

## TIME AND ENERGY IN THE INTERMITTENT INCUBATION OF BIRDS' EGGS

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### ABSTRACT

The intermittent incubation of an egg imposes costs on the parent in both time and energy. Heretofore, time and energy costs in intermittent incubation have tended to be considered separately, in part because no suitable theoretical framework has existed to describe how time and energy interact in the intermittent warming of an egg by a brood patch. This paper outlines a new approach to this problem, based upon the thermal properties of transient-state physical systems. Among the interesting results of this approach is a descriptive parameter, the thermal impedance, that provides a unitary description of how time and energy flow through an egg interact. Data describing the transient-state thermal properties of chicken eggs are presented, showing that an egg incubated by a brood patch behaves as a low-pass thermal filter, with a cutoff period of about 100 min. Birds have several ways of adjusting the time and energy costs of intermittent incubation. High efficiency of heat transfer from the brood patch to the egg requires a visitation cycle with a very long period, at least 2–3 time constants for at least 50% efficiency. The warmed mass of the egg can be limited by having short-period visitation cycles, but at the cost of efficient heat transfer into the egg.

### INTRODUCTION

In a regime of intermittent incubation, the eggs are alternately incubated by a brood patch for a time and then abandoned for a period while the parent feeds or patrols its territory (Skutch, 1957, 1962). The eggs of these birds alternately warm and cool as the parent alternately visits and vacates the nest (Huggins, 1941; Kendeigh, 1952, 1963; Skutch, 1957, 1962; Drent, 1973; White and Kinney, 1974; Pikula, 1977; Walsberg and King, 1978; Yom-Tov et al., 1978; Vleck, 1981a,b, 1985; Webb and King, 1983; Zerba and Morton, 1983a,b; Hohman, 1986; Naylor et al., 1988; Weathers and Sullivan, 1989).

The periodic cooling and rewarming of eggs imposes costs on the parent in both time and energy (Vleck, 1985). Energy costs are incurred both by keeping the egg warm and by rewarming the egg after an absence (Biebach, 1986). Time costs arise because time spent rewarming and incubating an egg is time that cannot be spent on other activities,

and vice-versa (Kendeigh, 1952, 1963; White and Kinney, 1974). Time and energy costs in intermittent incubation are also inextricably linked. For example, the energy cost of rewarming starling eggs is proportional to the extent the eggs cool during an absence of the parent from the nest (Biebach, 1986). The extent of egg cooling will, in turn, depend upon the time the bird has spent away from its nest (Drent, 1973; White and Kinney, 1974; Vleck, 1985).

This paper is broadly concerned with the interaction of energy and time among intermittent incubators. The study of intermittent incubation has commonly focused on the behaviors of the parent, in particular on the interaction between the eggs' rates of temperature change, environmental temperature, and the parent's schedule of visits to, and absences from, the nest. This aspect has been well reviewed elsewhere (White and Kinney, 1974), and it will not be the principal focus of this paper. Rather, I shall attempt to build a synthetic overview of the interaction between energy and time in intermittent incubation.

As in any problem in thermal energetics, understanding intermittent incubation boils down to being able to describe and predict the flows of heat between the parent, the egg, and environment. This is clearly a complicated process. Absolute temperatures of eggs, as well as their rates of temperature change, can be influenced by the embryo's production of heat and circulation of blood, by the evaporation of water from the egg, by the properties of the nest and substratum on which the eggs sit, by the presence or absence of other eggs, and by environmental conditions such as temperature, wind speed, insolation, etc.

While recognizing these complexities, it is also worth noting the value of the reductionist dictum that the simple aspects of a problem must be well understood before tackling the complex parts. It is my contention that we still have a lot to learn about the simple aspects of the thermal energetics of incubation. Consequently, my deliberate approach in this paper has been to simplify the problem to a point that some might consider unrealistic. Nevertheless, it is my hope that in understanding this problem at its simplest level we will be able to think more clearly about the use of time and energy by intermittent incubators in more natural (and complicated) circumstances.

#### THE ALTERNATING THERMAL REGIME OF AN INTERMITTENTLY INCUBATED EGG

At its simplest, the intermittently incubated egg alternates between two qualitatively different thermal regimes. When the parent is absent from the nest, the egg is left essentially surrounded by air or nest material, i.e., the egg is "convectively cooled" (Turner, 1992). This situation is analogous to an egg being incubated in an artificial incubator. During the parent's absence, the egg will cool (or warm) toward the environmental temperature. When the parent returns to the nest, the brood patch is applied to one surface of the egg. The egg, or at least that part of the egg contacting the brood patch, will be forced toward a regulated brood patch temperature, i.e., the egg will be "contact-warmed" or "contact-incubated" (Turner, 1992).

## THE CONVECTIVELY COOLED EGG

*ENERGY IN THE CONVECTIVELY COOLING EGG*

The transient state thermal energetics of convectively cooling eggs are fairly well understood (Kendeigh, 1963; Turner, 1985; Sotherland et al., 1987).

The rate of heat loss,  $q(W)^*$ , from a convectively cooling egg is determined by the difference in temperature between the egg and the environment, and the egg's total resistance to heat loss ( $R_1, ^\circ C W^{-1}$ ).

$$q = (T_{egg} - T_{env})/R_1 \quad (1)$$

$R_1$  is itself the sum of the resistance to heat flow within the egg ( $R_i$ ) and the resistance to heat flow outside the egg ( $R_e$ ).

$$R_1 = R_i + R_e \quad (2)$$

The internal resistance limits the flows of heat internally by conduction and circulation. External resistance limits the losses of heat from the egg surface by radiation, convection, etc.

The heat lost from the egg during a bout of cooling,  $Q_c$  (J), can be calculated as the product of the change of egg temperature during cooling,  $\delta T_{egg}$  ( $^\circ C$ ), and the egg's thermal capacitance,  $C$  ( $J ^\circ C^{-1}$ ).

$$Q_c = C \delta T_{egg} \quad (3)$$

For birds' eggs in still air, the external resistance to heat flow,  $R_e$ , is roughly 50–100 times larger than  $R_i$ , i.e.,  $R_1 \approx R_e$  (Turner, 1985; Sotherland et al., 1987). Variations of wind speed from 0 to 400  $cm s^{-1}$  reduce  $R_e$  by about 5-fold (Sotherland et al., 1987). Consequently, even in fairly stiff winds,  $R_e$  is about an order of magnitude larger than  $R_i$ , and, as a result, the convectively cooled egg has a homogeneous internal temperature (Sotherland et al., 1987). This allows one to make certain simplifying assumptions in applying eq 3. For example, estimation of  $\delta T_{egg}$  is not complicated by significant inhomogeneities of internal temperature. One can therefore measure this quantity by measuring a single temperature anywhere within the egg. Additionally,  $C$  can be estimated as the product of the egg's gravimetric mass,  $M$  (kg), and the specific heat of its contents,  $c_p$  ( $J kg^{-1} ^\circ C^{-1}$ ). Thus, for a convectively cooling egg, eq 3 can be rewritten

$$Q_c = c_p M \delta T_{egg} \quad (4)$$

Energy spent rewarming an egg,  $Q_w$  (J), presumably must bring the egg temperature repeatedly back to some set value (White and Kinney, 1974; Webb and King, 1983; Zerba and Morton, 1983a,b). Thus, one way to estimate the energy cost of rewarming the egg,  $Q_w$  (J), would be to assume that, on average,  $Q_w \approx Q_c$ . Thus, a simple measure of a bird's rewarming energy costs would involve simply tabulating the temperature excursions of the egg through the incubation period, calculating the heat lost for each excursion, and adding them. This approach assumes, of course, that energy flow into the egg from the parent is 100% efficient. If there is any inefficiency in heat transfer

\*see Appendix for complete glossary of symbols and abbreviations used throughout article.

between the parent and egg, this approach will underestimate the energy cost of rewarming. As we shall see below, anything approaching 100% efficiency of heat transfer into an egg can only occur under very limited circumstances.

#### TIME IN THE CONVECTIVELY COOLING EGG

Some authors (Drent, 1973; Zerba and Morton, 1983a,b) suggest that a bird that has vacated the nest will not allow the egg to cool below a minimum temperature,  $T_{\min}$ , and will gauge the time spent away from the nest accordingly. When a bird leaves the nest, the egg's environmental temperature suddenly drops from a warm nest temperature to a cooler air temperature. The time course of the egg's temperature,  $T_t$  ( $^{\circ}\text{C}$ ) will follow an exponential approach to a new equilibrium temperature,  $T_{\text{eq}}$  ( $^{\circ}\text{C}$ ),

$$T_t = (T_0 - T_{\text{eq}}) e^{-t/\tau_c} + T_{\text{eq}} \quad (5)$$

where  $T_0$  = egg temperature at the beginning of the parent's absence. The time for the egg to change temperature is quantified by  $\tau_c$  (s), the time constant, which is the product of the egg's thermal capacitance and  $R_t$

$$\tau_c = (R_i + R_e) C = R_i c_p M \quad (6)$$

The time a bird spends away from the nest,  $t_{\text{abs}}$  (s), can be predicted by rearranging eq 5 to calculate the time required for  $T_t = T_{\min}$ :

$$t_{\text{abs}} = -\tau_c \ln((T_{\min} - T_{\text{eq}})/(T_0 - T_{\text{eq}})) \quad (7)$$

From eq 7, one can derive the well-known prediction that warmer environmental temperatures allow a bird to take longer absences from the nest (Fig. 1).

Fairly good predictive equations exist for  $\tau_c$  for eggs cooling in still air (Kendeigh, 1963; Turner, 1985). However, this quantity can be influenced by wind conditions, local turbulence (Sotherland et al., 1987), presence or absence of other eggs (Blagosklonov, 1978; Ponomareva, 1982), and insulating quality of the nest (Ponomareva 1971). Consequently, application of eq 7 to predict an absence time requires a knowledge of  $\tau_c$  in situ.

The progressive mass loss that eggs experience during incubation (Ar and Rahn, 1980) will shorten  $\tau_c$ . Equation 6 predicts that the proportional decline of  $\tau_c$  through incubation will be identical to the egg's proportional loss of mass.

The embryo's developing circulation could also reduce  $\tau_c$ . Measurements of  $R_t$  in developing chicken eggs show that circulation reduces internal resistance by about 20% through the incubation period (Turner, 1992). However, the relatively very large external resistance of convectively cooling eggs means that these reductions of  $R_t$  will have virtually no effect on  $R_t$  (eq 2), and hence on  $\tau_c$ . Indeed, for both chicken eggs and bobwhite quail eggs cooling in air, there is no measureable variation in  $\tau_c$  through the incubation period (Turner, 1987, 1992), although declines are evident when these eggs are cooled in environments that reduce  $R_e$  substantially, like water (Turner, 1987), or in helium-oxygen mixtures (Tazawa et al., 1988).

The embryo's metabolic heat production and evaporative heat loss can influence the

absence time by altering the equilibrium temperature,  $T_{eq}$ . Of the two, metabolism is the most important, producing roughly 5 times more heat over the incubation period than is lost by evaporation (Rahn et al., 1987). The elevation in  $T_{eq}$  is simply the product,  $R_t q_{egg}$ , where  $q_{egg}$  is the egg's net heat production (W). Thus, eq 7 can be rewritten

$$t_{abs} = -\tau_c \ln \frac{T_{min} - T_{env} - R_t q_{egg}}{T_0 - T_{env} - R_t q_{egg}} \tag{8}$$

As incubation proceeds, two opposing influences on absence times should therefore be at work. As net heat production increases, absence times should increase (Fig. 2). Simultaneously, the progressive mass loss of the egg should shorten absence times (Fig. 2).

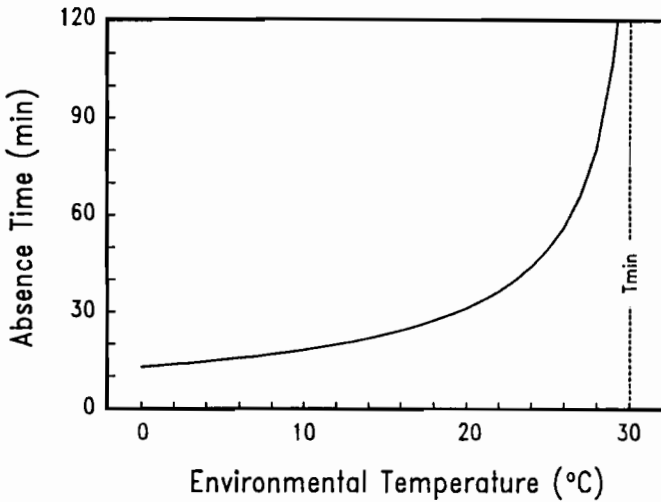
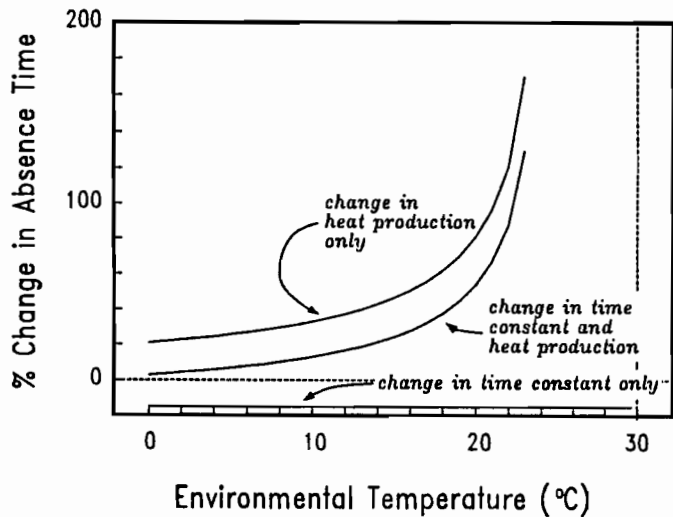


Fig. 1. Variation of absence time from a chicken egg as a function of environmental temperature,  $T_{ex}$ , predicted from eq 7 in text. Parameters used in estimate are:  $\tau_c = 45$  min,  $T_{min} = 30$  °C, and  $T_0 = 40$  °C.

Fig. 2. The expected proportional change in absence time for a chicken egg as a function of environmental temperature, predicted from eq 8 in text. The model assumes a proportional reduction of egg mass by 15%, a heat production rate of 150 mW, and an  $R_t = 40$  °C  $W^{-1}$ . Other parameters are as outlined in legend for Fig. 1.



Of the two, the most important will be the temperature increment from net heat production. Consequently, if an intermittent incubator is adjusting its absence time by the temperature excursions of its eggs, one should see the bird take longer absences as the incubation period progresses, perhaps manifested as a decline in attentiveness to the eggs. This effect should be especially dramatic at temperatures close to the minimum temperature,  $T_{\min}$  (Fig. 2). This has been observed to be the case among some birds (e.g., Zerba and Morton 1983a,b; Brown and Frederickson, 1987), but not among others (e.g., Kendeigh, 1952; Weathers and Sullivan, 1989). Consequently, it is still a matter of question whether there is predictive value in models of absence time that are based upon the exponential approach of an egg to a particular temperature (Yom-Tov et al., 1978; Webb and King, 1983).

### THE CONTACT-INCUBATED EGG

#### *HOW DOES THE CONTACT-INCUBATED EGG DIFFER FROM THE CONVECTIVELY COOLED EGG?*

The contact-incubated egg experiences a very different thermal regime from the convectively cooled egg (Turner, 1987, 1992). Although the steady-state thermal energetics of contact-incubated eggs are reasonably well understood (Turner, 1992), their transient state energetics are not (Turner, in press a,b). This presents obvious difficulties for trying to understand the time and energy costs associated with rewarming eggs with a brood patch.

A distinctive attribute of the contact-incubated egg is the presence of substantial internal temperature gradients that are largely absent from convectively-cooling eggs (Rahn et al., 1983; Sotherland et al., 1987; Turner, 1987, 1992). The region of the egg just under the brood patch can be several degrees warmer than the more remote regions of the egg (Rahn et al., 1983).

These temperature gradients impose some interesting complications on the transient-state energetics of the contact-incubated egg. To illustrate what these might be, let us consider the contact-rewarming of an egg under two hypothetical scenarios: a single bout of contact-rewarming, and repeated bouts of contact-rewarming.

#### *SCENARIO 1: CONSEQUENCES OF A SINGLE BOUT OF CONTACT-REWARMING*

Consider an egg, initially at a uniform cool temperature. When a warm brood patch is applied to this egg, heat will flow into the egg, down the temperature gradient between the brood patch and egg surface.

The added heat will not uniformly warm the egg. Initially, most of the added heat will accumulate in a circumscribed volume of the egg close to the brood patch, warming it to a higher temperature than the egg's more remote regions (Fig. 3).

When the parent leaves the egg, the added heat will begin to redistribute from the warmed part of the egg to the cooler interior. However, there also will be a temperature gradient between the warmed surface of the egg and the now cooler external environment (Fig. 3). Inevitably, some of the heat added during rewarming will leave the egg

directly, and so will not warm the egg's interior (Fig. 3), i.e., some of the heat added to the egg by the parent during rewarming is inevitably "recycled" back to the environment before it can ever penetrate the egg and warm the embryo. This makes the intermittent contact-warming of an egg inherently inefficient. The cost of rewarming the egg will be determined in part by how inefficient this process is.

*SCENARIO 2: CONSEQUENCE OF REPEATED BOUTS OF CONTACT-REWARMING*

Consider now an egg that has been warmed as in the previous example and then is left to cool for a time in air. Initially, the region of the egg warmed by the brood patch will be warmer than the rest of the egg. After a time, this residual heat will travel through the

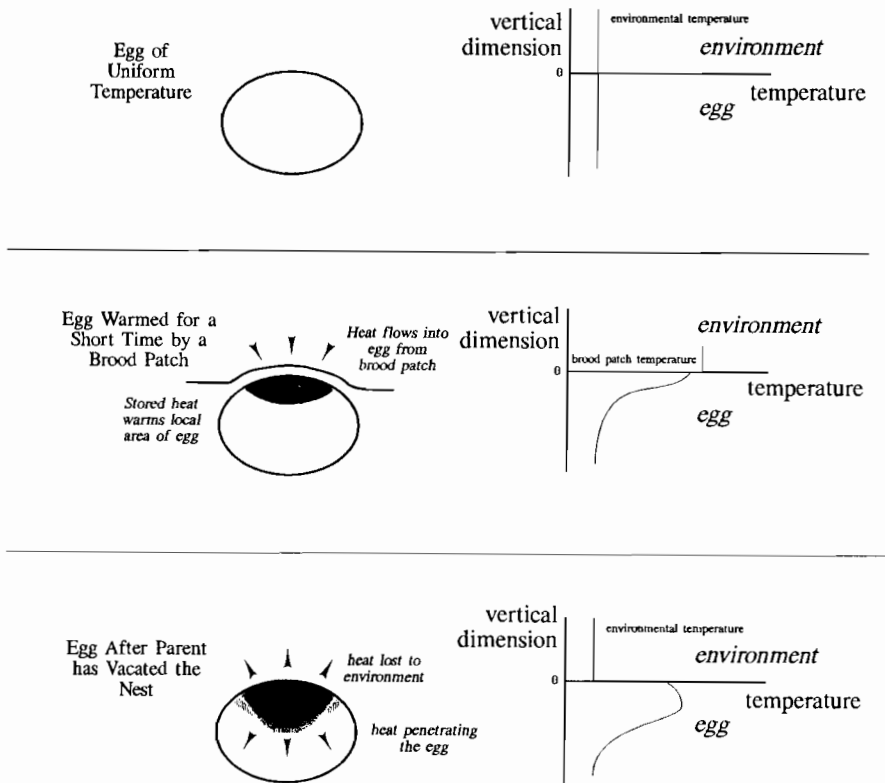


Fig. 3. Schematic depiction of patterns of heat flow and temperature gradients in an egg, warmed by a brood patch from an initial uniform temperature. The diagrams on the left show a diagram of an egg, with warmed portions being shaded. The diagrams on the right show expected temperature distributions along a vertical transect from the region above the egg, and through the egg to the bottom. *Top set:* Conditions prior to the initial bout of warming. *Middle set:* Conditions upon initial warming of the egg by contact with a brood patch. *Bottom set:* Conditions after the incubating parent has left the egg.

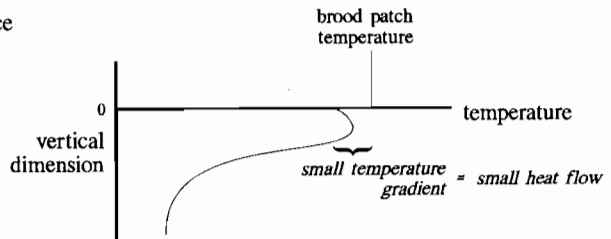
egg as a wave of elevated temperature (Fig. 4). At some time, the parent will return to the nest and begin again to rewarm the egg.

If the parent's absence has been long enough for the wave of added heat to have moved into the egg, the egg surface now contacting the brood patch will be cool and will present to the brood patch a large temperature gradient for heat to flow into the egg (Fig. 4). However, if the parent returns and warms the egg before this residual heat has penetrated, the egg surface will still be warm, and the temperature gradient between the brood patch and egg surface will be smaller. Less heat will therefore enter the egg as it is being rewarmed (Fig. 4).

In other words, there will be an apparent 'resistance' to the transfer of heat into the egg, owing to residual heat from the previous bout of incubation. Thus, the efficiency of heat flow into the egg will depend upon the egg's prior thermal history.

The relatively simple analysis of time and energy in convectively cooling eggs, outlined in eqs 1–8, offers little help in understanding problems of contact-rewarming such as these. For the most part, the problems arise because of the internal temperature gradients that exist in the contact-warming egg, gradients that are much smaller in convectively-cooling eggs. Conceivably, one could extend the analysis of eqs 1–8 to contact-warming eggs by collecting more detailed information on the egg's temperature gradients during warming and their variations with respect to time. However, there is a simpler and more powerful way of getting at these problems.

#### Rewarming after a Short Absence



#### Rewarming after a Long Absence

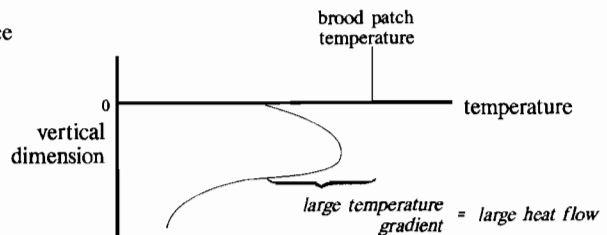


Fig. 4. Schematic depiction of patterns of heat flow and temperature gradients in an egg, warmed by a brood patch at some time after a prior bout of rewarming. Convections and layout are as described for Fig. 3. *Top panel:* Conditions during a bout of rewarming after a short prior absence. *Bottom panel:* Conditions during a bout of rewarming after a long prior absence.

### THE CONTACT-WARMED EGG AS A PHYSICAL SYSTEM

A physical system is any system through which energy moves down a potential energy gradient and forces a response in it (Trimmer, 1950). For example, heat moving through a physical system requires a temperature gradient across it. The heat moving through the system will force changes in the temperature of the system.

The energetics of all physical systems are governed by similar sets of equations. Consequently, one can model the behavior of one physical system, say the flow of heat through an egg, by analogizing it to another, say the flow of electrical current through a circuit (Trimmer, 1950). This is the basis of the well-known electrical analogy for modeling heat flow (Table 1; Thomas, 1980).

The flow of energy through a physical system occurs in two components: steady and transient. In the steady component, the potential energy gradient driving energy flow is invariant with respect to time, and energy flow is limited by a resistance only. A DC electrical circuit is an example of a physical system that has only a steady component, or more precisely, that has no transient component. In the transient component, the potential energy gradient varies with respect to time, and the capacity of the system to store energy becomes important. Transient-state systems have both a steady and a transient component of energy flow.

The flow of energy through a transient-state physical system is limited by a quantity, the *impedance*, that is the transient-state analog of the *resistance* of a steady-state system. The impedance defines the "resistance" of a physical system to admit both steady and transient components of energy flow. Thus, an AC electrical circuit has a characteristic electrical impedance, an acoustic physical system like the vertebrate ear has a characteristic acoustic impedance, and, by analogy, a physical system characterized by the flow of heat has a characteristic thermal impedance.

The impedance of a physical system varies in a characteristic way with the time-dependency of the transient component of energy flow. Consider, for example, a low-pass electrical filter with a certain cutoff frequency. The low-pass filter is a physical system which admits AC currents below the cutoff frequency, but does not admit AC currents with frequencies higher than the cutoff. Treating the filter as having an impedance provides a useful way of dealing simultaneously with the dimensions of time and energy flow that characterize this physical system.

Table 1  
The electrical analogy for heat flow in steady physical systems

	Ohm's Law	"Newton's Law"
Equation	$I = (V_1 - V_2)/R$	$Q = (T_1 - T_2)/R_t$
Potential energy gradient	V (volts)	T (kelvins)
Energy flow	I (amperes)	Q (watts)
Energy flow limiter	R (ohms)	$R_t$ (kelvins watt <sup>-1</sup> )

The intermittently contact-incubated egg, because it receives intermittent inputs of heat with a characteristic time dependency (determined by the birds' schedule of visits to the nest), can be considered a transient-state physical system. It therefore should be possible to study the interaction of time and energy in this system by using the already well-established principles that characterize analogous behavior of other physical systems.

#### THE TRANSIENT-STATE THERMAL PROPERTIES OF A CONTACT-INCUBATED EGG

The thermal impedance is one of several transient-state thermal properties that characterize the intermittently incubated egg. The most straightforward method for measuring these properties is to subject an egg to a sinusoidally-varying input of heat from a brood patch,  $q_b(t)$ , such that

$$q_b(t) = A_q + B_q \sin(2\pi t/P) \quad (9)$$

where  $A_q$  = mean heat input (W),  $B_q$  = amplitude of variation (W),  $P$  = period of the heat input (s), and  $t$  = time (s) (Trimmer, 1950; Turner, in press a). The input of heat is provided by an artificial brood patch (ABP), similar to that developed originally by Drent (1973) and developed further by Turner (1992, in press a,b). This will force on the egg a sinusoidal variation of temperature (Fig. 5),  $T(t)$ , such that

$$T(t) = A_T + B_T \sin(2\pi t/P + \varphi) \quad (10)$$

### Sinusoidal forcing of egg temperature

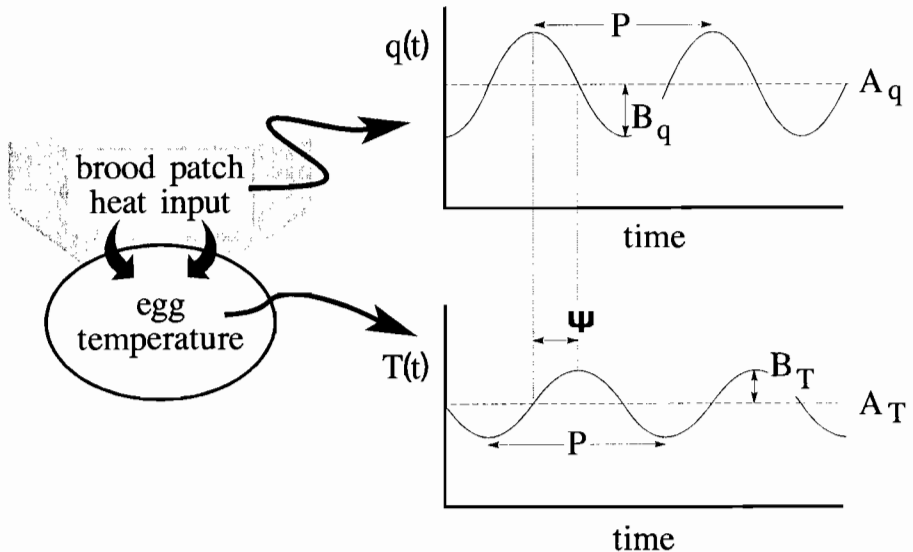


Fig. 5. Schematic diagram of co-varying sinusoidal brood patch heat inputs and temperatures within the egg. Notation as described in eqs 9 and 10 in the text.

where  $A_T$  = mean temperature ( $^{\circ}\text{C}$ ),  $B_T$  = amplitude of temperature variation ( $^{\circ}\text{C}$ ), and  $\varphi$  = phase difference between  $q_b(t)$  and  $T(t)$  (radians).

From the parameters of eqs 9 and 10, it is straightforward to calculate both the steady-state and the transient-state thermal properties of the egg. The steady component of energy flow is limited by the steady thermal resistance,  $R_i$  ( $^{\circ}\text{C W}^{-1}$ ), and is calculated

$$R_i = A_T/A_q \quad (11)$$

The transient component of energy flow is limited by a capacitive reactance, proportional to the capacity of the egg to store heat. Capacitive reactance, designated as  $X_c$ , is calculated

$$X_c = R_i \tan(-\varphi) \quad (12)$$

The thermal impedance,  $Z_i$ , is calculated as the vector sum of  $R_i$  and  $X_c$

$$Z_i = (R_i^2 + X_c^2)^{0.5} \quad (13)$$

A time constant,  $\tau_w$ , already introduced as a parameter that describes the rapidity of temperature change in the convectively incubated egg (eqs 3,4), can be estimated for the contact-incubated egg from the phase delay,  $\varphi$

$$\tau_w = \frac{-P \tan \varphi}{2 \pi} \quad (14)$$

The power factor,  $\rho$ , is the ratio of usable power to the total power flowing through the system. It also is calculated from  $\varphi$

$$\rho = \cos \varphi \quad (15)$$

The most 'efficient' physical system, i.e., one in which the energy lost is lowest, is accomplished when the phase delay is close to null.

#### *THE TRANSIENT-STATE THERMAL PROPERTIES OF CONTACT-INCUBATED CHICKEN EGGS*

To date, these transient-state thermal properties have only been measured in contact-incubated chicken eggs (Turner, in press a,b). The contact-incubated chicken egg behaves analogously to a low-pass thermal filter, whether the egg is embryonated or not. Consequently, transient components of brood patch heat input that have long periods penetrate the egg more readily, and so cause larger transient temperatures in the egg than do shorter-period components (Figs. 6,7). While the steady resistance,  $R_i$ , is independent of period (Fig. 8), the egg's capacitive reactance increases sharply at periods of roughly 60 min or less (Fig. 8). Consequently, the thermal impedance of the contact-incubated chicken egg increases sharply when the brood patch heat inputs have short periods (Fig. 8). At periods of heat input of about 100 min or more, the impedance is virtually identical to the steady resistance (Fig. 8), and the capacitive reactance contributes little to the flows of heat through the egg. Finally, the egg's power factor increases with the period of the heat input: efficiency of heat flow into the egg is greater than 90% at periods of roughly 270 min or greater (Fig. 9). Efficiency is less than 50% at

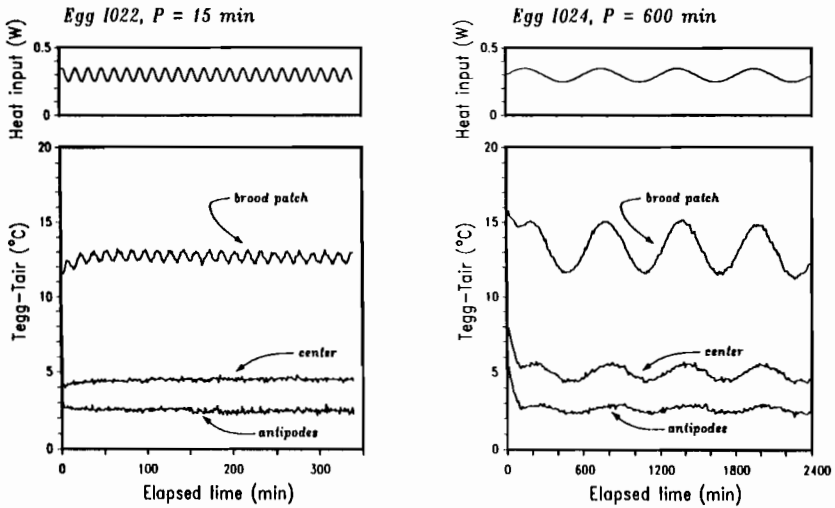


Fig. 6. Sinusoidally-varying heat inputs to two representative eggs with resultant sinusoidal temperatures at the brood patch, center, and antipodal surface of the egg. Egg temperatures are expressed as a temperature elevation above the chamber air temperature. Elapsed time is the time since the beginning of the experiment. Inserts above the temperature graphs show the heat inputs to the egg via an artificial brood patch. Mean heat input and amplitude of variation of both are  $0.3 \pm 0.05$  W, respectively. *Left panel*: Period = 15 min. *Right panel*: Period = 600 min. Data are from Turner (in press a).

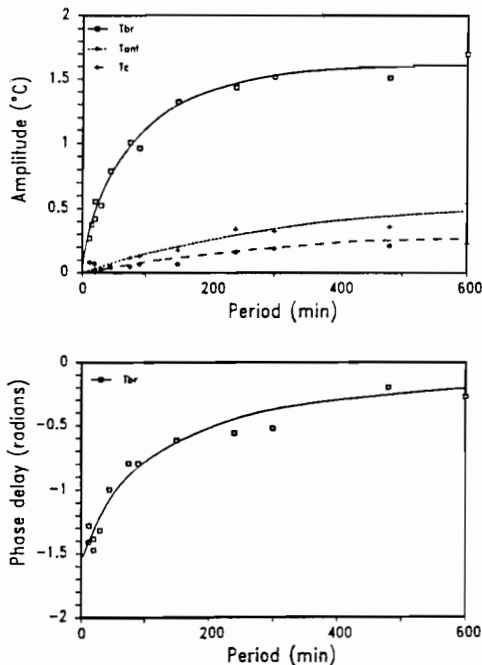


Fig. 7. Amplitude and phase delay of sinusoidally-varying temperature of 13 infertile chicken eggs, subjected to sinusoidally-varying heat inputs via an artificial brood patch. *Top panel*: Amplitudes of variation for temperatures at the brood patch (unfilled squares, solid curve), egg center (crosses, dotted curve), and antipodal surface of the egg (diamonds, dashed curve). Curves are fitted by eye. *Bottom panel*: Phase delay of brood patch temperature oscillation with respect to heat input oscillation. Curve fitted by eye. Data are from Turner (in press a).

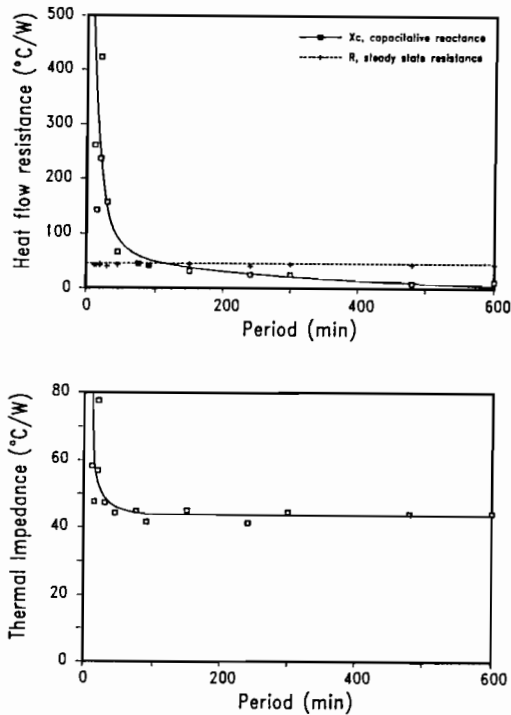


Fig. 8. Components of thermal impedance for 13 infertile chicken eggs subjected to a sinusoidally-varying heat input via an artificial brood patch. *Top panel:* Capacitive reactance (unfilled squares, solid curve), and steady-state resistance (crosses, dotted curve). Curves fitted by eye. *Bottom panel:* thermal impedance as calculated from the steady-state resistance and capacitive reactance. Curve fitted by eye. Data are from Turner (in press a).

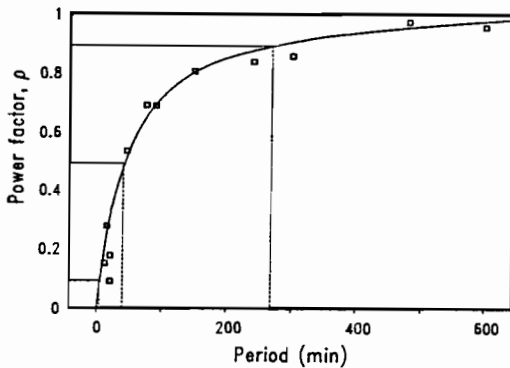


Fig. 9. Power factor,  $\rho$ , calculated for infertile chicken eggs. Dotted curves indicate power factors and associated periods for 90%, 50%, and 10% efficiency of heat flow into the egg from the brood patch. Data are from Turner (in press a).

periods of about 40 min or less (Fig. 9). Remarkably, the time constant for the contact-warmed chicken egg is less than half that for a convectively cooled chicken egg (Table 2).

The development of the embryo reduces the chicken egg's thermal impedance, which declines by roughly 10% between the beginning and end of the incubation period (Table 3). The decline of impedance is due in roughly equal parts to the decline of mass of the egg, reducing the egg's capacitive reactance, and to the increased circulation by the embryo within the egg, reducing the egg's  $R_1$  (Turner, in press b). As the embryo develops, the time constant declines from roughly 13 min at the beginning of incubation

Table 2  
Thermal properties of infertile convectively incubated and contact-incubated chicken eggs compared

	Convectively cooled	Contact-incubated	Contact/Convective
$\tau$ (min) (measured)	42.1	20.1	0.477
$R_i$ ( $^{\circ}\text{C W}^{-1}$ ) (measured)	13.7	42.7	3.12

Data for convectively cooled eggs are from Turner, 1985. Data for contact-incubated infertile eggs are from Turner, in press a.

Table 3  
Summary of changes in transient thermal properties of living chicken egg as egg matures from days 1–6 of incubation to days 13–18 of incubation

	Days 1–6	Days 13–18
$R_i$ ( $^{\circ}\text{C W}^{-1}$ )	41.9	33.8
$X_c$ ( $^{\circ}\text{C W}^{-1}$ )	72.4	65.4
$Z$ ( $^{\circ}\text{C W}^{-1}$ )	86.8	78.4
$\tau$ (min)	13.1	11.2
$\phi$ (radians)	-0.827	-0.577
$\rho$	0.677	0.838

Values represent means for three periods of heat input, 20, 60, and 120 min, with a sinusoidal heat input of  $300 \text{ mW} \pm 50 \text{ mW}$ . Data from Turner, in press b.

to about 11 min by the end of incubation (Table 3). Finally, the egg's power factor increases as the egg matures, from an average of 68% at the start of incubation to nearly 84% by the end (Table 3).

#### TIME AND ENERGY IN THE INTERMITTENTLY INCUBATED EGG

##### *MAINTAINING SUITABLE EMBRYO TEMPERATURES IN A REGIME OF INTERMITTENT INCUBATION*

Because of its substantial internal temperature gradients, it makes little sense to speak of a contact-incubated egg as having a single "egg temperature." Presumably, of all the possible temperatures within the egg, it is the temperature of the embryo that is the important one for the reproductive success of the bird. An incubating bird presumably gauges the temperature of its egg through thermoreceptors located in the brood patch (Drent, 1973; White and Kinney, 1974; Midtgard et al., 1985; Toien et al., 1986). Consequently, the egg temperature sensed by the bird is not likely to be similar to the embryo's temperature. How, then, does an incubating bird "know" that its egg is "warm enough", i.e., that the temperature of the embryo, somewhat removed from the temperature sensed by the parent, is suitable for development?

Under steady-state conditions, e.g., constant incubation, there is a good correlation between temperature in the egg's interior and brood patch temperature (Turner, 1992). The dissimilarity in these two temperatures should not therefore pose any problem; natural selection could presumably "calibrate" the brood patch to be regulated at whatever temperature is required to keep the embryo at a suitable temperature for development.

However, in transient-state conditions, e.g., intermittent incubation, the correlation between the various temperatures through the egg is not so reliable. Consider, for example, an egg subjected to two identical step changes of heat input from an artificial brood patch (Fig. 10). The two series differ only in the initial conditions for egg temperature. When the initial egg temperature is uniform (Fig. 10, top panel), the temperatures at the brood patch show an "overshoot" upon the onset of heating. When there is an initial temperature gradient from the brood patch to the antipodal surface of the egg (Fig. 10, bottom panel), the overshoot does not appear. Clearly, the correlation between the sensed temperature and the embryo's temperature in these circumstances is not a reliable one. We are then returned to the original question, slightly modified for the

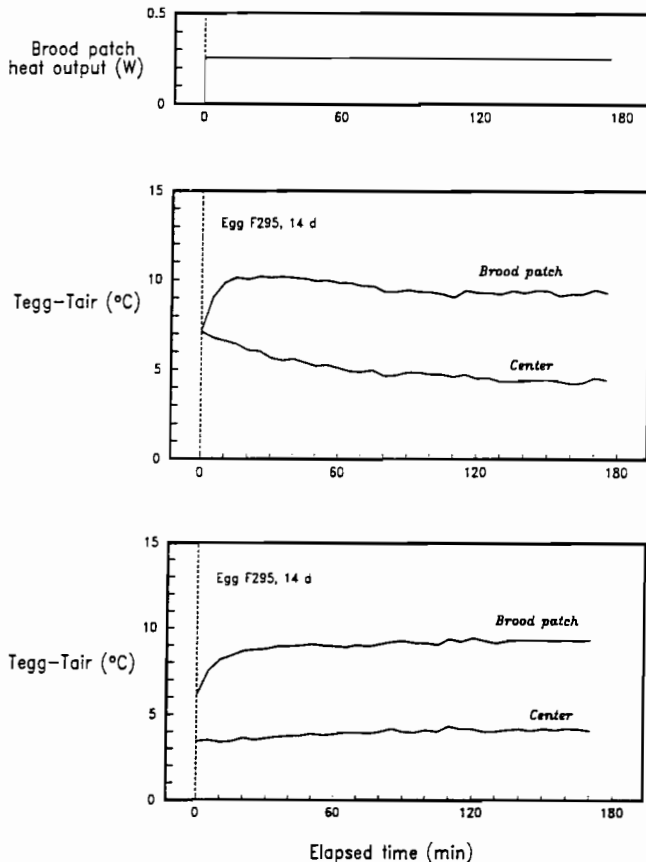


Fig. 10. Stepped heat input of 0–250 mW to a fertile chicken egg at 14 days incubation. Egg temperatures are expressed as a temperature elevation above the chamber air temperature. Elapsed time is the time since the beginning of the experiment. Insert above the temperature graphs shows the heat inputs to the egg via an artificial brood patch.

situation of intermittent incubation: How does a bird *rewarming* its egg “know” when the egg has been “warmed enough”, i.e., that the rewarming will leave the embryo at a temperature suitable for development, when the only temperature that can be sensed by the bird is the brood patch temperature?

The question thus posed might profitably be recast in energetic terms. For some point in an egg distant from the brood patch to be warmed, the heat required to rewarm that point must actually get there. Consequently, ensuring that an intermittent input of heat from the brood patch actually warms an embryo means ensuring that the heat penetrates into the egg to where the embryo is.

Getting the heat to where the embryo is will be difficult if the thermal impedance resisting the influx of heat is high. At least for chicken eggs, the egg's thermal impedance increases sharply when the period of a transient heat input is short (Fig. 8). A parent, to ensure the effective penetration of its intermittent heat inputs into the egg, should therefore eschew visitation schedules that have short periods, or that have a significant portion of the energy in short-period components (Fig. 9). Thus, the most efficient schedule for intermittent incubation should have periods of intermittency that are as long as possible. This prediction is in conformity with, although derived differently from, that of Drent (1973), who suggested that the energy cost of rewarming eggs should be minimized by taking relatively few and long absences from the nest.

#### *THERMAL IMPEDANCE AND THE “EFFECTIVE THERMAL MASS” OF A CONTACT-INCUBATED EGG*

Nevertheless, the incubation schedules of many birds do not conform to this prediction. Many passerine birds, for example, may take many dozens of short absences per day from the nest. There may, therefore, be alternative strategies at work shaping the incubation rhythms of these birds. The concept of the thermal impedance may help illuminate what these alternative strategies might be.

A transient input of heat from a brood patch will penetrate into an egg for only a certain distance. The degree of penetration can be evaluated by mapping the magnitude of the forced change of temperature,  $\delta T$ , within the egg. For example, a pulse of heat from the brood patch will raise local temperatures of the egg as it passes through. One can define an isotherm where the largest transient increase of temperature,  $\delta T$ , is some arbitrary value,  $+x$  °C (Fig. 11). At points above this isotherm,  $\delta T > +x$  °C, and below it,  $\delta T < +x$  °C (Fig. 11).

The extent to which the  $+x$  °C isotherm penetrates into the egg will depend upon the egg's thermal impedance during contact-warming. If the egg's thermal impedance is low, the penetration of the  $+x$  °C isotherm into the egg will be greater, and will encompass more of the egg's volume, than if the egg's thermal impedance is high (Fig. 11). This is why, for example, the egg's center temperature oscillates with a greater amplitude when the sinusoidal period of brood patch heat input is long (Fig. 6).

It also indicates that an intermittently warmed egg has an “effective thermal mass” that is not equivalent to the thermal mass defined in eqs 3 and 4. Equations 3 and 4 assume, among other things, that the egg's entire gravimetric mass,  $M$ , contributes its

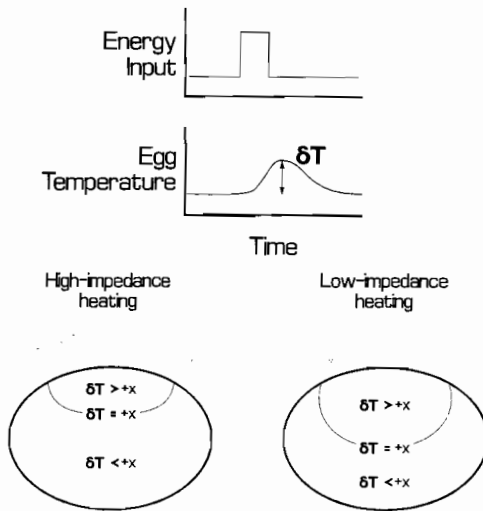


Fig. 11. Diagrammatic representation of the penetration of the  $\delta T = +x$  °C isotherm, under conditions of high impedance heating and low impedance heating. Inset shows how  $\delta T$  might be defined from the temperature response of a pulsed input of heat from a brood patch.

heat storage capacity to the egg's thermal capacitance. However, consider the situation in an intermittently warmed egg when the  $+x$  °C isotherm is not measurably different from null. The region of the egg below the isotherm will therefore be essentially at steady temperature. This region is therefore not storing any heat, and it is in no way participating in the transient flows of heat through the egg. The region above the  $+x$  °C isotherm is so engaged, however, and so constitutes an "effective thermal mass",  $C_{\text{eff}}$ , that is considerably smaller than the gravimetrically determined thermal mass of eqs 3 and 4. The relatively small time constant for contact-rewarming (Turner, in press a,b; Table 2) is one result of these egg's relatively small "effective thermal masses."

$C_{\text{eff}}$  of an egg depends inversely upon the impedance of the egg during rewarming (Turner, unpublished). Thus, a pulse of heat put into the egg at low impedance will penetrate further into the egg, and encompass a larger effective thermal mass, than will an identical quantity of heat put into the egg at high impedance (Table 4). A pulse of heat at high impedance heating will therefore warm a smaller volume of the egg to a higher temperature than will the same pulse of heat at low impedance heating (Table 4).

Although low impedance heating is the most efficient way to get intermittent pulses of heat into the egg, there may be circumstances where the best "strategy" for a bird would be to engage in high impedance intermittent heating. This could be readily accomplished by an incubation schedule characterized by *short* periods of intense heating. One such circumstance might occur in the early stages of incubation, when the yolk can rotate within the egg, and the embryo is automatically positioned in a region of the egg close to the brood patch (Rahn et al., 1983). This "automatic positioning" of the embryo operates to some degree through most of the incubation period. A transient pulse of heat from a brood patch that penetrates beyond the localized region containing the embryo might therefore be energy that is wasted, warming essentially "inert mass" of

Table 4  
Response of brood patch temperature to a 252-J pulsed input of heat  
at different thermal impedances of the egg

	High impedance	Low impedance	<i>p</i>
$T_{b, \max}$ ( $^{\circ}\text{C}$ )	13.48	12.68	0.0084
$s_w$ (min)	10.68	12.29	0.0073

High impedance heating is provided by heating the egg for a short time at a high rate of brood patch heat input. Low impedance heating is provided by heating the egg for a longer time at a lower rate of brood patch heat input. Brood patch temperature is measured on the eggshell surface where the egg contacts the warmed artificial brood patch. Reported values are main effects means for fertile chicken eggs over the entire incubation period.  $T_{b, \max}$  is the highest temperature attained at the brood patch during the heating pulse.  $\tau_w$  is the time constant for the post-heating cooling of the brood patch temperature. *p* is the Type I probability as calculated by an analysis of variance. Data are from Turner (unpublished).

the egg. By limiting the portion of the egg that it transiently warms, an intermittently incubating bird might therefore reduce its energy cost of rewarming, even though the efficiency of the transfer of heat into the egg is low.

#### CONCLUSIONS

Rewarming an egg after an absence from the nest imposes costs in both time and energy for the incubating bird. A general theory that predicts what these costs are and how they might interact has heretofore been lacking. The interaction of time and energy in transient-state physical systems is the subject of a well-known body of theory (Trimmer, 1950). Treating the egg as a transient-state physical system might illuminate the temporal and energetic consequences of intermittent incubation in a way heretofore not possible.

Measurements of the transient-state thermal properties of chicken eggs show many interesting features describing the efficiency of heat flow into the egg, the role that the embryo can play in effecting this transfer of heat, and how a bird can alter the fractional mass of the egg it actually warms with a brood patch.

These analyses might illuminate several long-standing issues in intermittent incubation. Consider, for example, the question: how should the visitation time of an intermittent incubator change with respect to the incubation age? The egg's thermal impedance suggests that transfer of heat into the egg from the brood patch is most efficient when the visitation cycle has a period that is long with respect to the egg's time constant. As the embryo matures, the circulation of blood in the egg facilitates the transfer of heat into the

egg. If the bird's attentiveness to the nest is organized to make heat transfer from its body into the egg efficient, one might therefore expect a visitation time that will be long initially, and gradually shorten as the incubation period progresses. On the other hand, the volume of the egg that the parent needs to warm might be small initially and increase as the embryo grows and fills more of the egg. Short visitation periods allow a bird to warm a small proportion of the egg; one might then see short visitation times initially that lengthen through the incubation period as the embryo grows. Based on the transient-state properties of the eggs, both strategies are feasible.

This approach suggests other interesting questions for future study:

(1) What about the transition between convective cooling and contact-warming that inevitably must occur in intermittent incubation? Although energetic advantage might accrue to a bird that warms only a limited volume of its egg, perhaps a bird could warm a larger fraction of the egg than necessary to warm the embryo, essentially "pre-loading" the egg with "extra" heat to prolong the subsequent absence?

(2) What effect might turning of the egg have? For example, if a bird first warms one surface of the egg for a while, and rotates the egg to warm the opposite surface, two "waves" of heat will be set traveling through the egg toward one another. What happens when these two waves meet in the center of the egg? Will there be a type of "constructive interference" where these two waves of energy elevate the temperature at the center of the egg? Will the turning schedule of a bird be determined in any way by such considerations?

(3) Is there any evidence of "impedance matching" of the egg with its brood patch? While we know that circulation through the brood patch and parental heat production vary adaptively in the face of variations of egg temperature, we know little about how the thermal properties of a bird's brood patch might influence the flow of heat into the egg. Is the brood patch "engineered" to match its impedance with that of the egg, just as the efficient transfer of sound energy from air into the ear requires the elaborate impedance matching apparatus of the outer and middle ears (Alexander, 1983)?

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## APPENDIX

## GLOSSARY OF SYMBOLS AND ABBREVIATIONS

Symbol	Definition	Units
$A_q$	steady component of variation of brood patch heat output (eq 9)	(W)
$A_T$	steady component of variation of temperature (eq 10)	(°C)
ABP	artificial brood patch	
AC	alternating current	
$B_q$	amplitude of sinusoidal variation of brood patch heat output (eq 9)	(W)
$B_T$	amplitude of sinusoidal variation of temperature (eq 10)	(W)
$C$	thermal capacitance (eq 3)	(J °C <sup>-1</sup> )
$C_{eff}$	effective thermal mass	(J °C <sup>-1</sup> )
$C_p$	specific heat (eq 4)	(J kg <sup>-1</sup> °C <sup>-1</sup> )
$M$	gravimetric mass of the egg (eq 4)	(kg)
$Q_c$	heat lost during cooling of a convectively cooled egg (eq 3)	(J)
$Q_w$	heat to be replaced after cooling of a convectively cooled egg	(J)
$q$	heat loss rate from the convectively cooled egg (eq 1)	(W)
$q_b$	brood patch heat output	(W)
$q_b(t)$	time-varying brood patch heat output (eq 8)	(W)
$q_{egg}$	net heat production of egg (eq 8)	(W)
$P$	period (eq 9)	(min)
$R_e$	the thermal resistance external to the convectively cooled egg (eq 2)	(°C W <sup>-1</sup> )
$R_i$	the thermal resistance internal to the convectively cooled egg (eq 2)	(°C W <sup>-1</sup> )
$R_t$	the steady-state or total thermal resistance (eqs 1,2)	(°C W <sup>-1</sup> )
$T(t)$	time varying temperature (eq 10)	(°C)

$T_0$	initial temperature of a convectively cooled egg during an absence from the nest (eq 5)	(°C)
$T_a$	temperature of egg surface antipodal to the brood patch	(°C)
$T_b$	temperature of egg at the brood patch	(°C)
$T_c$	temperature of center of an egg	(°C)
$T_{egg}$	temperature of the convectively cooled egg (eq 1)	(°C)
$T_{env}$	environmental temperature of the convectively cooled egg (eq 1)	(°C)
$T_{eq}$	equilibrium temperature of an egg exposed to a step change of $q_b$ (eq 5)	(°C)
$T_{ex}$	release temperature of egg at which a bird vacates the nest	(°C)
$T_{min}$	minimum allowable temperature of an intermittently incubated egg (eq 6)	(°C)
$T_t$	temperature at time $t$ of an egg exposed to a step change of $q_b$ (eq 6)	(°C)
$t$	time (eq 6)	(min)
$t_{abs}$	absence time (eq 7)	(min)
$t_{vis}$	visitation time	(min)
$X_c$	capacitative reactance (eq 12)	(°C W <sup>-1</sup> )
$Z_t$	thermal impedance (eq 13)	(°C W <sup>-1</sup> )
$\delta T_{egg}$	change of temperature of a convectively cooled egg during a bout of cooling	(°C)
$\rho$	power factor (eq 15)	
$\tau_w$	time constant for temperature change (eq 14)	(min)
$\tau_c$	cooling time constant for a convectively incubated egg (eq 5)	(min)
$\phi_T$	phase delay of temperature (eq 10)	(rad)

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