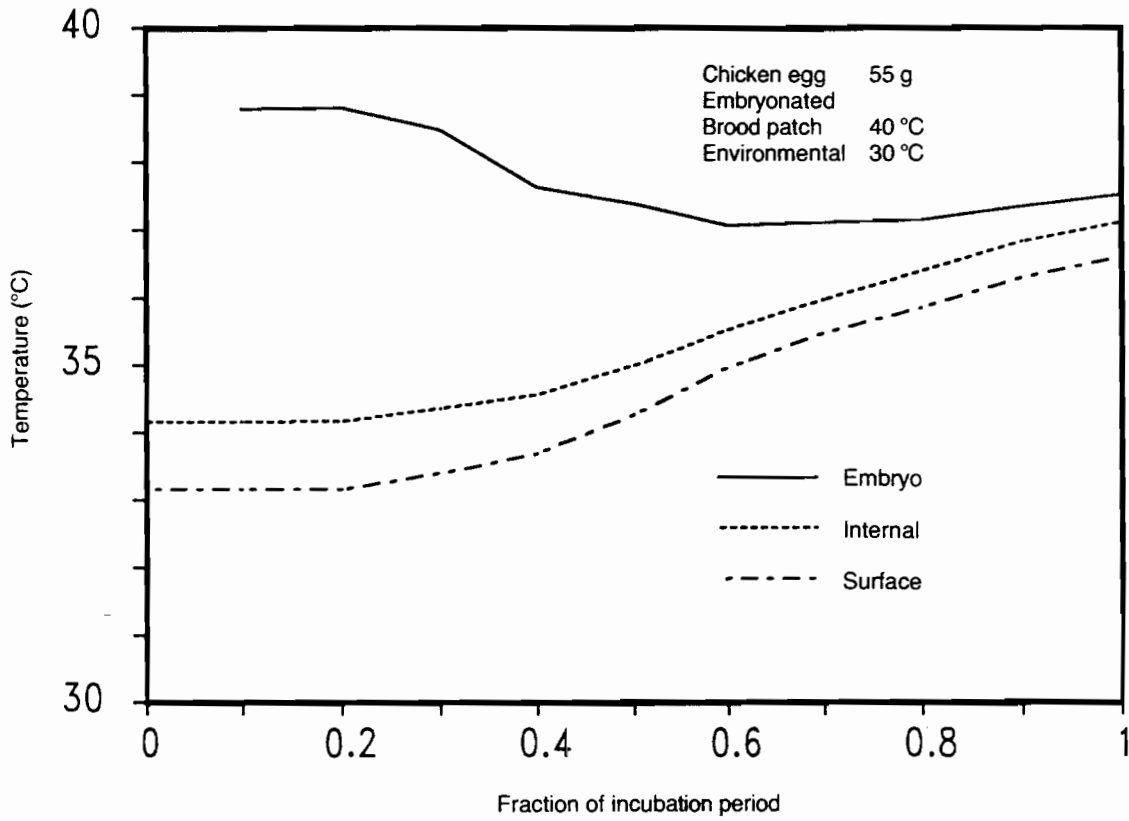


Fig. 9.12. The effect of incubation stage (defined as a fraction of incubation period ending with internal pipping) on egg temperature and heat input from brood patch, as predicted by the numeri-

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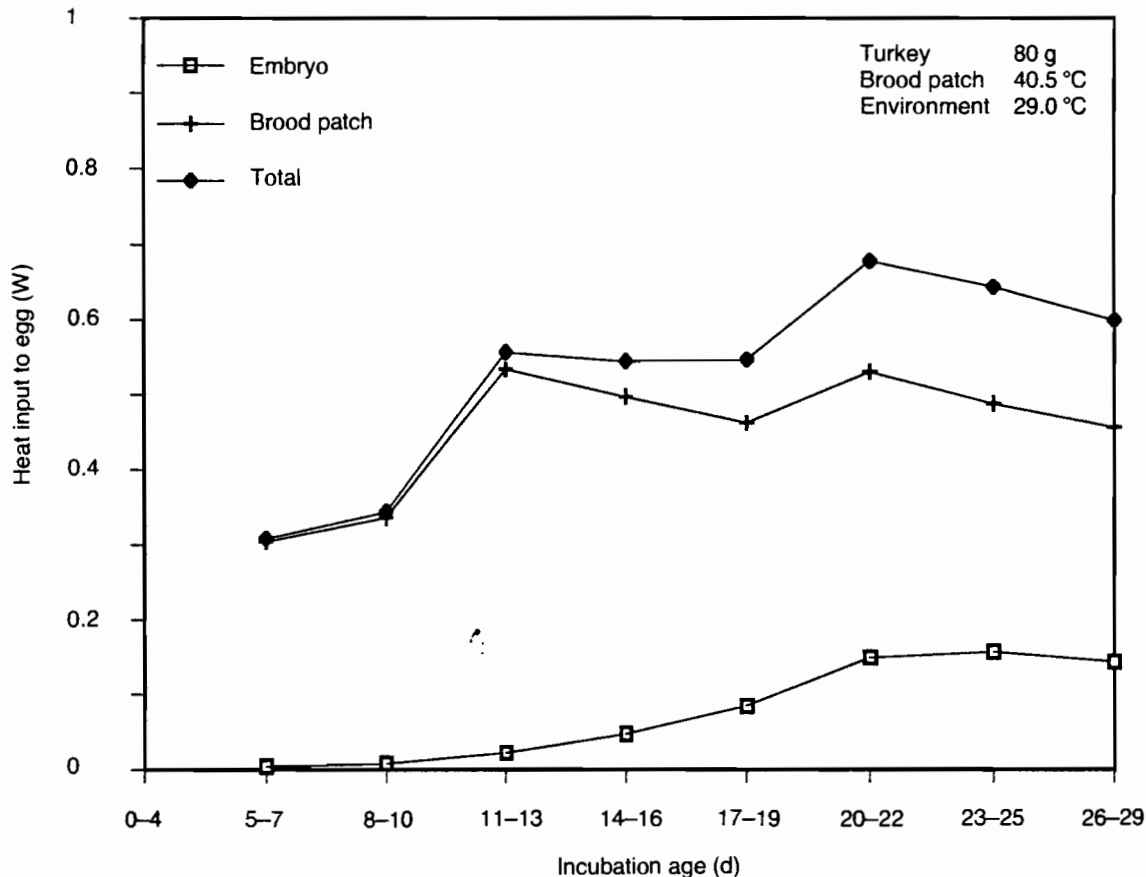


Fig. 9.13. Observed incubation energy budget observed for living turkey (*Meleagris gallopavo*) eggs as measured by the artificial brood patch system. The brood patch covers roughly 20% of the egg's surface area. The brood patch temperature averaged roughly 40.5 °C. The environmental temperature averaged roughly 29 °C. Symbols are means of 10–12 replicates in each age group. *Open squares*: embryo heat production. *Crosses*: brood patch heat production. *Open diamonds*: Total heat input to egg.

temperature, and as incubation proceeds, it declines.

The numerical model predicts that energy demand on the parent will increase through incubation, not decrease (Fig. 9.12). During the first 20% of incubation, there should be no change in parental energy cost, during roughly the middle third of incubation, parental energy cost should increase and during the last third of incubation, when the embryo's rate of heat production becomes significant, the parent's energy cost should be roughly constant (Fig. 9.12). Note especially that total heat input to the egg

(embryo's plus parent's) *increases in parallel* with increasing embryo metabolism (Fig. 9.12).

I measured incubation energy budgets for turkey (*Meleagris gallopavo*) eggs through the incubation period (Figs 9.13 & 9.14), and the results agree with the numerical model. During the initial third of incubation, heat input from the artificial brood patch is low (Figs 9.13 & 9.14). As incubation proceeds, heat input from the brood patch first increases, and steadies during the latter half of the incubation period (Figs 9.13 & 9.14). These changes cannot be attributed to some structural change in the egg,

Fig. 9.12 *contd*

cal model. The egg is a 55 g fowl egg. The brood patch covers 15% of the egg's surface area. The brood patch temperature is 40 °C. The environmental temperature is 30 °C. *Top panel*: Average egg temperatures. *Solid line*: embryo temperature. *Broken line*: internal temperature. *Dashed and dotted line*: Exposed surface temperature. *Bottom panel*: Heat input to the egg. *Solid line*: heat production by the embryo. *Broken line*: heat input from the brood patch. *Dashed and dotted line*: Total heat input to the egg (embryo plus brood patch).

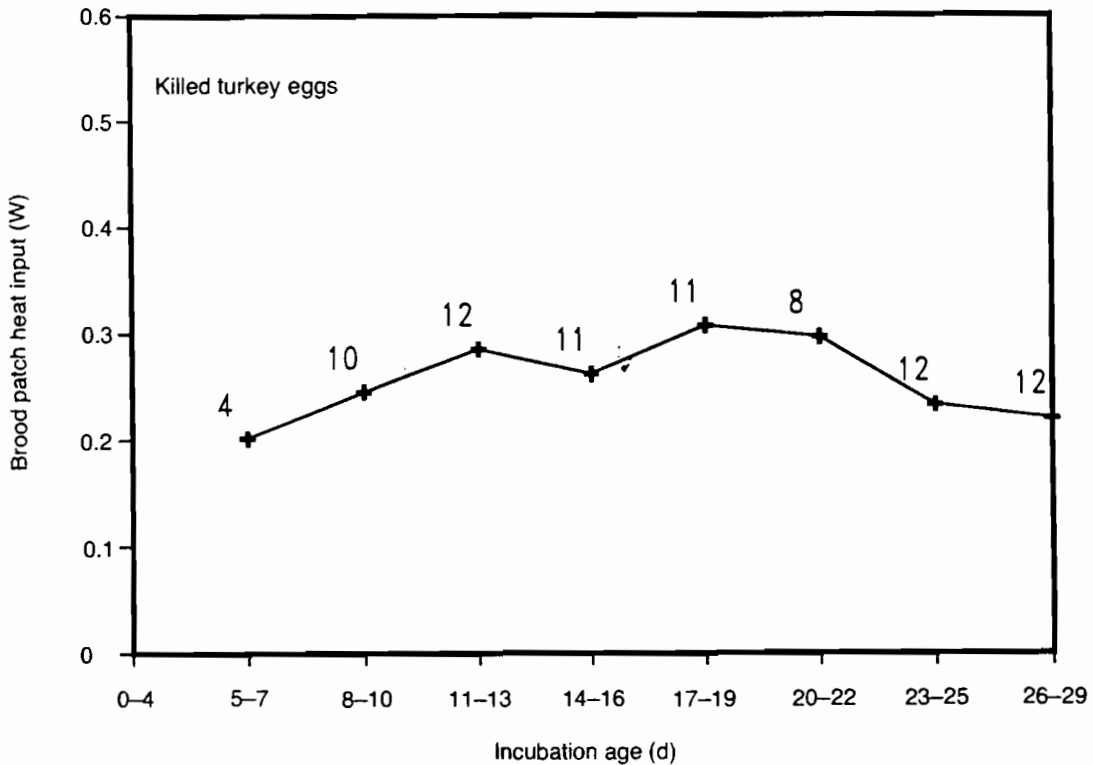
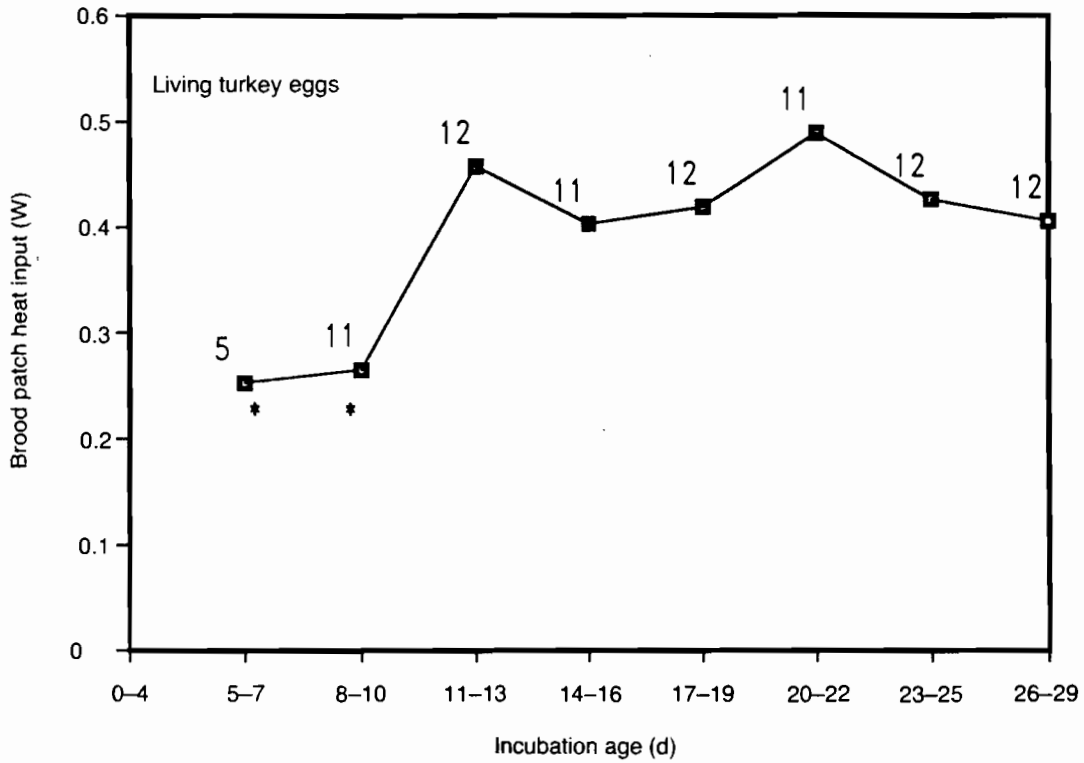


Fig. 9.14. Brood patch heat inputs for turkey eggs corrected to a brood patch temperature 10 °C warmer than environmental temperature. Symbols are the average for each age group. Number of replicates are indicated next to each point. *Top panel:* Brood patch heat inputs for living eggs. Asterisks indicate age groups that are significantly different ($p = 0.05$) from those without asterisks. *Bottom panel:* Brood patch heat inputs for the eggs once the embryos are killed.

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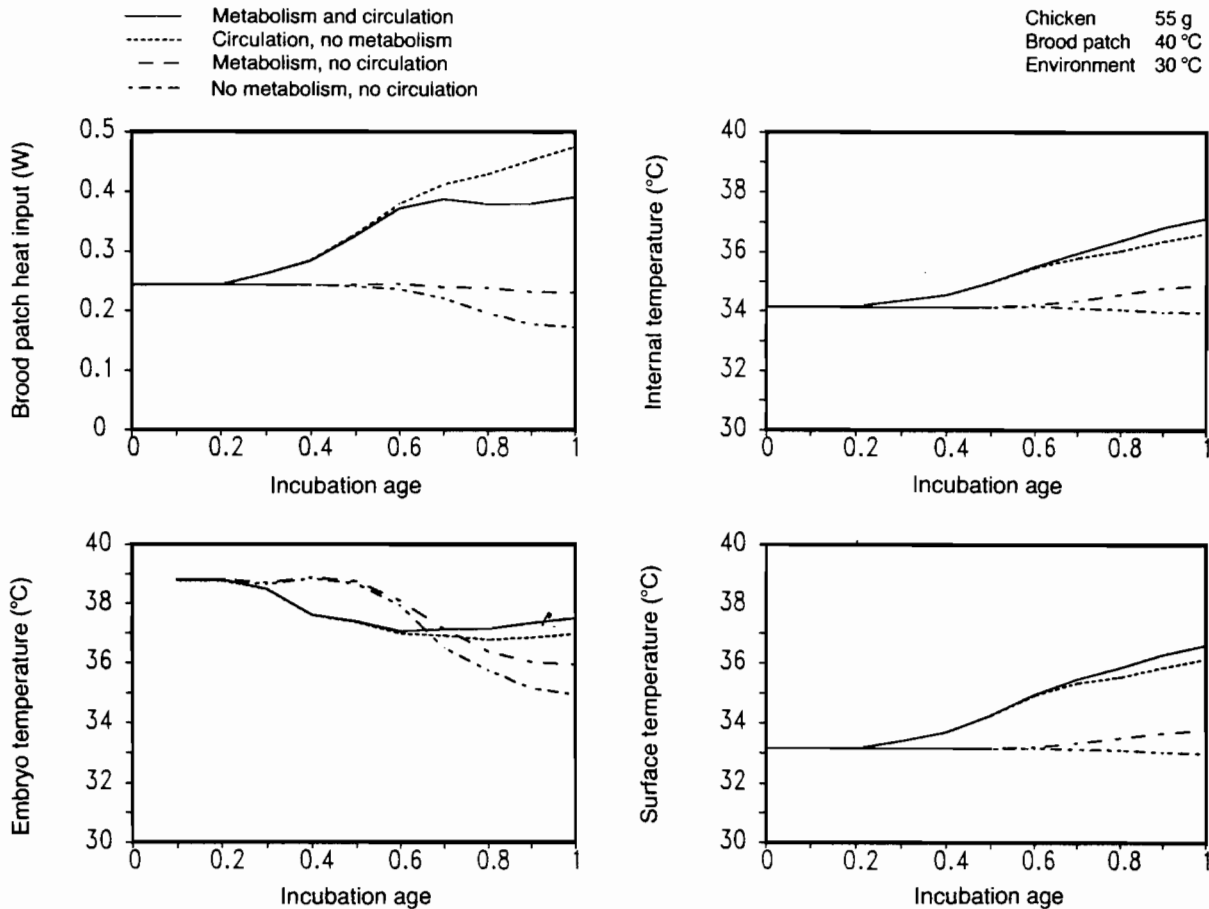


Fig. 9.15. The interaction of embryonic metabolism and circulation during the incubation period of a 55 g fowl egg, as predicted by the numerical model. The model considers four conditions: (1) Simulated egg, with metabolism and circulation (*solid line*); (2) Simulated egg, with metabolism and no circulation (*dashed line*); (3) Simulated egg, with circulation and no metabolism (*broken line*); (4) Simulated egg, with neither circulation nor metabolism (*dashed and dotted line*). The brood patch covers 15% of the egg's surface area. The brood patch temperature is 40 °C. The environmental temperature is 30 °C. *Top left panel*: The course of brood patch heat input. *Top right panel*: The course of average internal temperature. *Bottom left panel*: The course of average embryo temperature. *Bottom right panel*: The course of average internal egg temperature.

such as the development of the air cell, because the brood patch heat input for killed eggs is steady over the entire incubation period (Fig. 9.14). It is clear that the analogical approach cannot correctly predict how the energy costs for contact incubation change as the embryo develops. It is unclear whether the lumped conductance approach can do any better but the numerical model approach does clearly predict the pattern correctly.

The embryo's heat production and circulation influence the thermal energetics of the contact incubated egg in a complex way through incubation. Are there times when metabolism is more important than circulation or vice versa? By comparing simulated eggs with both metabolism

and circulation with simulated eggs that have either, or neither, we may sort out these complexities.

Circulation in the egg appears to be an important influence on the energy cost for incubation of the parent, irrespective of incubation stage (Fig. 9.15). For the first 60% of the incubation period, the energy cost for incubating an egg with circulation but no metabolism is nearly identical to the cost for incubating an egg with both whereas the cost for the egg with metabolism alone is dissimilar (Fig. 9.15). During the last third of incubation, the influence of embryonic metabolism is greater but nevertheless it is secondary to that of the circulation. If the simulated egg has only circulation, the

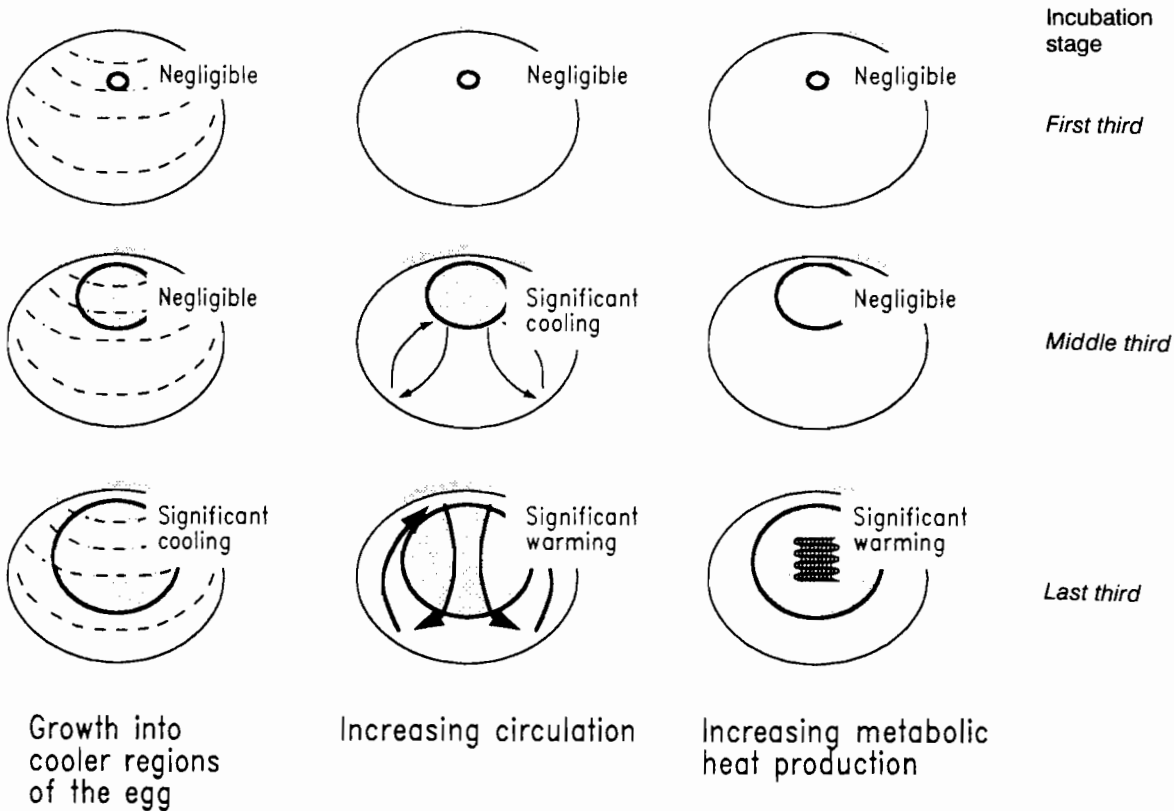


Fig. 9.16. Schematic diagram of the factors determining the course of embryo temperature in a fertile fowl egg as predicted by the numerical model. Full explanation is in the text.

parent's energy cost continues to rise through the entire incubation period but when the simulated egg has both metabolism and circulation, the parent's energy cost steadies through the last third of incubation (Fig. 9.15). Thus, metabolism appears to just compensate for the increased heat loss caused by the embryo's increasing circulation.

Circulation also appears to be most important in determining the egg's internal and surface temperatures (Fig. 9.15). The surface and interior temperatures of a simulated egg with circulation alone is similar to the simulated egg with both metabolism and circulation but when the simulated egg has metabolism alone, the temperatures are dissimilar (Fig. 9.15). While both the lumped conductance approach and the numerical model approach predict surface and interior egg temperatures that increase through incubation, it should be emphasised that the reasons for the similarity are very different: metabolism for the former, and circulation for the latter.

The predicted decline of average embryo temperature through incubation has a complex

explanation, involving the interplay of three factors: the position of the embryo in the egg, circulation, and metabolism (Fig. 9.16). The embryo usually occupies the upper portion of the egg, which happens to be warmer because it is closer to the brood patch. As the embryo grows, it cannot help but grow into cooler regions of the egg (Fig. 9.16). The consequence, even for an egg with neither circulation nor metabolism, is an average embryo temperature that cools as the embryo grows (Fig. 9.15). The major influence of embryo position, as shown by temperatures of the egg with neither circulation nor metabolism, occurs during the last third of the incubation period (Figs 9.15 & 9.16).

Circulation makes its mark on the course of embryo temperature from the time it begins to increase substantially, after the first third of incubation (Tazawa, 1980; Figs 9.15 & 9.16). Its influence on embryo temperature is in two phases. In the middle third of incubation, circulation cools the embryo, mostly because blood is flowing between the embryo and the membranes at the cooler surface of the egg (Fig. 9.15). In the last third of incubation, circulation

appears to warm the embryo. This is mainly a secondary effect of the overall warming of the egg elicited by the circulation. The influence of metabolism on embryo temperature is secondary to, and moderates, the effects of circulation. With metabolism, the embryo is slightly warmer than it would be without but this is only significant in the last third of the incubation period (Figs 9.15 & 9.16).

Case 5: The effect of ambient temperature

Clearly, the lower the ambient temperature, the greater will be the rate of heat loss from the exposed surface of the egg, and the greater must the rate of heat input be from the brood patch to balance this loss. According to the analogical approach, the energy cost to the parent for incubation is a linear function of the difference between egg temperature and environmental temperature (equation 9.1). Where environmental temperature and egg temperature are equivalent, the parent's energy cost should be nil.

The numerical model also predicts that the energy cost for incubation is a linear function of environmental temperature (Fig. 9.17). However, the environmental temperature at which parental energy cost is nil is lower than brood patch temperature. Furthermore, the relative thermal importance of circulation and metabolism vary with ambient temperature in some complex ways.

Circulation and metabolism affect energy cost in two ways. If an egg has neither heat production nor circulation, parental energy costs are nil when environmental and brood patch temperatures are equal (Fig. 9.17), as predicted by equation 9.1. When circulation alone is present, this still is true, but now the egg's incubation conductance is greater, i.e. circulation has increased the energy *gain* for incubation (Fig. 9.17). Energy cost at any temperature (except where $T_e = T_b$) is, therefore, greater than it would be if circulation were absent. When metabolism alone is present, the environmental temperature at which parental energy cost is nil is now less than brood patch temperature (Fig. 9.17). Also, energy cost at any temperature is less (except where the egg must be cooled, i.e. $Q_c < 0$) than it would be if metabolism were absent (Fig. 9.17). Metabolism has changed the egg's energy *offset* for incubation.

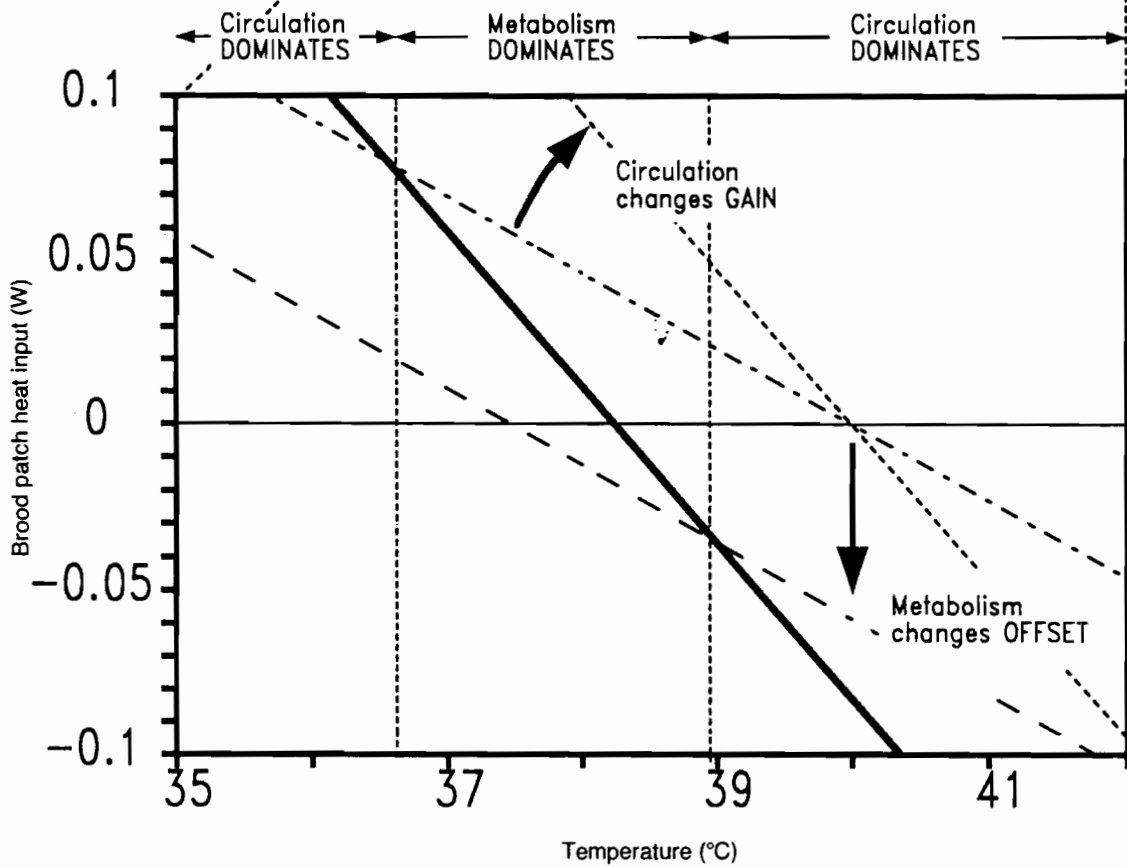
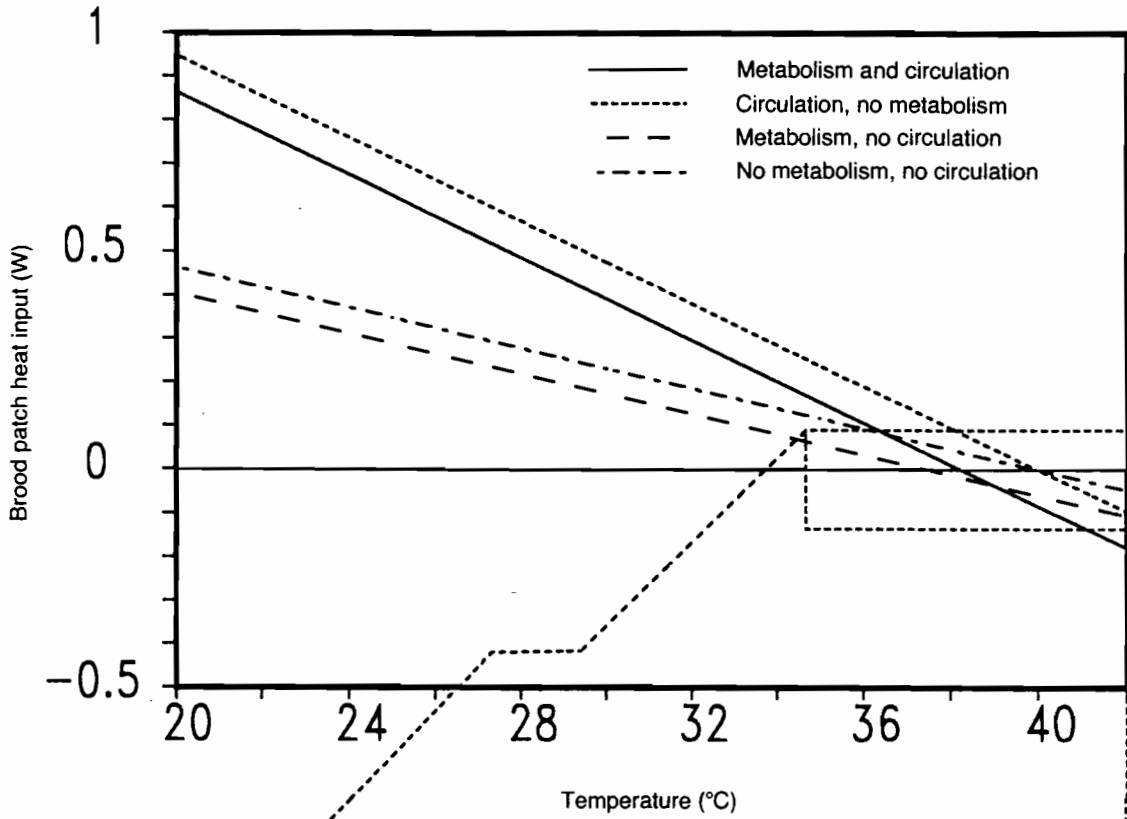
When both circulation and metabolism are

present, they independently affect both gain and offset of the energy balance of the egg during incubation: the consequence is a complex change in the thermal physiology of the egg at environmental temperatures close to brood patch temperature (Fig. 9.17). At an environmental temperature of 36.7 °C the opposing effects of metabolism and circulation exactly balance. At this temperature, removing both circulation and metabolism (equivalent to killing a living egg) should have no effect whatsoever on the parent's energy cost for incubation (Figs 9.17 & 9.18). When environmental temperature is less than 36.7 °C, killing the egg reduces the energy cost of incubating it, i.e. circulation dominates over metabolism and the lower the environmental temperature, the more circulation will dominate (Fig. 9.18).

At environmental temperatures exceeding 39.0 °C the parent must now dissipate heat to incubate the egg. More heat must be dissipated for an egg with circulation and metabolism than is required for an egg with metabolism only (Fig. 9.17). Thus, at high temperatures, circulation again dominates the egg's thermal energetics. Only from 36.7–39.0 °C, a range of 2.3 °C, can the metabolic rate of the embryo be said to dominate the egg's thermal energetics. Within this range, the closer environmental temperature approaches brood patch temperature, the more metabolism will dominate (Fig. 9.18).

Experimental measurements show results virtually identical to the predictions of the numerical model. As ambient temperature declines, the parental energy cost increases linearly (Fig. 9.19). The incubation conductance for the living egg is higher than it is for the killed egg. The energy offset for incubating a living fowl egg is negative with respect to that of a killed egg (Fig. 9.19). When environmental temperature is 35.5 °C, the contrary effects of metabolism and circulation balance (Figs 9.19 & 9.20). At cooler environmental temperatures, circulation dominates the incubated egg's thermal energetics (Figs 9.18 & 9.20). Once environmental temperature exceeds 38.5 °C, the extrapolated results show the parent must *dissipate* heat to incubate the egg and warmer environments should again make circulation important (Fig. 9.17).

Environmental temperature dramatically affects the thermal physiology of the contact incubated egg. At most environmental temperatures, embryonic circulation is the most



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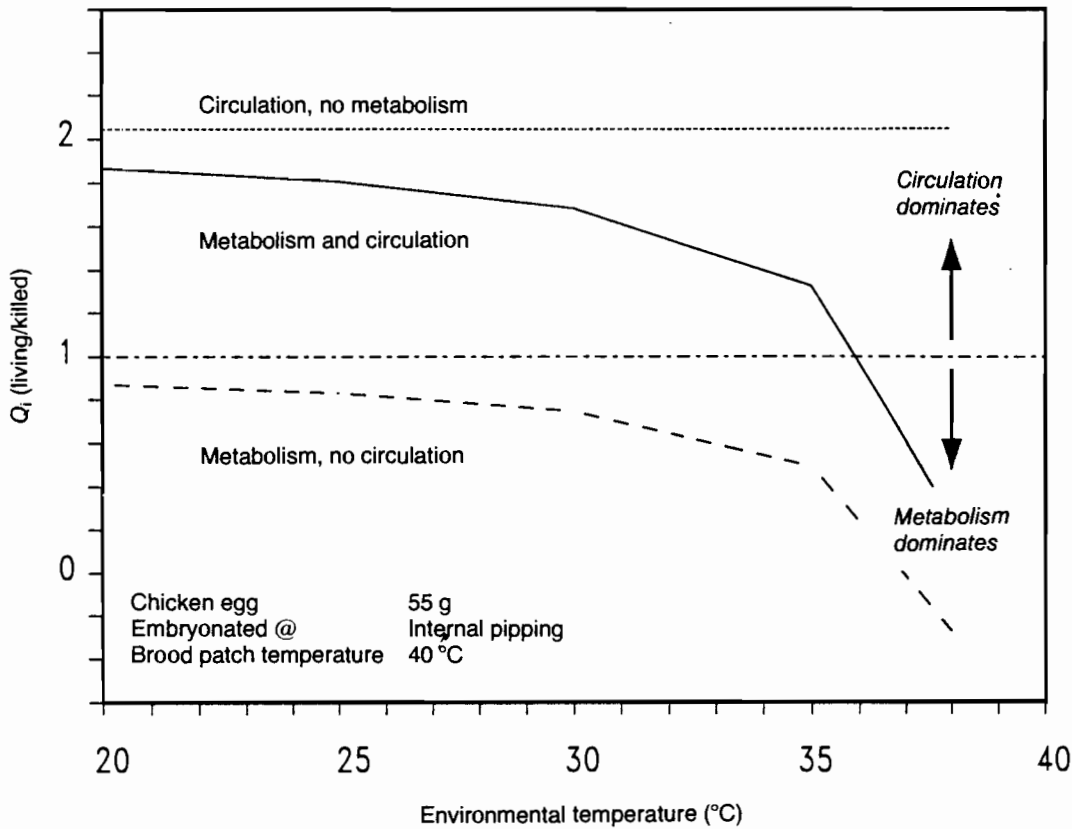


Fig. 9.18. The ratio of brood patch heat inputs (Q_i) for simulated eggs when metabolism dominates (metabolism, no circulation), when circulation dominates (circulation, no metabolism) and when both are present (metabolism and circulation), and its variation with ambient temperature. When the ratio is unity, the effects of circulation and metabolism offset one another.

important influence. But in a narrow range of environmental temperatures close to brood patch temperature, embryonic metabolism comes to the fore. No such thing is seen in convectively incubated eggs. These effects of ambient temperature have a straightforward explanation: as environmental temperature increases, egg temperature increases, and the egg becomes more uniform in temperature (Fig. 9.21). Circulation requires temperature gradients to transport heat. As increased environmental temperature makes temperature

gradients inside the egg disappear, then circulation will become less and less capable of altering flows of heat in the egg. This will leave metabolism as the only factor capable of influencing the egg's thermal energetics.

These results make it noteworthy that the simulations by Ackerman & Seagrave (1984) typically assume an air temperature in the nest only a few degrees less than brood patch temperature. This may partly explain why the lumped conductance approach and the numerical model approach come to such radically different con-

Fig. 9.17. Effect of environmental temperature on the brood patch heat input for incubating a 55 g fowl egg just prior to internal pipping. The model considers four conditions: (1) Simulated egg, with metabolism and circulation (*solid line*); (2) Simulated egg, with metabolism and no circulation (*dashed line*); (3) Simulated egg, with circulation and no metabolism (*broken line*); (4) Simulated egg, with neither circulation nor metabolism (*dashed and dotted line*). The brood patch covers 15% of the egg's surface area. The brood patch temperature is 10 °C. *Top panel*: Effect over the environmental temperature range 20–42 °C. *Bottom panel*: magnified picture of top panel from 35–42 °C, showing in more detail the complex changes in brood patch heat input at environmental temperatures near the brood patch temperature. Also, the independent effects of embryonic metabolism and circulation on the brood patch heat input are shown.

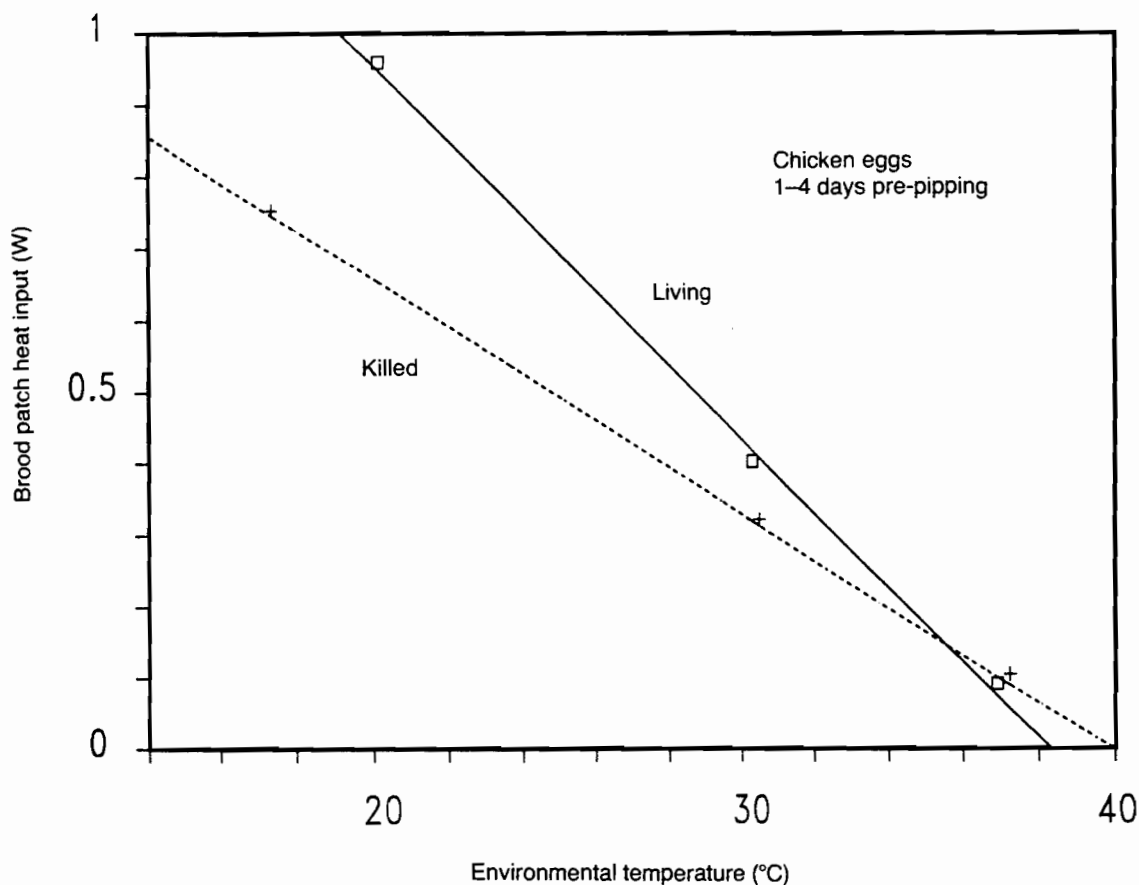


Fig. 9.19. Brood patch heat inputs experimentally measured for incubating fowl eggs at various environmental temperatures. Brood patch temperature is maintained at 40 °C. Symbols indicate means for groups of eggs. *Open squares*: Living fowl eggs, 1–4 days prior to external pipping. *Crosses*: Eggs after they have been killed. Lines indicate least-squares best fit to the means.

clusions regarding circulation. It cannot explain all the discrepancy, however, for even at environmental temperatures as low as 35 °C, the numerical model and experimental results show circulation to be at least as important as metabolism (Figs 9.19 & 9.20). It is likely that the three-node model of the thermal energetics of the egg (Ackerman & Seagrave, 1984) has somehow simplified away one of the most important thermal properties of a contact incubated egg: the influence of the embryo's circulation.

Discussion

The problem of how to estimate the energy cost of incubating eggs has been approached in many imaginative ways (Grant, 1984). Most of these approaches have involved simplified analyses of heat exchange between an egg and its incubating parent. It now appears that these approaches have not been adequate for the problem. For

example, the analogical approach of Kendeigh (1963), however appealingly simple or broadly applied, fails to predict accurately virtually any attribute of the energetics of contact incubation. The lumped conductance approach, even though it is more physically realistic, appears to simplify away some interesting, even fundamental, attributes of contact incubation. It is also clear that the energetics of contact incubation need to be analysed as the complex problem it really is. The numerical model approach accounts for this complexity and is able to successfully predict many attributes of contact incubation.

The importance of the embryo's circulation is one striking, and heretofore unappreciated, feature of contact incubation. Almost universally, the embryo's metabolism has been regarded as the most important influence on the thermal energetics of contact incubated eggs (Drent, 1970; Ackerman & Seagrave, 1984.

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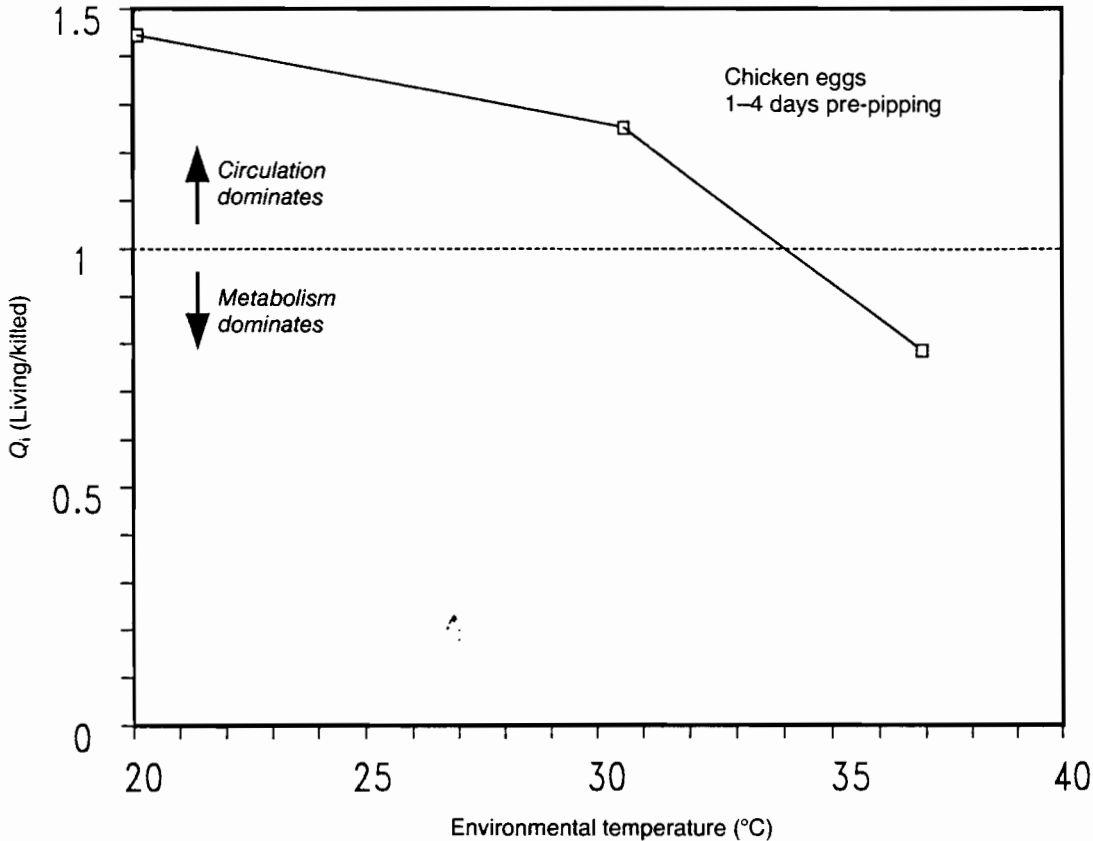


Fig. 9.20. Ratio of brood patch heat inputs experimentally measured for living fowl eggs, 1–4 days prior to internal pipping, and for eggs after they have been killed. Brood patch temperature is maintained at 40 °C. When the ratio is unity, the effects of circulation and metabolism offset one another.

Grant, 1984). This is not generally true: except for a narrow range of environmental temperatures, embryonic circulation, not metabolism, plays the dominant role in the egg's temperatures and in the energy cost to the incubating parent for incubation. The failure to appreciate this has fostered many notions about incubation energetics that are manifestly false, e.g. that costs to the parent should decrease as the embryo grows and produces more heat. When modelled in appropriate detail, and when measured in living eggs, the opposite appears to be true.

Both the analogical approach and the lumped conductance approach have overlooked the important role of embryonic circulation for the same reason, although their respective paths to that reason differ. It is informative to explore what this reason is. The analogical approach has presumed contact incubated eggs to behave essentially as convectively incubated eggs. The developing circulation of the embryo has little influence on the thermal conductance of a con-

vectively incubated egg (Turner, 1987) because convectively incubated eggs are nearly isothermal (Sothelard *et al.*, 1987; Turner, 1987): the internal temperature gradients needed for circulation to transport heat simply are not there. The lumped conductance approach has missed the importance of circulation for the same reason. In varieties of this approach which presume the egg to be a single node (Walsberg & King, 1978*a,b*), an isothermal egg is axiomatic: nodes are, by definition, isothermal. Where the egg is distributed into a few nodes (Ackerman & Seagrave, 1984) temperature variation within the simulated egg conceivably could arise. Nevertheless, Ackerman & Seagrave's (1984) typical simulation assumes nest temperatures high enough to possibly render the egg isothermal. Again, because the temperature gradients necessary for circulation to transport heat are not there, circulation will not emerge as an important factor in these simulated eggs.

Nevertheless, naturally incubated eggs sustain

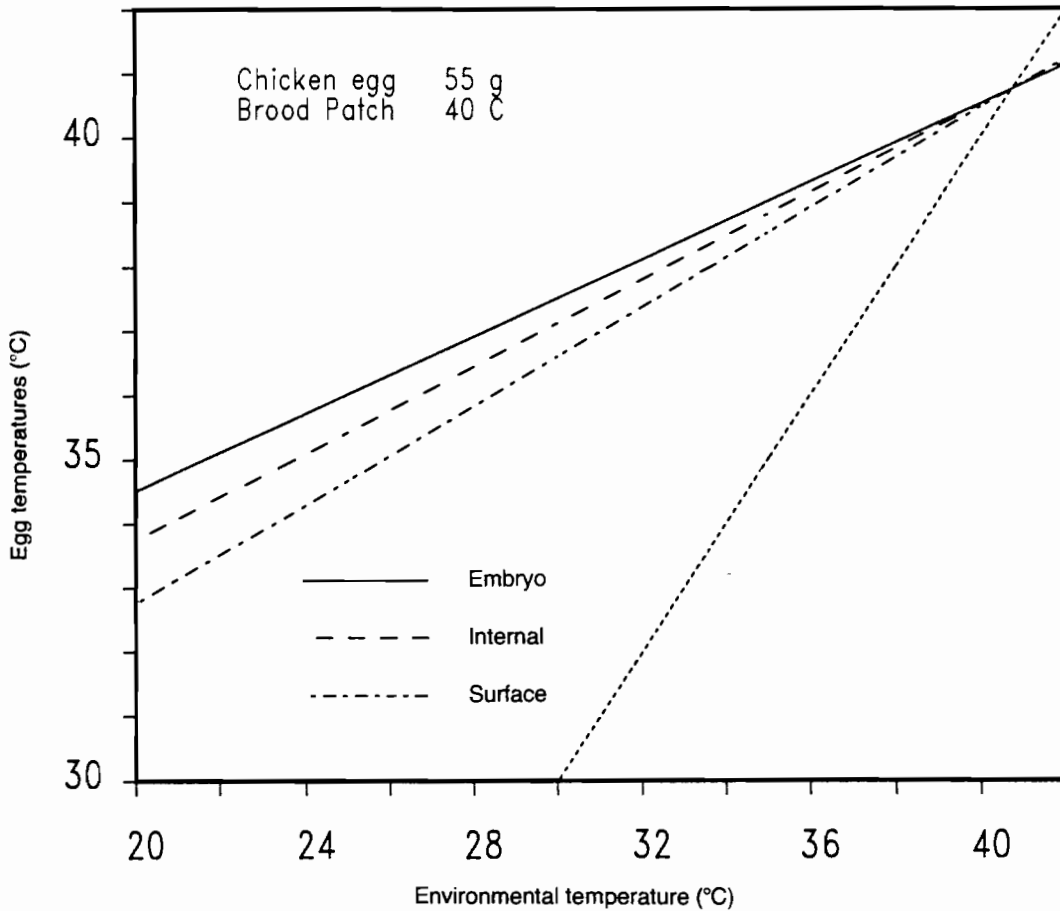


Fig. 9.21. Weighted average egg temperatures as environmental temperature varies as predicted by the numerical model. *Dotted line*: indicates equality between egg and environmental temperature. *Solid line*: indicates embryo temperature. *Dashed line*: indicates average internal temperature. *Dashed and dotted line*: indicates temperature of exposed surface.

large internal temperature gradients, even in very well insulated nests, where one might reasonably expect warm nest air. The egg of the eider (*Somateria mollissima*), for example, sustains a temperature difference of nearly 9 °C between the top and bottom (Rahn *et al.*, 1983). Large temperature gradients in contact incubated eggs are evident for a variety of other eggs and nest types (Grant *et al.*, 1982; Vleck *et al.*, 1983; Swart *et al.*, 1987). To the extent that heat flow in embryonic blood depends upon these temperature differences, so circulation will play an important (and heretofore unappreciated) role in the egg's thermal energetics.

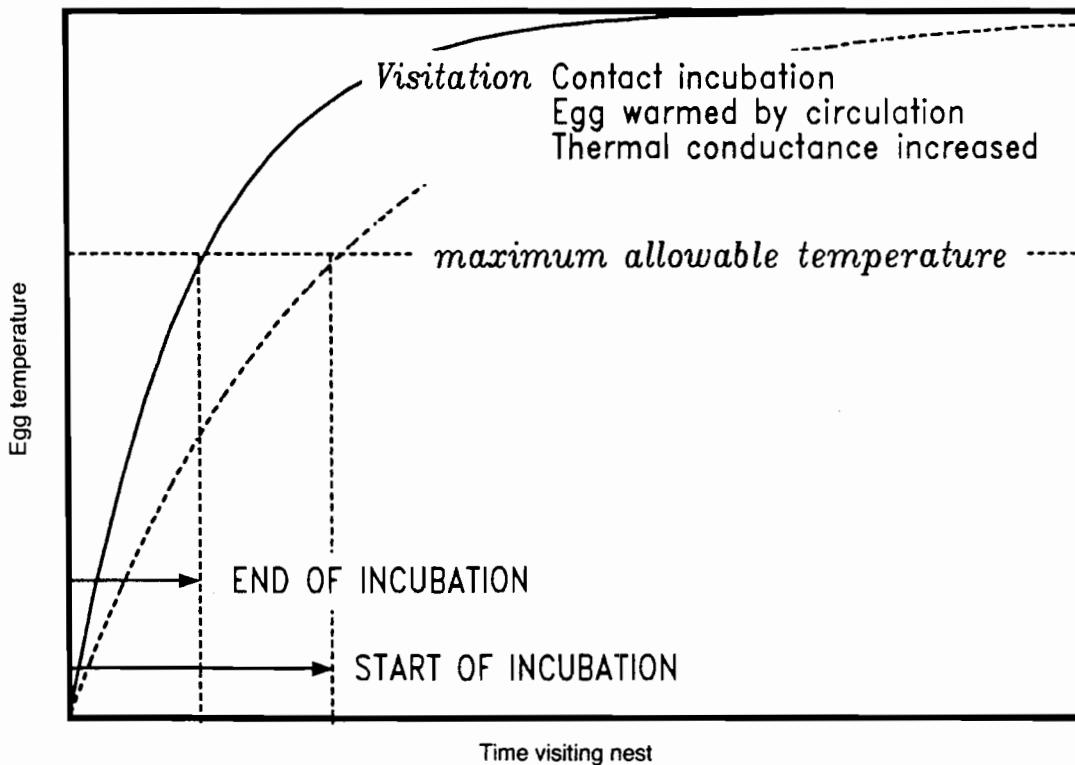
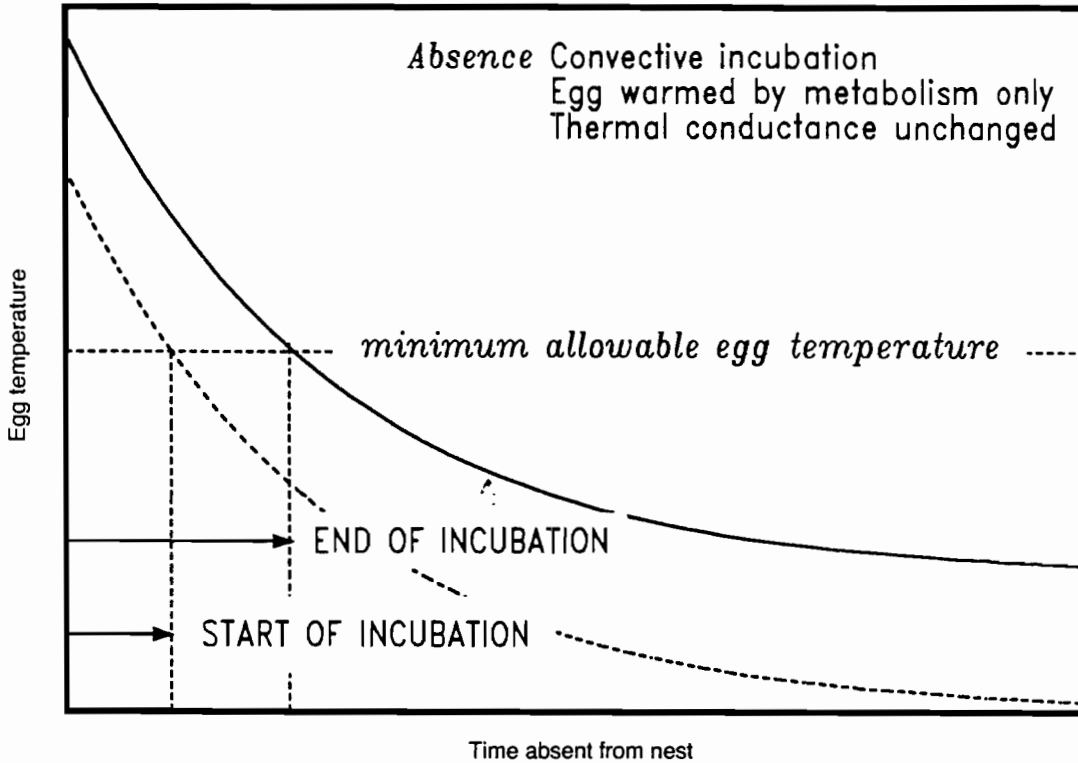
The predicted course of embryo temperature during incubation is another radical difference between contact incubated and convectively incubated eggs. During incubation, the embryo's metabolic heat production warms a convectively incubated egg, and the embryo along with it (Tazawa *et al.*, 1988). The numerical model predicts that the combination of a number of factors, including temperature gradients within the egg, the position in the embryo within the egg, and the metabolism and circulation of the embryo, should result in the embryo actually *cooling* during incubation (Fig. 9.15).

Fig. 9.22. How visitation times and absence times for intermittent incubators might be affected by embryonic development. *Dashed lines*: represent expected rates of temperature change at the start of incubation. *Solid lines*: represent expected rates of temperature change at the end of incubation. *Top panel*: Egg temperature vs time absent from the nest. *Bottom panel*: Egg temperature vs time visiting the nest.

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Start of incubation -----

End of incubation ———



Egg temperatures of naturally incubated eggs are usually assessed by implanting one, or at most a few, temperature sensors in an egg, which a bird is then allowed to incubate. Often, the egg is a 'dummy egg' of some sort, which is usually filled with some inert substance although some dummy eggs are of exceptionally clever design (Buttemer, Astheimer & Dawson, 1988). The course of temperature of these dummy eggs is often thought to reflect embryo or egg temperature in some way. The validity of this supposition may be limited by three factors now known to be crucial in determining embryo temperature. First, contact incubated eggs will have no such thing as an 'egg temperature', only an egg temperature distribution, which cannot be measured adequately by one or a few temperature sensors. Secondly, a static array of thermocouples inside a dummy egg will not reflect the changing distribution of embryo mass within the egg. Thirdly, a single dummy egg does not reflect the complex changes in heat flow elicited by a living embryo's circulation and metabolism. Without taking these factors into account, temperatures of dummy eggs can do little to inform us about embryo temperature in naturally incubated eggs.

Dummy eggs also are sometimes used as experimental tools to measure energy costs of incubation. For example, a dummy egg might be perfused with water of different temperatures (Toien *et al.*, 1986; Vleck, 1981). The change in metabolic heat production of the incubating bird is then measured to assess the energy cost of incubating the egg. In a living egg, circulation is very important in determining this cost. Consequently, if the water-perfused dummy is vigorously circulated with water, which is common practice, the cost to the parent is likely to be greatly exaggerated. To the extent that experimenters err on the side of vigorous perfusion of a dummy egg used in this way, so will they err in overestimating the energy cost of incubation.

In nature, most avian eggs are contact incubated. Overall, it appears that the thermal physiology of the contact incubated egg is radically different from the convectively incubated egg. To understand the energetics of incubation, the fundamental attributes of the contact incubated egg must be taken into account. Most previous approaches to this problem seem not to have done this, and current thinking on incubation energetics may require some revision. For

example, incubating eggs appears to be energetically much cheaper than we have previously thought. Additionally, energy cost to the parent should increase as incubation proceeds, not decrease as the conventional thinking would have it. Finally, embryo temperature in contact incubated eggs actually should decline slightly as the embryo matures: conventional thinking would have it increase.

A particularly interesting case in point concerns birds that intermittently vacate their nests for short time periods (on the order of the egg's time constant) to forage, defend territories, and so forth. The visitation schedules of intermittent incubators such as these appear to be regulated in some way by rates of egg temperature change (White & Kinney, 1974). Time absent from the nest is determined by the time required for the egg to cool to some minimum allowable temperature (Fig. 9.22), while time visiting the nest is set by the time required to rewarm the egg to some maximum allowable temperature (White & Kinney, 1974). These eggs routinely experience both contact incubation (when the parent is sitting on the nest) and convective incubation (when the parent is absent from the nest). When the parent is away, the temperature of the egg as it cools should therefore be influenced only by the embryo's metabolic rate. As the embryo grows and produces more heat, the egg will stay warmer longer, and absence times should increase. When the parent is on the egg, circulation will be the main influence determining the egg's rate of rewarming. As the embryo grows and circulates more blood, the egg should warm more quickly and visitation times should decrease.

To conclude, the thermal physiology of the contact incubated egg is radically different from the convectively incubated egg. Trying to understand how contact incubation works, either as an analogy with convectively incubated eggs, or by simplifying the problem excessively, has not proved fruitful. The process of contact incubation is complex, and understanding it requires an approach that recognises this complexity.

Acknowledgements

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