
Transient-State Thermal Properties of Contact-incubated Chicken Eggs

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Abstract

Chicken eggs subjected to a sinusoidally varying input of heat from a brood patch experience sinusoidally varying egg temperatures. As the embryo matures, steady and transient egg temperatures become more uniform, declining about 0.8°C at the brood patch and increasing from 0.4° to 0.8°C in the more peripheral regions of the egg. The increasing homogeneity of egg temperature is reversed by killing the embryo. Steady resistance of the egg declines from 41.9°C W⁻¹ at the start of incubation to an average of 33.8°C W⁻¹ by the end and is independent of the period of variation of brood patch heat output. Capacitative reactance of the egg declines about 10% through incubation in concert with an average 10% mass loss by the egg. Capacitative reactance is strongly dependent on the period of the heat input, increasing from 27.8°C W⁻¹ at a period of 120 min to 151°C W⁻¹ at a period of 20 min. Thermal impedance declines roughly 12% throughout the incubation period, which is attributable in similar parts to increasing circulation within the egg and to the declining mass of the egg. The time constant for the warming of a contact-incubated egg declines from 13.1 min at the start of incubation to 11.4 min at the end. There is no evidence of hysteresis in the heating and cooling rates of the egg. The time constant for temperature change of a contact-incubated chicken egg is considerably shorter than that of an egg cooling in air. The importance of these results for understanding the energetics of intermittent incubation is discussed.

Introduction

Two common "styles" of incubation are found among birds (Skutch 1957, 1962): two-parent incubators and single-parent incubators. When both parents incubate, the eggs are attended nearly continuously and usually stay at

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al. 1978; Vleck 1981*a*, 1981*b*; Webb and King 1983; Zerba and Morton 1983*a*, 1983*b*; Biebach 1986; Weathers and Sullivan 1989)? In the first instance, the parent will incur a single rewarming bout per day—but one with a large energy cost. In the second instance, the parent will incur a small energy cost for each bout of rewarming, which will be repeated many times per day. Which allotment of time and energy is better?

Our ability to answer questions such as these would be advanced by our understanding how the brood patch interacts thermally with a warming egg. This interaction is reasonably well understood for eggs in steady state (Ackerman and Seagrave 1984; Turner 1992), where the egg can be modeled as a thermal resistance analogue. Unfortunately, our understanding of the transient-state energetics of contact-incubated eggs (see fig. 1, below) is slim.

This article is intended to describe the transient-state thermal properties of living eggs incubated by a brood patch. In particular, I will show how the presence of an embryo influences the transient-state thermal energetics of its egg. I conclude by discussing what these influences may mean for the use of time and energy in intermittent incubation.

Material and Methods

Eggs

Fertile chicken eggs (*Gallus domesticus*) were convectively incubated (sensu Turner 1992) at 37°C in a temperature-controlled incubator. Viability of eggs throughout the incubation period was assessed by candling of the eggs.

The Artificial Brood Patch

Eggs were contact incubated (sensu Turner 1992) by means of an artificial brood patch (ABP) system, which has been described in detail by Turner (1992, in press). The ABP allows the direct measure of the heat energy requirement for incubating eggs with a brood patch (Drent 1973).

Heat Production at the ABP

Measurement of the transient-state thermal properties of an egg requires the heat input to the egg from the brood patch (q_b ; W) to have a transient component. A convenient choice for q_b is a sinusoid of known frequency and amplitude (Trimmer 1950), such that

a relatively constant temperature throughout incubation (Burke 1925; Drent 1973; Siegfried and Frost 1974; Bertram and Burger 1981; Swart, Rahn, and deKock 1987; Evans 1989). When only one parent incubates, the eggs are intermittently abandoned while the parent feeds and patrols territory. The eggs cool during the parent's absence and are rewarmed with the brood patch on the parent's return to the nest (Huggins 1941; Skutch 1957, 1962; Drent 1973; White and Kinney 1974; Armstrong and Whitehouse 1977; Pikula 1977; Walsberg and King 1978; Yom-Tov, Ar, and Mendelssohn 1978; Vleck 1981*a*, 1981*b*; Webb and King 1983; Zerba and Morton 1983*a*, 1983*b*; Naylor, Szuba, and Bendell 1988; Weathers and Sullivan 1989).

A physical system is any system in which energy flows down a potential energy gradient and does work (Trimmer 1950). Energy flow through a physical system can be broken down into two components (Trimmer 1950): steady and transient. The steady component is characterized by a potential energy gradient that does not vary with respect to time: the flow of energy through the system is limited primarily by a resistance to energy flow and the magnitude of the potential energy gradient. The transient component is characterized by a time-varying potential energy gradient. In addition to a resistance to energy flow, the capacity of the system to store energy, or its capacitance, influences the flow of energy through the system (Trimmer 1950). The dimension of time thus becomes an important factor in the energetics of transient-state physical systems.

The continuously incubated egg, because of its fairly steady temperature, is a steady-state physical system. In contrast, the intermittently incubated egg, because of its time-varying temperature, is a transient-state physical system. Consequently, intermittent incubators must deal with both time and energy in ways that continuous incubators do not (Vleck 1985).

Consider, for example, how an intermittent incubator might balance the time spent away from the nest against the energy cost of rewarming the eggs. The energy cost of rewarming the eggs is proportional to how much the eggs have cooled during the parent's absence (Drent 1973; Vleck 1981*b*, 1985; Biebach 1986). How much the eggs cool will itself depend on how long the bird has spent away from the nest (Drent 1973; Hohman 1986; Thompson and Raveling 1987; Naylor et al. 1988; Hepp, Kennamer, and Harvey 1990). How then should the bird spend its daily allotment of time away from the nest? Should the bird spend it all in one long absence per day, as is seen among many seabirds, fowl, and waterfowl (Drent 1973; Hohman 1986; Thompson and Raveling 1987; Naylor et al. 1988; Hepp et al. 1990), or should it spend the time in many short absences, as is seen among many passerines (Kendeigh 1952; Skutch 1957, 1962; White and Kinney 1974; Armstrong and Whitehouse 1977; Mertens 1977; Yom-Tov et

$$q_b(t) = q_0 + A_{qb}\sin(2\pi t/p), \tag{1a}$$

where $q_b(t)$ is the heat input (W) as a function of time, t (min); q_0 is the mean heat input (W); A_{qb} is the amplitude of heat input (W); and p is the period (min). This imposes on the egg a sinusoidal variation of temperature, $T(t)$, that varies around a mean temperature, T_0 , with a characteristic amplitude, A_T , and phase delay, ϕ_T , with respect to $q_b(t)$:

$$T(t) = T_0 + A_T\sin(2\pi t/p - \phi_T). \tag{1b}$$

The sinusoidal variation of $q_b(t)$ was provided by a computer-controlled switching power supply as described by Turner (in press). A representative set of data, which shows the codependent sinusoidal variations in $q_b(t)$ and egg temperature, is provided in figure 1.

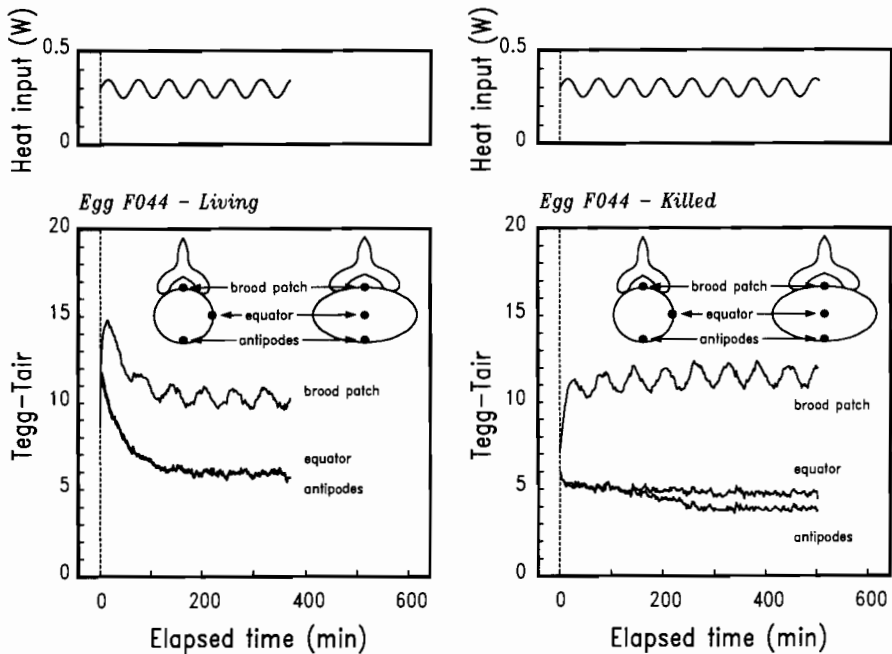


Fig. 1. Sample data showing the codependent sinusoidal variation of $q_b(t)$ and T_b , T_e , and T_a of the egg. Data are from egg F044, which was subjected to the heating conditions for experiment 1. Heat input and temperature variation in the living egg (left) and in the killed egg (right).

The Egg-ABP Assembly

Three 32-gauge, type-T thermocouples were attached to the egg: one to measure the temperature of the egg at the brood patch (T_b), one to measure either the egg center temperature (T_c) or the surface temperature at the equator of the egg (T_e), and one to measure the antipodal temperature (T_a) at the egg surface opposite the brood patch. Surface temperature thermocouples were secured to the eggshell with a drop of paraffin wax. To place a thermocouple at the egg center, a hole of 1 mm in diameter was drilled in the eggshell with a dental drill. A glass capillary tube sealed at one end was then inserted through the hole and secured with paraffin wax. The capillary tube acted as a sleeve to hold a 32-gauge, type T thermocouple at the center of the egg. Damage to the embryo by the implantation of the capillary tube was assessed by visual inspection of the embryo after an experiment was completed. If the embryo exhibited severe bruising or blood in the extraembryonic fluids, data from that egg were discarded.

The egg outfitted with the thermocouples was secured in the ABP with dental alginate as described by Turner (1992, in press). The egg-ABP assembly was then mounted on a carriage, which held it securely in place in a temperature-controlled chamber. The carriage also carried a thermocouple to measure the temperature of the chamber (T_{air}), which was controlled at about 23°C by the circulation of water through a water jacket from a thermostatically regulated water bath.

Experiments

Experiment 1: Transient Temperatures of Living versus Killed Eggs. Experiment 1 compared the transient temperatures of 15 living and 15 killed eggs at three incubation ages (beginning, 1–6 d; middle, 7–12 d; end, 13–18 d). The eggs were subjected to a sinusoidal $q_b(t)$ (eq. [1a]) with a single p of 60 min ($q_0 = 300$ mW; $A_{qb} = 50$ mW). The class variables were the viability of the eggs (whether they were living or killed) and the incubation ages of the eggs. The dependent variables for this experiment were the characteristic amplitudes for the temperature of the surface of the egg at the brood patch (A_{T_b}), at the equator (A_{T_c}), and at the antipodes (A_{T_a}); and the mean temperatures of the egg at the brood patch ($T_{0,b}$), at the equator ($T_{0,e}$), and at the antipodes ($T_{0,a}$).

An egg was subjected to six full cycles of $q_b(t)$. Temperature data from the last cycle were used to estimate the egg's T_0 and A_T . Parameter estimates were made according to the least squares method described by Bloomfield (1976).

The egg-ABP assembly was then removed from the chamber, and the egg was injected with 0.5 mL of saturated KCl to induce cardiac arrest in the embryo. Care was taken to not disturb the connection between the ABP and the egg or any of the attached thermocouples. The egg's transient temperatures were then measured again according to the method just described.

The effect of incubation age was assessed by means of a one-way ANOVA with the incubation age as a class variable. Separate analyses were done for the living eggs and for the killed eggs. The effect of killing the embryo was assessed by paired comparison *t*-tests between living and killed eggs for each age class.

Experiment 2: Transient-State Thermal Properties of Living Eggs. Experiment 2 measured transient-state thermal properties (Turner, in press) of 42 living eggs partitioned into three different incubation age classes (beginning, 1–6 d; middle, 7–12 d; end, 13–18 d) at three different *p*'s of $q_b(t)$ (20 min, 60 min, and 120 min; $q_0 = 300$ mW; $A_{qb} = 50$ mW) by means of a sinusoidal forcing function (eq. [1a]). The class variables were the *p* and the incubation ages. The dependent variables were A_{Tb} , A_{Ta} , the characteristic amplitude for the egg center temperature (A_{Tc}), $T_{0,b}$, $T_{0,a}$, the mean temperature of the egg at the center ($T_{0,c}$), the steady-state thermal resistance (R), the capacitive reactance (\mathbf{X}_c ; °C W⁻¹), and the thermal impedance (\mathbf{Z}_t ; °C W⁻¹). Eggs were prepared as described above, except that T_c rather than T_e was measured. Eggs were allowed to equilibrate under the schedule of heat input for at least 6 h or four complete cycles of $q_b(t)$, whichever was longest.

Data from the last cycle were used to estimate the egg's T_0 , A_T , and ϕ_T . From these data, R , \mathbf{X}_c , and \mathbf{Z}_t were calculated (Turner, in press). In addition, the data for the three *p*'s were used to estimate a time constant for temperature change, τ (min). Details of these calculations are given in Turner (in press).

Data were analyzed by a two-way ANOVA. The class variables were incubation age and *p*. Because the \mathbf{X}_c and \mathbf{Z}_t are trigonometric functions, the measured values for these quantities had considerable heterogeneities of variance. Consequently, comparisons for these quantities were made with their log-transformed values (Sokal and Rohlf 1969).

Experiment 3: Time Constants for Temperature Change of Eggs under a Pulsed Heat Input Regime. Experiment 3 measured, by means of a step forcing function ($q_b(t) = q_0 - A_{qb}$ [$t = 0p \rightarrow 0.5p$] or $q_b(t) = q_0 + A_{qb}$ [$t = 0.5p \rightarrow p$]; $p = 200$ min; $q_0 = 325$ mW; $A_{qb} = 25$ mW), the temperature response of eggs subjected to a step change of $q_b(t)$. Eggs were subjected to repeating step changes in $q_b(t)$ of 300 mW to 350 mW to 300 mW with a

single p of 200 min. The class variable was viability (living or killed eggs). The dependent variables were the time constant for rewarming (τ_w) and the time constant for cooling (τ_c).

Seventeen fertile chicken eggs were incubated for 15–19 d. Eggs were prepared for measurements as described above, with the exception that only T_b was measured.

Subsequent to a step transition of $q_b(t)$, T_b was followed as it equilibrated to a new temperature. Brood patch temperatures from the last 20 min of each 100-min phase of the cycle were averaged to provide an equilibrium brood patch temperature (T_{eq}); τ was calculated by the fitting of a least squares linear regression to the equation

$$\ln((T_t - T_{eq})/(T_i - T_{eq})) = -\tau^{-1}t, \quad (2)$$

where T_t is the egg's temperature at time t , and T_i is the egg's temperature at the beginning of the transient.

Once the data were taken for the living egg, the embryo was killed as described above, and the measurements were repeated.

Data were analyzed by paired t comparisons between measurements of living (preinjection) and killed (postinjection) eggs.

Results

Experiment 1: Comparison of Living versus Killed Eggs

Mean temperatures of eggs in all age classes contained substantial temperature gradients between the brood patch, equatorial surface, and antipodal surface of the eggs, irrespective of whether they contained living embryos (fig. 1, table 1). These gradients declined among the living eggs as the embryos grew inside them (table 1), and eggs containing living embryos became more thermally homogeneous during the incubation period. The increasing homogeneity among the living eggs arose through a decline in the $T_{0,b}$ of roughly 1.8°C, which was simultaneous with increases in the $T_{0,e}$ and $T_{0,a}$ of roughly 1.0°C and 1.5°C, respectively (table 1). All changes with respect to incubation age were statistically significant (table 2). Among the living eggs, most of the change in T_0 's occurred between the middle and the end of the incubation period (table 1).

Among killed eggs, however, these age-dependent changes in the T_0 's were not evident (table 1). There was a statistically significant drop in $T_{0,a}$ in the middle period of incubation (tables 1, 2), but there was no

TABLE 1

Main effects means for comparisons of average egg temperatures ($^{\circ}\text{C}$) and egg temperature amplitudes ($^{\circ}\text{C}$) for living and killed eggs of three different age ranges (experiment 1)

| Dependent Variables | Age | | |
|--------------------------------------|-----------|--------|-------|
| | Beginning | Middle | End |
| Living: | | | |
| $T_{0,b} - T_{\text{air}}$ | 12.79 | 12.29 | 10.94 |
| $T_{0,e} - T_{\text{air}}$ | 4.64 | 4.43 | 5.59 |
| $T_{0,a} - T_{\text{air}}$ | 3.83 | 3.71 | 5.30 |
| A_{Tb} | .72 | .77 | .61 |
| A_{Te} | .06 | .09 | .12 |
| A_{Ta} | .05 | .05 | .10 |
| Killed: | | | |
| $T_{0,b} - T_{\text{air}}$ | 12.54 | 12.77 | 12.67 |
| $T_{0,e} - T_{\text{air}}$ | 4.64 | 4.24 | 4.51 |
| $T_{0,a} - T_{\text{air}}$ | 4.06 | 3.65 | 4.05 |
| A_{Tb} | .72 | .80 | .77 |
| A_{Te} | .07 | .06 | .13 |
| A_{Ta} | .05 | .06 | .07 |

statistically discernible relationship between incubation age and $T_{0,b}$ and $T_{0,e}$ (tables 1, 2).

The A_{Tb} of living eggs declined with incubation age, and A_{Ta} and A_{Te} increased slightly (table 1). The age-dependent changes of A_{Tb} and A_{Ta} were statistically significant only at the $P \leq 0.1$ level (table 2). Among killed eggs, there were no discernible effects of age on A_{Tb} , A_{Te} , or A_{Ta} (tables 1, 2).

Mean temperatures and A_T 's of living eggs differed from those of killed eggs only at the end of incubation and not at the beginning or middle of incubation (tables 1, 2). At the end of incubation, the $T_{0,b}$ of a killed egg was roughly 1.7°C higher than that of a living egg, while the $T_{0,e}$ and $T_{0,a}$ of killed eggs were 1.1°C and 1.3°C lower, respectively (table 1). The A_{Tb} also was greater in killed eggs than in living eggs: the difference ($A_{Tb}[\text{living}] - A_{Tb}[\text{killed}]$) was significantly different from zero ($t = -3.05$, $P = 0.038$). However, killing the egg apparently had no discernible effect on A_{Te} or A_{Ta} , irrespective of incubation age (tables 1, 2).

TABLE 2
Significance levels for agewise comparisons and comparisons of living and killed eggs' temperature means and amplitudes as tabulated in table 1

| Dependent Variables | Agewise Comparisons | Comparisons of Living and Killed Eggs | | |
|-----------------------|---------------------|---------------------------------------|--------|-------|
| | | Beginning | Middle | End |
| $T_{0,b} - T_{air}$: | | | | |
| Living | .015 | | | |
| Killed | .929 | .606 | .422 | .031 |
| $T_{0,c} - T_{air}$: | | | | |
| Living | .005 | | | |
| Killed | .207 | >.99 | .524 | <.001 |
| $T_{0,a} - T_{air}$: | | | | |
| Living | <.001 | | | |
| Killed | .006 | .948 | .203 | <.001 |
| A_{Tb} : | | | | |
| Living | .076 | | | |
| Killed | .508 | .916 | .739 | .074 |
| A_{Tc} : | | | | |
| Living | .217 | | | |
| Killed | .255 | .442 | .337 | .720 |
| A_{Ta} : | | | | |
| Living | .075 | | | |
| Killed | .137 | .411 | .524 | .094 |

Experiment 2: Transient-State Thermal Properties of Living Chicken Eggs

As the embryos grew, the $T_{0,b}$'s declined, while the $T_{0,c}$'s and $T_{0,a}$'s increased (fig. 2). All age-related changes were statistically significant (table 3). There was no significant effect of the p of $q_b(t)$ for any of the T_0 's (fig. 2, table 3).

In contrast, the A_T of all egg temperatures showed a significant effect of both the p of $q_b(t)$ and the incubation age (fig. 3, table 3). Amplitudes increased significantly with respect to the p of $q_b(t)$ at all sites measured in the egg (fig. 3, table 3). The A_{Tb} 's declined significantly with respect to age (fig. 3, table 3), while the A_{Tc} 's and A_{Ta} 's increased significantly with respect to incubation age (fig. 3, table 3).

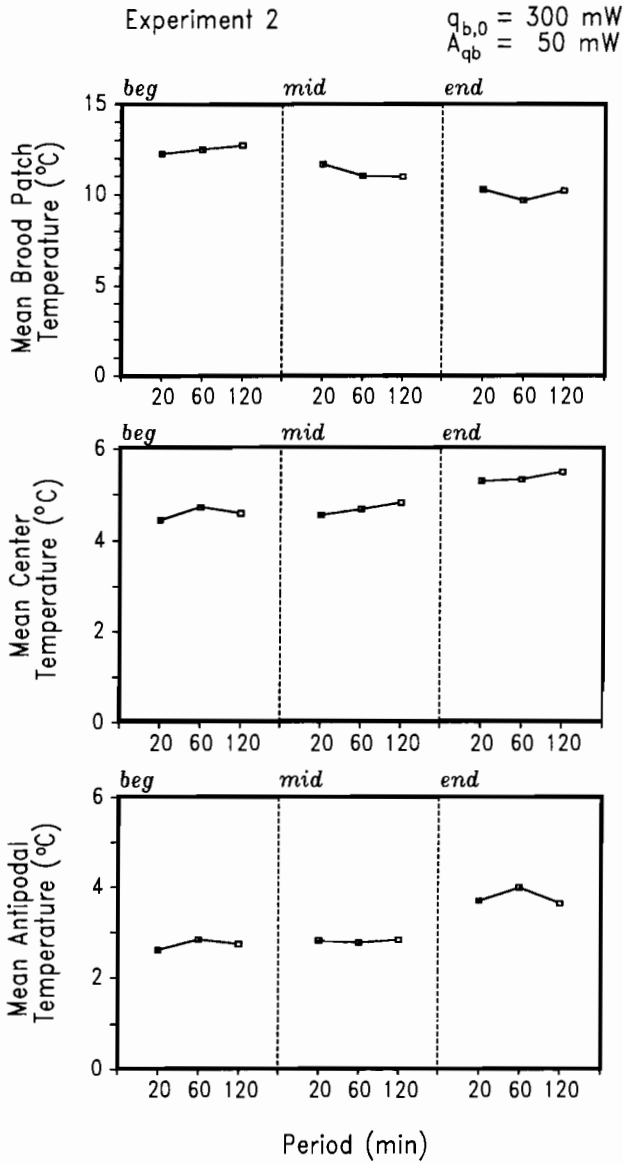


Fig. 2. Mean elevations (above T_{air}) in T_b , T_c , and T_a for living chicken eggs at three p's and three age classes. Significance values for comparisons are tabulated in tables 2 and 3.

As the embryo grew, the R_i of the egg declined by roughly 20%, which was significant (table 4). However, there was no statistically discernible effect of the p of $q_b(t)$ on R_i (table 4). In contrast, X_c declined significantly with the p of $q_b(t)$ (table 4). The X_c also declined by roughly 10% as the

TABLE 3
Significance levels for two-way comparisons of temperatures between incubation ages and period of the forcing heat inputs to living eggs (experiment 2)

| Variables | <i>F</i> | <i>P</i> |
|-----------------------|----------|----------|
| $T_{0,b} - T_{air}$: | | |
| Age | 18.62 | <.001 |
| Period | .43 | .652 |
| $T_{0,c} - T_{air}$: | | |
| Age | 19.77 | <.001 |
| Period | 1.13 | .334 |
| $T_{0,a} - T_{air}$: | | |
| Age | 43.13 | <.001 |
| Period | .76 | .475 |
| A_{Tb} : | | |
| Age | 17.32 | <.001 |
| Period | 82.95 | <.001 |
| A_{Tc} : | | |
| Age | 11.72 | <.001 |
| Period | 151.49 | <.001 |
| A_{Ta} : | | |
| Age | 11.12 | <.001 |
| Period | 40.31 | <.001 |

Note. See figs. 2 and 3 for mean values. Dependent variables are $T_{0,b}$, $T_{0,c}$, $T_{0,a}$, T_{air} , A_{Tb} , A_{Tc} , and A_{Ta} . Independent variables are *age* and *period*.

embryo grew (table 4). The combined declines of both R_i and \mathbf{X}_c with respect to age resulted in a significant decline of \mathbf{Z}_i (table 4). During the incubation period, τ at the brood patch also declined significantly (table 5).

Experiment 3: Time Constants Measured under a Pulsed Heat Input Regime

Time constants estimated from a step change in $q_b(t)$ were similar to those estimated from the ϕ_T and p in experiment 2 (table 5). When the eggs contained living embryos, τ 's were roughly 10.5–11.0 min. When the eggs were killed, τ 's increased significantly to roughly 13.4–14.1 min (table 6).

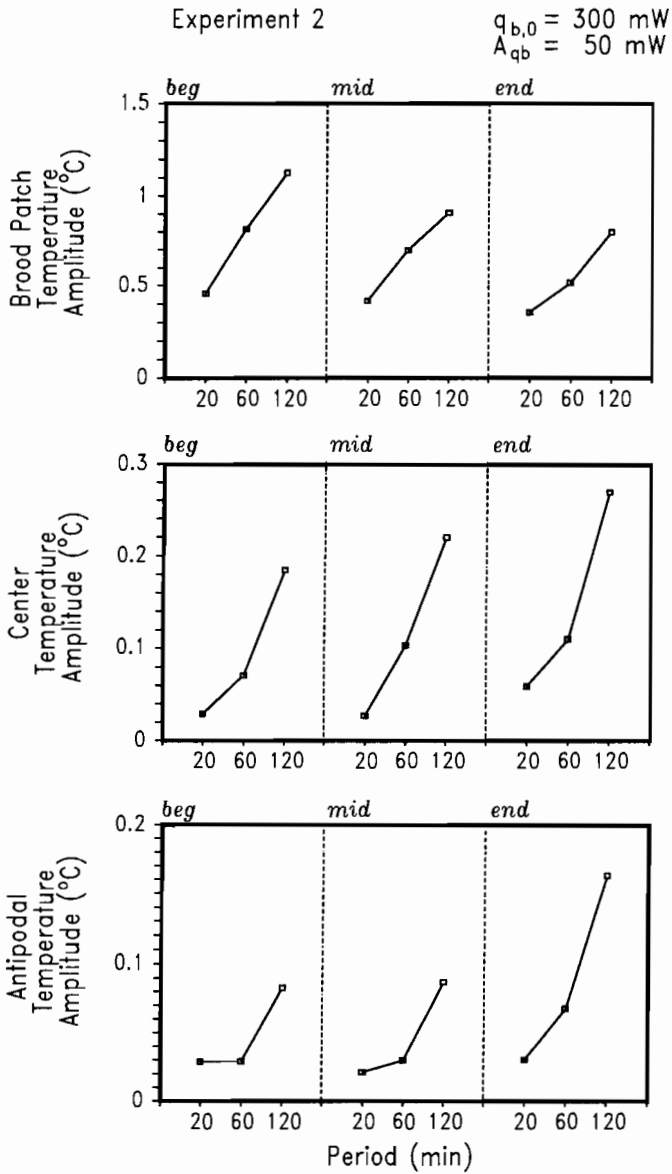


Fig. 3. The A_{Tb} , A_{Tc} , and A_{Ta} for living chicken eggs at three p's and three age classes. Significance values for comparisons are tabulated in tables 2 and 3.

There was no statistically discernible difference between the τ 's for the heating phase and the cooling phase for either the living or the killed eggs (table 6).

TABLE 4
Main effects means and significance levels for two-way comparisons of thermal resistances, capacitive reactances, and thermal impedances of living eggs

| | R_t (°C W ⁻¹) | X_c (°C W ⁻¹) | log X_c | Z_t (°C W ⁻¹) | log Z_t |
|---------------------|--------------------------------|--------------------------------|-----------|--------------------------------|-----------|
| Age (d): | | | | | |
| Beginning | 41.91 | 72.46 | 1.77 | 86.79 | 1.89 |
| Middle | 37.67 | 77.89 | 1.78 | 89.56 | 1.89 |
| End | 33.76 | 65.44 | 1.64 | 78.44 | 1.79 |
| <i>P</i> | <.001 | .461 | <.001 | .842 | .001 |
| Period (min): | | | | | |
| 20 | 38.01 | 150.53 | 2.16 | 155.85 | 2.18 |
| 60 | 37.06 | 44.16 | 1.64 | 57.75 | 1.76 |
| 120 | 37.66 | 27.84 | 1.43 | 46.89 | 1.67 |
| <i>P</i> | .655 | <.001 | <.001 | <.001 | <.001 |

Note. Independent variables are *age* and *period*. Dependent variables are R_t , X_c , and Z_t .

Discussion

It has long been known that intermittent incubators must balance both time and energy in ways that continuous incubators do not (Vleck 1985). Our

TABLE 5
Time constants of living chicken eggs by incubation age

| Incubation Age | τ (min) | <i>F</i> | r^2 |
|---------------------|-----------------|----------|-------|
| Beginning | 13.15 | 106.79 | .92 |
| Middle | 12.83 | 248.38 | .96 |
| End | 11.45 | 86.15 | .89 |
| All ages | 12.43 | 391.95 | .91 |

Note. Time constants have been estimated from the least-squares fit between p and ϕ_{1b} according to the equation $\phi_{1b} = -\tan^{-1}(\tau 2\pi/p)$. *F* ratios and r^2 values have been derived from the least-squares estimate (experiment 2).

TABLE 6

Time constants of living (L) and killed (K) chicken eggs subjected to step changes of $q_b(t)$. Time constants for warming, τ_w , were estimated, as $q_b(t)$ shifted from 300 mW to 350 mW (W), and for cooling, τ_c , as brood patch heat input shifted from 350 mW to 300 mW (C)

| Chicken Eggs | τ (min) | Pairwise comparison t (P) | Pairwise comparison t (P) |
|------------------------|-----------------|-------------------------------------|---------------------------------------|
| <i>L and W</i> | 10.46 | <i>L, W vs. C</i> .296 (.776) | <i>W, L vs. K</i> 2.635 (.0249) |
| <i>L and C</i> | 10.97 | . . . | <i>C, L vs. K</i> 3.947 (.0023) |
| <i>K and W</i> | 13.43 | <i>K, W vs. C</i> .433 (.677) | |
| <i>K and C</i> | 14.07 | . . . | . . . |

Note. Time constants were estimated from the least squares fit of T_b versus t , as described in the text.

understanding of just how these factors interact has been hampered by a poor understanding of one of the crucial steps in intermittent incubation, the warming of the egg by the brood patch. This study has attempted to clarify this process by applying well-established principles of the transient-state thermal energetics of physical systems (Trimmer 1950). From the results reported here, three points are worthy of discussion.

First, conventional transient-state properties of physical systems (Trimmer 1950), such as \mathbf{X}_c and \mathbf{Z}_t , can be measured for eggs being warmed by a brood patch (Turner, in press). This in turn makes the body of theory for the energetics of other transient-state physical systems (such as AC electrical circuits) applicable to this problem.

Second, the presence of a living embryo facilitates both the steady component and the transient component of heat flow from a brood patch into an egg. For chicken eggs, this effect is most important near the end of the incubation period, when the embryo is growing fastest and when age-dependent changes in the circulation and heat production in the egg are fastest.

Third, the τ at the brood patch, which was measured independently in two ways, is considerably shorter (12 min; see also Turner, in press) than

the τ for an egg surrounded on all sides by air (about 43 min for a 60-g egg; Turner 1985). The time constant also shortens as the embryo matures.

The Intermittently Incubated Egg as a Transient-State Physical System

The flow of energy in all physical systems is governed by a common set of principles and equations (Trimmer 1950). This makes possible the well-known method of studying one type of physical system, such as the flow of heat through an egg, by analogy to another, such as the flow of electrical current through a circuit (Trimmer 1950).

In any AC electrical circuit, the basic "problem" that must be solved is how to extract energy from a source where the potential energy gradient that drives energy flow has a significant transient component. By analogy, the energetic problem for an intermittent incubator is how to ensure that the intermittent pulses of heat from the parent penetrate the egg so as to effectively warm the embryo.

The flow of energy through AC circuits is limited by an impedance, the transient-state equivalent of the resistance of a DC circuit. The impedance of a physical system typically limits the flow of energy to those transient components that have a characteristic range of p 's. For example, the electrical impedance of a circuit will allow AC voltages of certain frequencies into the circuit, where they can do work, while AC voltages of other frequencies will be excluded and, hence, will be unable to do work. For example, a filter leaves unchanged a signal that has a characteristic frequency but does screen out "noise"—that is, those signals with other characteristic frequencies.

Contact-incubated eggs behave essentially as thermal "low-pass filters," in which transient heat inputs with long p 's penetrate the egg more effectively than do those with short p 's (Turner, in press). Consequently, A_T everywhere in the egg is larger when the p of $q_b(t)$ is longer (Turner, in press; table 3, fig. 3). For infertile chicken eggs (Turner, in press), the Z_i is nearly equivalent to R_i at p 's of $q_b(t)$ of about 100 min or more. At shorter p 's, $q_b(t)$ from the brood patch is effectively excluded from the egg—dramatically, so that the transient component's p falls below 60 min (Turner, in press).

Thus, a bird that is intermittently incubating a 60-g egg will affect the temperature of the egg only when the p of its visitation schedule is 60–100 min or more. Visitation schedules with p 's shorter than this should have little effect on egg temperature.

For an AC physical system, it is sometimes convenient to describe the "efficiency" of energy flow into it by a quantity designated the power factor

(ρ), which is calculated from ϕ_T (rad) between the heat input and temperature response:

$$\rho = \cos(\phi_T). \tag{3}$$

The power factor is essentially the fraction of energy in a transient potential energy gradient that results in usable work (Grob 1977).

In a low-pass electrical filter, ρ increases with the p of the AC voltage. Similarly, the ρ at the egg's brood patch increases with longer p 's, from about 0.28 when p is 20 min to about 0.85 when p is 120 min (fig. 4).

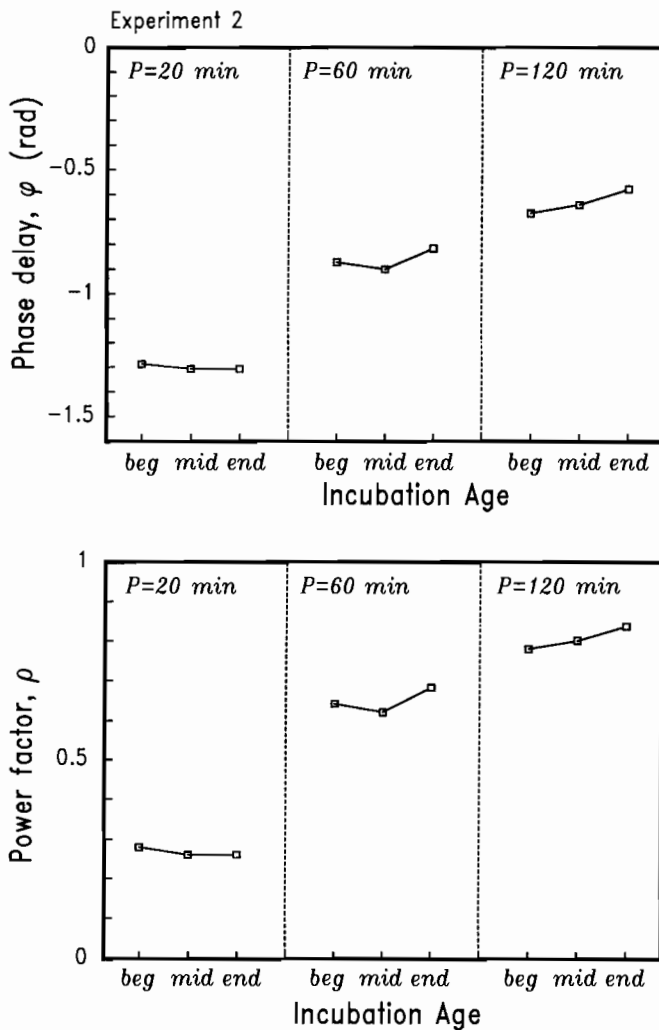


Fig. 4. Age-dependent and p -dependent variation in ϕ_T (top) and ρ (bottom) between q_b and T_b . Data are from experiment 2.

Consequently, if an intermittent incubator is to efficiently use heat from the broad patch to warm the egg, it should make the p of $q_b(t)$ as long as possible. This is consistent with, albeit derived differently from, Drent's (1973) contention that the most energetically efficient "strategy" for an intermittent incubator would be to take only one long absence per day rather than many shorter absences.

As the embryo grows, the Z_t of the egg declines (table 4), and the efficiency of transient-state heat flow into the egg increases, especially at long p 's of $q_b(t)$ (table 4). This opens two possible scenarios for how the use of time and energy might change during the incubation period. First, if the visitation schedule of the bird remained unchanged throughout incubation, the egg's declining Z_t would result in a more efficient transfer of the parent's metabolic heat to the egg during rewarming. Alternatively, the bird could conserve the energy expenditure during rewarming. The egg's lower Z_t would mean that the same amount of energy could warm the egg faster with less time spent rewarming.

Physiological and Physical Influences on the Egg's Z_t

The age-dependent decline of Z_t could be accounted for by changes in several physical and physiological properties of the egg. First, the thermal properties of the egg contents, such as the thermal conductivity or thermal diffusivity, could change as the embryo converts yolk and albumin to embryo. Second, the embryo produces more and more heat as it grows: by the end of incubation, a chicken embryo is producing roughly 130–150 mW of heat, which is sufficient to raise the egg's temperature by 2°–3°C above T_{air} (Tazawa and Rahn 1987; Tazawa, Turner, and Paganelli 1988). Third, the embryo's internal circulation of blood increases during the incubation period: in chicken eggs, blood circulation to the chorioallantois increases by roughly 500% from day 9 to day 18 of incubation (Tazawa 1980). Finally, the egg will lose a certain mass of water during the incubation period, which is commonly about 15% of the egg's initial mass (Ar and Rahn 1980).

Two of these possibilities can probably be ruled out at the outset. For example, if the decline of Z_t resulted from changes in the thermal conductivity or thermal diffusivity of the egg contents, one would expect to see age-dependent changes in these properties among the killed eggs. No such change was discernible (tables 1, 2). It also seems unlikely that the embryo's increasing heat production could explain the observed changes of Z_t . Certainly, increased metabolic heating of the egg could explain the higher $T_{0,c}$, $T_{0,a}$, and $T_{0,e}$ of the egg or the increased homogeneity of egg temperature

as the embryo grew (table 1, fig. 2). However, it is difficult to reconcile increasing heat production with the simultaneous decline of $T_{0,b}$ and A_{Tb} (table 1; figs. 2, 3) or with the egg's higher A_{Tc} , A_{Te} , and A_{Ta} (table 1; fig. 3).

This leaves the embryo's increasing circulation and the declining mass of the egg as the likely factors for the observed decline of the egg's Z_t .

Fortunately, the definition of the Z_t allows one to quantify independently the contributions of each. The Z_t is the vector sum of two properties of the egg, R_t and X_c (Turner, in press):

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

The embryo's increasing circulation should result in a decline of R_t through incubation, as it does under steady-state conditions (Turner 1992), but it should not affect the egg's X_c , which depends on the embryo's thermal capacity. On the other hand, the loss of water and, hence, the declining thermal capacitance (C_t) of the egg should lower the egg's X_c without affecting R_t . By estimating what change of Z_t results from the observed changes of either R_t or X_c alone, one can separate the effects of the embryo's circulation from the effects of the loss of mass from the egg.

For the eggs in this experiment, the average R_t decreased by roughly 19.4% (table 4), which is similar to that measured under steady-state conditions by Turner (1992). Also, these eggs' average masses declined from 63.7 g to 58.0 g, which is an average fractional mass loss of about 9.9%. The average X_c decreased by about 9.7% (table 4), which is close to the 9.9% fractional mass loss. Finally, the average Z_t declined by roughly 9.5% (table 4). From equation (4), the measured decrease in R_t alone should drop Z_t by roughly 4.5%. Alternatively, the decrease in X_c alone should drop Z_t by roughly 7.2%. Together, circulation and mass loss cause a drop in Z_t of about 12%. Thus, it appears that the embryo's increasing circulation and decreasing mass contribute similarly to the age-dependent decline in the egg's Z_t .

Time Constant for Contact-incubated Eggs and the Time Budget for Intermittent Incubation

It is commonly thought that the time an intermittently incubating bird spends visiting the nest is determined by the time required to rewarm the egg to some "release temperature" (T_r ; Kendeigh 1952; Skutch 1957, 1962; Drent 1973; White and Kinney 1974; Armstrong and Whitehouse 1977; Mertens 1977; Yom-Tov et al. 1978; Vleck 1981*a*, 1981*b*; Webb and King 1983; Zerba and Morton 1983*a*, 1983*b*; Lofaldi 1985; Biebach 1986; Hohman 1986; Thompson and Raveling 1987; Naylor et al. 1988; Weathers and Sullivan

1989; Hepp et al. 1990). The parent presumably "knows," through sensory feedback from the thermoreceptors in the skin of the brood patch, when the egg has warmed to the T_r (White and Kinney 1974; Vleck 1981*a*; Midgard, Sjorsen, and Johansen 1985; Toien, Aulie, and Steen 1986). Presumably, the bird gauges the temperature of its egg from T_b .

If this notion is correct, it is straightforward to calculate a visitation time (t_{vis}). Let us assume that a parent returns to the nest to find its egg at temperature T_i . If the bird rewarms the egg to the T_r , the time required to do this is

$$t_{vis} = -\tau_w \ln((T_r - T_p)/(T_i - T_p)), \quad (5)$$

where T_p is the body temperature of the parent.

Crucial to this prediction is an accurate value for τ_w . There are various reports from the literature on the τ 's of eggs, which are calculated by means of methods ranging from the estimation of cooling rates of single eggs cooling in air (Kendeigh 1963; Turner 1985) to the estimation of cooling rates of clutches of eggs and nests together (Ponomareva 1971, 1982; White and Kinney 1974; Blagosklonov 1978; Howey et al. 1984). However, the τ 's for contact-incubated eggs reported here and elsewhere (Turner, in press) are considerably less than for these other measurements. Thus, equation (5) may considerably overestimate t_{vis} if a τ measured under these apparently unrealistic conditions is used.

Why is the τ for contact-incubated eggs so much smaller than that for eggs cooling in air? One way to define the τ of an object is as a product of the object's R_t ($^{\circ}\text{C W}^{-1}$) and C_t ($\text{J } ^{\circ}\text{C}^{-1}$):

$$\tau = R_t C_t. \quad (6)$$

When an egg is surrounded on all sides by air, nearly the entire mass of the egg is "thermal mass," mass that stores heat (Turner 1985) or, more precisely, mass that participates in the transient component of heat exchange. Consequently, the C_t of an egg cooling in air is closely approximated by the product of the egg's gravimetric mass (M ; kg) and the egg's specific heat (c_p ; $\text{J kg}^{-1} ^{\circ}\text{C}^{-1}$). The τ for an egg cooling in air is therefore reasonably well predicted by the equation (Turner 1985)

$$\tau = R_t c_p M. \quad (7)$$

For contact-incubated eggs, the presumption that the entire egg is thermal mass may not be a good one. When heat flows into an egg from a brood patch, it does not flow evenly through the entire mass of the egg (Turner

1987, 1992). Rather, a considerable fraction of the heat flows to the surface of the egg adjacent to the brood patch, thence it is lost to the environment. For $q_b(t)$, the regions of the egg adjacent to the brood patch experience the largest transients of temperature. The more remote regions of the egg experience relatively little transient flows of heat and, consequently, little transient fluctuation of temperature (figs. 1, 3; table 1). Consequently, there may be an "effective" thermal mass in a contact-incubated egg, which is defined as that part of the egg that actually participates in the transient components of heat flow. This effective thermal mass is less than the product of the egg's c_p and its M : Turner (in press) has estimated that the effective thermal mass of infertile chicken eggs may be as little as 15% of the egg's total M .

If contact-incubated eggs have an effective thermal mass, this raises some interesting questions about the interaction of time and energy in intermittent incubation. Suppose, for example, that the t_{vis} is equal to the time required to warm the surface of the egg to T_r (eq. [5]). Presumably, warming the egg surface to T_r would be pointless if it were not accompanied by a warming of the egg interior, where the embryo resides. Yet all $q_b(t)$'s to the egg surface are not equally capable of warming the egg interior—fast-component heat inputs do not penetrate the egg as effectively, that is, they do not involve as much effective thermal mass as do slow-component heat inputs. So, what would be better for the incubating parent? Should the bird warm the egg surface to T_r as quickly as possible to allow more time for foraging and other activities away from the nest but with the likelihood that the added heat will not effectively warm the embryo? Or should the bird deliberately prolong the warming time, perhaps by "throttling" the flow of heat from the brood patch into the egg, which would involve more of the egg as effective thermal mass but at the cost of lost foraging time?

In conclusion, intermittent incubation involves simultaneous costs in time and energy. Treating the egg as a transient-state physical system allows one to examine the interaction of these costs in a powerful way, which opens to critical study, in ways not easily done before, such questions as what is the efficiency of heat flow to the egg, to what extent should the egg be rewarmed, and what are the effects of the embryo's physiology?

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