



THERMAL IMPEDANCE OF A CONTACT-INCUBATED BIRD'S EGG

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(Received 15 March 1993; accepted in revised form 18 January 1994)

Abstract—1. Intermittently incubated eggs are alternately warmed by the brood patch during nest visits and allowed to cool during absences from the nest.

2. The thermal energetics of such eggs are not governed by conventional measures of thermal energetics, like thermal conductance or thermal resistance, which only measure the steady-state component of heat flow through an egg.

3. The transient component of heat flow that intermittently incubated eggs experience is limited by a time-dependent analog of thermal resistance, the thermal impedance. This paper outlines methods for measuring the thermal impedance and other transient-state properties of contact-incubated birds' eggs. Data are presented on these properties for infertile chicken eggs warmed by an artificial brood patch.

4. The infertile chicken egg behaves analogously to a low-pass thermal filter, in which slowly-varying heat inputs modify the temperature of the egg more than rapidly-varying heat inputs.

5. At heat inflow period of 60 min or less, the thermal impedance rises sharply above the thermal resistance.

6. Time constants of contact-incubated chicken eggs are about 20 min, considerably shorter than the 42 min observed in chicken eggs cooling in air.

7. The 'effective thermal mass' of a chicken egg, that is the portion of the egg experiencing transient heat flows increases with period of the heat input. As a result, time-varying heat inputs with periods less than 60 min will have little influence on egg temperatures of an egg incubated via a brood patch.

Key Word Index: Energetics; intermittent incubation; egg; chicken; thermal impedance; thermal mass

INTRODUCTION

Birds' eggs usually are incubated in one of two ways. When both parents incubate, the egg is generally attended continuously. Among birds where only a single parent incubates, however, the parent must periodically leave the nest and eggs to feed, patrol territories, etc. (White and Kinney, 1974).

When the parent is absent from the nest, the egg will change temperature as it cools (or warms) to ambient temperature (White and Kinney, 1974). Once the parent returns, the egg must be rewarmed by pressing the brood patch against it. Thus, an intermittently incubated egg experiences an alternating series of thermal transients, convectively cooling during periods of parental absence, and being warmed by contact through a brood patch during parental visits.

Analytically, heat flow through any object, including an egg, can be subdivided into two components: steady and transient. The steady component of heat flow through an egg is conventionally described by

well-known quantities like the thermal resistance or thermal conductance. By themselves, these quantities are capable of describing the flows of heat through eggs that experience no time-dependent variation in either heat flow or temperature. However, thermal resistance or conductance is incapable of describing the thermal components of heat flow and temperature, such as an intermittently incubated egg might experience. These components require other measures of heat flow and temperature response.

In the theory of physical systems (systems that transfer energy down potential energy gradients and do work with them; Trimmer, 1950), the transient component of energy flow is conventionally accounted for by an *impedance*, rather than a *resistance*. For example, the flow of AC electrical energy through a circuit is limited by an *electrical impedance* that limits flow of electrical energy in AC circuits (Horowitz and Hill, 1980). Similarly, the flow of sound energy into hearing organs is limited by an *acoustic impedance* (Alexander, 1983). By the same analogy that allows one to define a thermal *resistance*

for steady conditions of heat flow, one should be able to account for the transient components of heat flow through an object like an egg by a thermal *impedance*.

While the transient state behavior of eggs cooling in air is fairly well understood (Kendeigh, 1963; Turner, 1985), virtually nothing is known about how eggs change temperature when they are being warmed intermittently by a brood patch. In this paper, I outline methods for measuring the transient-state thermal properties of contact incubated eggs, including the thermal impedance. I then report measurements of these for infertile chicken eggs that are contact incubated by an artificial brood patch. My hope is that the thermal impedance of intermittently incubated eggs will prove to be a useful tool in understanding the interaction of time and energy in intermittent incubation (Vleck, 1985).

THEORY OF MEASUREMENT

The thermal impedance, Z_t , is a time-dependent resistance to heat flow. At its simplest, the thermal impedance is the vector sum of two components: the steady state thermal resistance, R_t , which has no time dimension, and the capacitive reactance, X_c , which depends upon how the energy input driving the system changes with respect to time (Trimmer, 1950). In the customary vector notation, the thermal impedance is:

$$Z_t = R_t + X_c. \quad (1)$$

The most straightforward way to measure R_t and X_c involves subjecting the egg to a sinusoidally-varying heat input, and quantifying the resulting sinusoidally-varying temperature (Trimmer, 1950). Thus, the heat input to the egg, q_i , (also known generally as the forcing function) is described by the equation:

$$q_i = A_q + B_q \sin(2\pi t/P) \quad (2a)$$

and the resulting temperature of the egg (also known generally as the forced response) is described by the equation:

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

where A = time average of the subscripted quantity (W or °C), B = amplitude of variation of the subscripted quantity (W or °C), t = time (s), P = period of the oscillation (s), and φ = phase delay (rad). In both Eq. (2a, b), there is a steady component (A) and a time-dependent transient component (B).

From the parameters of Eq. (2a, b), it is a simple matter to calculate R_t and X_c . The thermal resistance (°C W⁻¹) is calculated from the ratio of the steady components:

$$R_t = A_T/A_q \quad (3a)$$

The capacitive reactance is calculated as:

$$X_c = R_t \tan(-\varphi) \quad (3b)$$

The thermal impedance, being the vector sum of these two quantities [Eq. (1)] is simply:

$$Z_t = (R_t^2 + X_c^2)^{0.5} \quad (4)$$

(Trimmer, 1950).

Two other useful quantities can be calculated from the phase delay of T with respect to q_i . The time constant, τ , is calculated from τ and P :

$$\varphi = -\tan^{-1}(\tau/P) \quad (5)$$

The power factor, ρ , describes how effectively the transient component of heat flow penetrates the egg. It is calculated from φ :

$$\rho = \cos \varphi \quad (6)$$

Clearly, the transient component of heat flow is maximized by making the phase delay between q_i and T as close to null as possible.

MATERIALS AND METHODS

Twenty-four infertile chicken eggs were used for these measurements, so that thermal impedance would be determined by R_t and X_c only. The effects of resistance changes arising from embryonic circulation and possible 'induction-like' effects of embryo metabolism will be considered in a later paper.

Eggs were contact-incubated by an artificial brood patch (ABP) system (Drent, 1970, 1975), as modified by Turner (1992). The artificial brood patch is a cup-shaped Dewar flask, custom-fitted to cover part of the surface of an egg. A heating element in the cup dissipates heat when electrical current is passed through it. Heat so dissipated can only leave the cup through the egg.

The ABP was fitted with a 22 Ω resistive heating element. Current through the heating element was controlled by a 100 Hz DC switching power supply. Pulse width was digitally modulated via a Centronics-compatible parallel printer output from a microcomputer. The controllable duty cycle, δ , ranged from 0.42–0.95, and could be set with a linear resolution of 1 part in 170. Heat dissipated by the heating element was calculated from the duty cycle and full-on power dissipation, q_f :

$$q_i = \delta q_f = \delta V_f I_f \quad (7)$$

where V_f , I_f = on-voltage across and on-current through the heating element, respectively.

Three 36 Ga type T thermocouples were implanted into each egg prior to measurement: one at the upper surface of the egg, just under the heating element,

designated brood patch temperature, T_{br} ; one at the surface of the egg opposite the brood patch thermocouple, designated antipodal temperature, T_{ant} ; and a third into the center of the egg, designated T_c . The center thermocouple was contained within a capillary tube, that was itself mounted on a jig to ensure that the thermocouple tip was in a reproducible location in the egg center. All thermocouples were secured in place with drops of paraffin wax.

The egg was coupled to the ABP by pouring unset dental alginate into the cup, and then pressing the egg snugly into the cup. Once set, the excess alginate was trimmed away with a razor blade. Any exposed alginate remaining around the rim of the ABP was coated with petroleum jelly to prevent evaporation.

The egg-ABP assembly was placed into a carrier that supported the egg at three points, so that conductive heat losses from the egg to the support were minimized. The entire assembly was placed into a water-jacketed chamber. The temperature of the chamber was measured with a thermocouple in the air secured just below the egg. Air was drawn through the chamber at a rate of about 20 ml s^{-1} . The temperature of the water circulating through the water jacket was controlled using a thermostatically controlled refrigerated water bath.

Voltages from the three egg thermocouples and the air thermocouple were sensed by a 16-channel multi-

plexed A/D converter, with inputs amplified $50 \times$ (Remote Measurement Systems, Seattle, WA). Sampling was controlled by a microcomputer (Tandy, Dallas, TX). The switching power supply was controlled through the Centronics parallel printer port of the microcomputer. The controlling software allowed the user to set the average value, amplitude, and period of the sinusoidal power dissipation. Average heat dissipation in all experiments was 0.3 W , with an amplitude of 0.05 W . Periods ranged from 12–600 min. The controlling software also sampled the temperatures of the thermocouples at regular intervals ranging from 1 to 10 min. Data stored were later downloaded to disk and analyzed as described above. Typically an experiment lasted 6 h or 3 periods, whichever was longer.

From the time series of egg temperature and heat input data, the average value, amplitude and phase delay of the egg temperatures were calculated according to the least squares methods outlined by Bloomfield (1976). Data selected for time series analysis were those for the last complete period of the experiment.

RESULTS

Of the twenty-four eggs used, 11 separated from the alginate during the experiment. Thus, only 13 of the eggs provided suitable data.

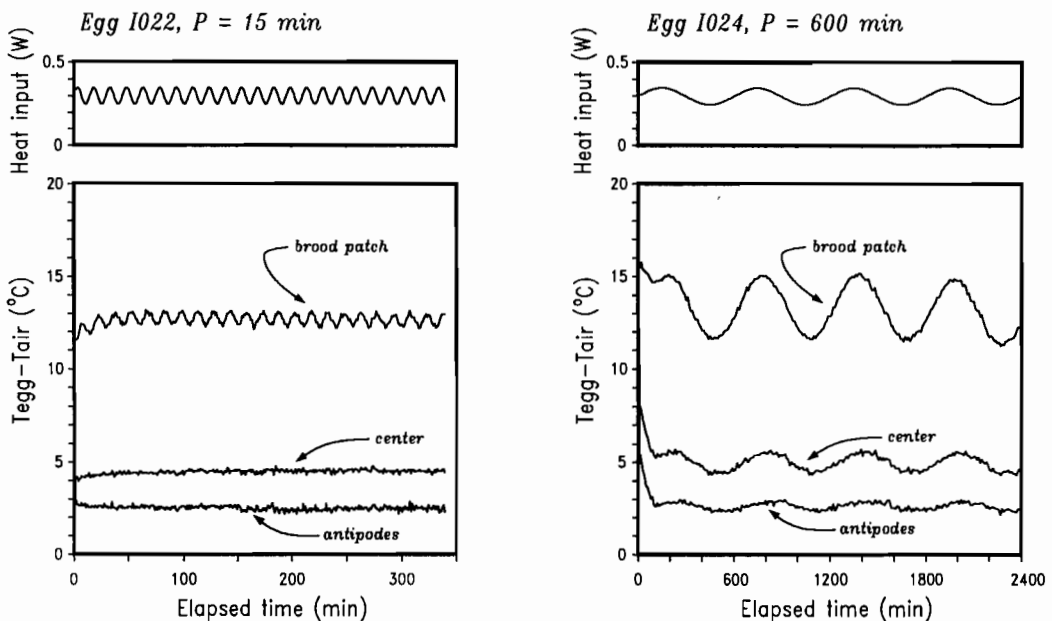


Fig. 1. Sample results from sinusoidally-varying heat inputs to two representative eggs. Temperatures of the brood patch, center and antipodal surface of the egg are expressed as a temperature elevation above the chamber air temperature. Elapsed time is the time since the beginning of the experiment. 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 $0.3 \pm 0.05 \text{ W}$, respectively. Left panel: period = 15 min. Right panel: period = 600 min.

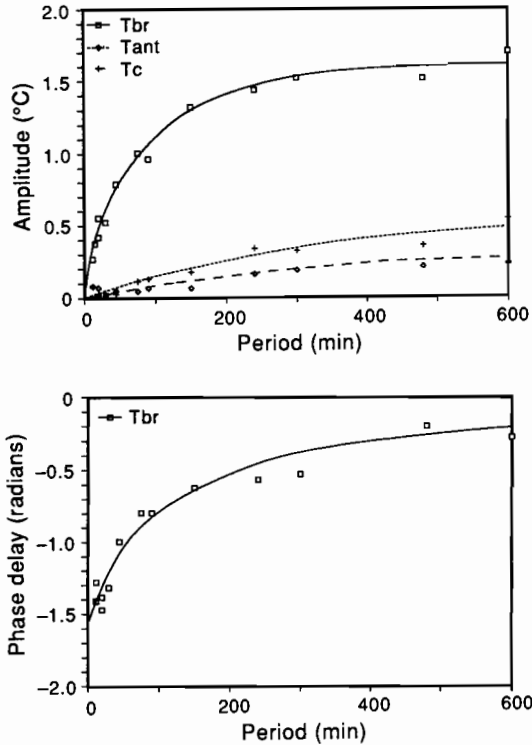


Fig. 2. Amplitude and phase delay of sinusoidally-varying temperature of 13 infertile chicken eggs, subjected to sinusoidally-varying heat inputs via an artificial brood patch. Top panel: amplitudes of variation for temperatures at the brood patch (\square , solid curve), egg center (+, dotted curve) and antipodal surface of the egg (\diamond , 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 from two typical experiments are shown in Fig. 1: a very long period (600 min) and a very short period (15 min). It is clear that the sinusoidal variation in heat input forces a sinusoidal variation of egg temperature. The amplitude of temperature variation is smaller when the period of the forcing heat input is shorter. The amplitude of variation is highest at the brood patch, and smaller at the other parts of the egg (Fig. 1).

As the period of variation of heat input shortens, the amplitude of variation in egg temperature shortens (Fig. 2), and the magnitude of the phase delay increases (to a maximum value of $-\pi/2$; Fig. 2). At the center of the egg, the maximum amplitude is about 0.5°C , and falls to less than 0.1°C at periods of roughly 60 min or less (Fig. 2). At the antipodal surface, the maximum amplitude of variation is about 0.2°C , and falls to less than 0.1°C at periods of roughly 110 min or less (Fig. 2).

The steady-state resistance of the eggs calculated by Eq. (3a) averaged about $42.7^{\circ}\text{C W}^{-1}$, with a

standard deviation of $1.6^{\circ}\text{C W}^{-1}$, similar to that measured under steady state conditions by Turner (1992). The steady state resistance appears to be independent of period (Fig. 3). The capacitive reactance, in contrast, is strongly influenced by period. Capacitive reactance is roughly equal to steady state resistance at a period of about 110 min, and falls to near zero as period increases (Fig. 3). As periods shorten, capacitive reactance increases sharply as period falls below roughly 30 min (Fig. 3). Consequently, thermal impedance is roughly constant at periods of 60 min or longer, but increases to roughly twice the steady state resistance at periods of 15 min or less (Fig. 3).

The best estimate for τ , estimated by minimizing the sum of square error between observed and predicted values of φ fitted to Eq. (5), was 20.1 min ($F = 16.89$, $P \approx 0.005$).

Power factor, ρ , increased with increasing period (Fig. 4). Transient flow of heat into the egg was 50% efficient at periods of about 40 min or more (Fig. 4).

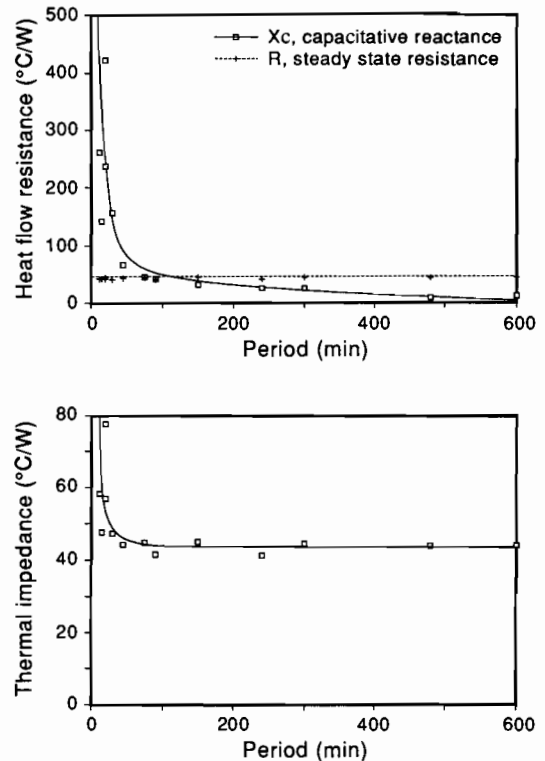


Fig. 3. Components of thermal impedance for 13 infertile chicken eggs subjected to a sinusoidally-varying heat input via an artificial brood patch. Top panel: capacitive reactance (\square , solid curve), and steady state resistance (+, dotted line), calculated as per Eq. (3a, b) in text. Curves fitted by eye. Bottom panel: thermal impedance as calculated from the steady-state resistance and capacitive reactance as per Eq. (4) in text. Curve fitted by eye.

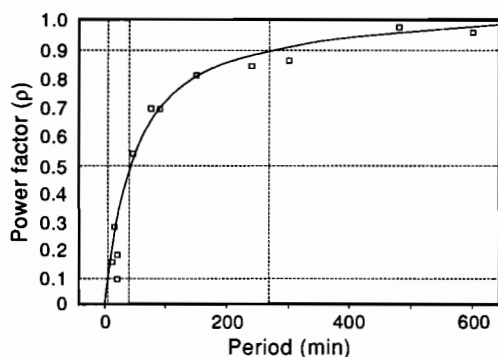


Fig. 4. Power factor, ρ , calculated for infertile chicken eggs. Dotted lines indicate power factors and associated periods for 90, 50 and 10% efficiency of heat flow into the egg from the brood patch.

For the transient inflow of heat to be 90% or more efficient required a period greater than 260 min (Fig. 4).

DISCUSSION

Among intermittently incubating birds, there appears to be an inextricable link between use of time and use of energy (Vleck, 1985). For example, the time a bird spends away from its nest will inevitably influence how much the eggs cool during the absence. The parent's energy cost of rewarming the egg upon return to the nest will in turn be influenced by how much the eggs have cooled during the prior absence (Biebach, 1986). An intermittently incubating bird must therefore balance both temporal and energetic demands in its schedule of incubation and foraging—a bird that spends time away from the nest foraging will ultimately pay for it in an energy cost of rewarming the egg.

Conventional measures of thermal energetics, like the thermal conductance (or its inverse, thermal resistance) of an egg, only describe steady-state flows of heat. Thus, they cannot help in understanding how time and energy are linked in intermittent incubation, simply because the dimension of time does not enter into them. A more appropriate measure of the energetics of an intermittently incubated egg would therefore be a time-dependent quantity like a thermal impedance.

This paper reports a method for measuring the thermal impedance and other transient-state thermal properties of contact-incubated birds' eggs. Applying this method to infertile chicken eggs shows some expected, and some unexpected, thermal properties of the transient state.

Among the expected results are that contact-incubated chicken eggs have a measurable thermal impedance, in which the egg behaves as a classical

thermally damped system. For sinusoidal heat inputs at periods less than about 30 min, the egg's capacitive reactance and thermal impedance increases markedly above the steady-state thermal resistance (Fig. 3). In this respect, the contact-incubated chicken egg is a thermal analog to a low-pass electronic filter (Horowitz and Hill, 1980).

One unexpected and revealing result concerns the contact-incubated egg's time constant for temperature change, τ . The time constant for the contact-incubated egg was estimated to be about 20.1 min, roughly half the 41.5 min time constant for a chicken egg cooling in air (Table 1; Turner, 1985). This result is surprising because the steady resistance to heat flow through contact-incubated eggs is considerably higher than that for that of an egg cooling in air (Table 1; Turner, 1985, 1992), which should lengthen the time constant, not shorten it. The opposite result indicates that contact-incubated eggs have an 'effective thermal mass', i.e. a portion of the egg that is actually participating in transient heat flows, that differs from the thermal mass of eggs cooling in air.

One can use the time constant to estimate what this 'effective thermal mass' is. If a region of the egg experiences a transient heat flow, the temperature of this region will also exhibit a transient component. The transient component of heat flow obviously does not penetrate with perfect efficiency into the egg, since the amplitude of temperature variation declines as one moves to regions of the egg further from the brood patch, like the egg center, or antipodal surface of the egg (Fig. 2). Consequently, not all regions of the egg are participating fully in the transient flows of heat.

The time constant, τ , is the product of the egg's thermal mass (more precisely its thermal capacitance) and the steady resistance to heat flow, R_t ($^{\circ}\text{C W}^{-1}$). It follows that the thermal capacitance, C ($\text{J }^{\circ}\text{C}^{-1}$), can be estimated from R_t and τ (s):

$$C = \tau/R_t \quad (8)$$

The time constant for a chicken egg surrounded on

Table 1. Thermal properties of convectively incubated and contact incubated eggs compared; data for convectively incubated eggs are from Turner (1985)

	Convectively incubated	Contact incubated	Contact/convective
τ (min) (measured)	42.1	20.1	0.477
R_t ($^{\circ}\text{C W}^{-1}$) (measured)	13.7	42.7	3.12
C ($\text{J }^{\circ}\text{C}^{-1}$) (estimated)	184	28.2	0.153

all sides by air is roughly twice the time constant for contact incubated eggs (Table 1; Turner, 1985, 1992). The thermal resistance of the chicken egg in air is roughly a third that of a contact incubated egg (Table 1; Turner, 1985, 1992). This leads to the surprising conclusion that the thermal capacitance of a contact-incubated egg is only about 15% that of the convectively incubated egg (Table 1). Since the specific heat of eggs is fairly uniform, this implies that only about 15% of the mass of a contact-incubated egg is actually 'thermal mass', i.e. involved in the transient flux of heat between the brood patch and egg. If so, this may imply that the energetic cost of rewarming an egg is considerably less than would be indicated by the egg's gravimetric mass.

How could a quantity like thermal impedance illuminate the interaction of time and energy in intermittent incubation? The method reported here subjected the egg to sinusoidally-varying inputs of heat that differed in period. The inputs of heat that an intermittent incubated egg would receive through a bird's brood patch obviously would not be sinusoidal. However, any periodic phenomenon can be described as a Fourier series, i.e. a series of sinusoids that sum to yield the periodic variation (Glantz, 1979). This can even be extended to aperiodic phenomena (Glantz, 1979). Thus, for example the heat input to an egg incubated by a bird that repeatedly visits the nest for x min and then abandons the nest for y min could be represented by a train of square wave heat impulses with a period of $x + y$ min. This train of pulses is dissectable into a Fourier series with dominant sinusoidal frequency, ω_1 , of $2\pi/(x + y)$ rad min⁻¹, and subordinate frequencies of $3\omega_1$, $5\omega_1$, ... etc. (Glantz, 1979). A similar analysis could be done for any time-varying input of heat to the egg, whether it be periodic or not.

The thermal impedance, because it varies with period (or frequency) of the heat input, allows one to weight the influence of the various sinusoidal components of the heat input from the brood patch (the forcing function) on the egg temperature (the forced response). For example, a train of square-wave heat inputs to an egg would, in the absence of any capacitative reactance, result in a square-wave train of temperature changes, meaning that all the sinusoidal components that comprise the forcing function carry over directly into the forced response (Trimmer, 1950). However, if there is a capacitative reactance, heat from the high-frequency components will not penetrate the egg, and thus will not force the egg's temperature to change. Thus, the temperature variation of an intermittently incubated egg will be 'smoothed out' (White and Kinney, 1974), reflecting the disproportionately large influence of the domi-

nant and low-frequency components of the heat input on egg temperature (Trimmer, 1950).

The 'thermal filtering' that is afforded by the egg's thermal impedance might help to distinguish what incubation behaviors would significantly influence the temperature of the egg. Using the data reported here on the chicken egg as an example, when the period of heat input is roughly 60 min or less, the efficiency of heat flow into the egg is around 50% (Fig. 4). The amplitude of temperature variation in the center of the egg is $<0.1^\circ\text{C}$ (Fig. 2). Any sinusoidal component of the heat input with a period less than this would penetrate less effectively into the egg, and would have a lesser influence on temperature in the center of the egg. Thus, if the visitation period of a bird that was intermittently incubating an egg of this size was less than 60 min, the temperature at the center of the egg would be nearly constant. Perhaps more importantly, there could be considerable variation of visitation period at periods less than 60 min with little consequence for egg temperature.

In summary, the intermittent incubation of a bird's egg involves repetitive transient inputs of heat to an egg through a brood patch. For intermittent incubation, conventional quantities in thermal energetics, like the thermal conductance, are less appropriate than measures that account for transient inputs of heat, like a thermal impedance. The thermal impedance of infertile chicken eggs was measured by subjecting the egg to a sinusoidally varying input of heat, and then measuring the amplitude and phase delay of the resulting sinusoidal variation of temperature. The thermal impedance of infertile chicken eggs increases markedly at heat input periods shorter than 60 min. The time constant for rewarming an intermittently incubated egg is about half that for an egg cooling in air. The short time constant also implies that energetic costs of rewarming the egg might be considerably less than supposed based on mass of the egg. The thermal impedance may be a useful general property for study of the time and energy costs of incubation for intermittent incubators.

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