On the Thermal Capacity of a Bird's Egg Warmed by a Brood Patch

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ABSTRACT

Eggs of intermittently incubating birds are periodically rewarmed by a transient pulse of heat from the parent's brood patch. Estimating the energy cost of rewarming such an egg requires knowledge of the egg's thermal capacity, typically assumed to be the product of the egg's mass and its specific heat, designated here as the gravimetric thermal capacity. When chicken eggs are transiently warmed by an artificial brood patch, the energetic costs of the rewarming indicate that they have thermal capacities about one-third the gravimetric thermal capacity. In this article, I show that birds' eggs warmed locally by a brood patch have effective thermal capacities that differ substantially from the eggs' gravimetric thermal capacities, both in absolute magnitude and in response to varying the temporal properties of the transient pulse of heat. An effective thermal capacity exists because heat from a brood patch flows unevenly through an egg and because of thermal impedance effects on the unsteady component of heat flow into the egg. If these conditions in any way characterize the rewarming of eggs by intermittently incubating birds in nature, intermittent incubation may be considerably less costly in time and energy than has heretofore been assumed.

Introduction

Incubating birds can be divided into two broad categories: steady incubators, which tend the eggs more or less continuously through incubation, and intermittent incubators, which frequently leave the nest and eggs to forage (Skutch 1957, 1962).

The eggs of intermittent incubators are subject to repeated cycles of warming and cooling, corresponding to the parents' alternating visits to, and absences from, the nest. Our current understanding of the course of one of these cycles is roughly as follows. Upon returning to the nest, the parent initiates the warming phase by pressing its brood patch against one surface of the egg. Heat is transferred from the parent to the egg via blood flowing through the brood patch. The delivery of heat to the egg is modulated by how tightly the parent fits the brood patch to the egg and by both locally and centrally controlled modulation of brood patch blood flow. A cool egg (its temperature sensed by cutaneous thermoreceptors in the brood patch) elicits brood patch vasodilatation and elevated parental heart rate. Consequently, the cooler the egg, the greater the delivery rate of heat to it (White and Kinney 1974; Gabrielsen and Steen 1979; Midtgård et al. 1985; Tøien et al. 1986). The heat to warm the eggs may come from increased metabolic heat production by the parent (Vleck 1981*a,* 1981*b,* 1985), or it may be surplus heat accumulated by the parent during the just-concluded foraging bout (Biebach 1986). The heating phase continues until the egg temperature sensed by the brood patch reaches a particular value, known as the exit temperature (White and Kinney 1974; Zerba and Morton 1983*a,* 1983*b*), whence the parent may leave for its next foraging bout, initiating the cooling phase. The duration of the foraging bout, and hence the cooling phase, may be limited by the time the egg takes to cool to some minimum value (Drent 1973; White and Kinney 1974; Zerba and Morton 1983*a,* 1983*b*).

During the warming phase of this cycle, heat is clearly transferred from the parent to the egg. Just as clearly, rewarming the egg requires time because the egg is thermally damped (Turner 1994*a,* 1994*c*), and time the bird spends rewarming is time that cannot be spent foraging. Consequently, the time and energy requirements of intermittently warming and cooling the eggs are thought by some to shape substantially the behavior and energetics of intermittently incubating birds (White and Kinney 1974; Vleck 1985). Others disagree (e.g., Walsberg and King 1978*a,* 1978*b;* Biebach 1986), asserting that the costs of rewarming are either small or can easily be met by more efficient use of metabolic energy.

Evaluating these claims depends, of course, on a realistic assessment of just what the time and energy costs of rewarming an egg are. Commonly, estimates of these costs have relied on two assumptions.

The first assumption is that cost of rewarming an egg can be estimated from its thermal capacity and its temperature change during rewarming (Walsberg and King 1978*a,* 1978*b;* Biebach 1986):

$$\delta Q = \delta T\, C, \tag{1}$$

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where δT is the change in egg temperature (K), δQ is the quantity of heat added to the egg (J), and C is the egg's thermal capacity (J K^{-1}). A subsidiary assumption is that the time required for the egg to change temperature is likewise directly proportional to its thermal capacity.

Obviously, the egg's thermal capacity is central to any estimate of the time and energy costs of rewarming the egg. This leads to the second common assumption, namely, that the egg's thermal capacity can be estimated as the product of its specific heat and mass (Walsberg and King 1978*a,* 1978*b;* Biebach 1986):

$$C = Mc, \tag{2}$$

where c is the egg specific heat (about 3.3 kJ K^{-1} kg^{-1}; Romanoff and Romanoff 1949) and M is mass (kg). This reflects the commonly held view that thermal capacity scales isometrically with body mass (Günther 1975).

The purpose of this article is to explore the validity of these assumptions. My principal conclusion is that they may be substantially in error. The reasons for this are as follows. Equation (2) is an operational definition of thermal capacity that assumes, among other things, that the entire gravimetric mass of an egg can be thermal mass, that is, that all parts of the egg participate uniformly in the transient flows of heat through it. This assumption is reasonably good for an egg that warms or cools uniformly, surrounded uniformly by a fluid medium like air or water (Turner 1985). However, it is not a good assumption for eggs that are contact-warmed (i.e., by the parent pressing the brood patch against one surface of the egg); whether in steady or transient conditions, flows of heat through the egg and the temperature gradients driving them are emphatically not uniform (Turner 1992, 1994*a,* 1994*c*). This undermines the assumptions that equations (1) and (2) rely on to estimate time and energy costs of intermittently warming an egg.

Recently, Turner (1994*c*) suggested that contact-warmed eggs behave as if their thermal capacities were substantially smaller than that defined in equation (2), that is, that eggs warmed by a brood patch may have an effective thermal capacity that is considerably smaller than their gravimetric thermal capacity. If this is so, estimates of energy and time costs of intermittent incubation, which have commonly relied on the gravimetric thermal capacity as defined in equation (2), may be in substantial error.

The idea of an effective thermal capacity arose from a more general study on the transient-state thermal properties of contact-warmed eggs (Turner 1994*a,* 1994*b,* 1994*c*). In this article, I explicitly test whether an effective thermal capacity exists in a contact-warmed egg, and if it does, to describe how it is affected by the temporal properties of the heat influx to the egg during rewarming and by the embryo's developing circulation and heat production.

Material and Methods

General Rationales for Experimental Design

The experimental designs and apparatus to be described below reflect two rationales: that measuring effective thermal capacity requires heat flows through the egg to resemble as much as possible the flows of heat through an egg being warmed by a bird's brood patch and that effective thermal capacity is affected by the egg's thermal impedance.

I tried to mimic the flows of heat through an egg warmed by a brood patch in two ways. First, I used an artificial brood patch to warm the egg, which enabled me to deliver known quantities of heat to the egg over part of its surface, as presumably occurs when a bird warms its egg with its brood patch. Second, I measured response of that egg temperature that would be sensed, and presumably would be regulated, by an incubating bird, that is, the surface contacting the brood patch (White and Kinney 1974; Gabrielsen and Steen 1979; Midtgård et al. 1985; Tøien et al. 1986).

The effective thermal capacity is influenced by thermal impedance effects in the contact-warmed egg. The thermal impedance is a transient-state analogue of the more commonly used thermal resistance (or its inverse, thermal conductance). The thermal impedance is not only a property of the egg but also of the time-dependency of the transient flows of heat into the egg; a slowly changing transient flow of heat will penetrate the egg more readily than will a rapidly changing flow (Turner 1994*a,* 1994*b,* 1994*c*). Consequently, effective thermal capacity should vary with the temporal properties of a transient input of heat (Turner 1994*b*). The experiments outlined here are based partly on this principle.

The experiments deliver a precisely controlled and quantified pulse of heat (δQ, J), from the artificial brood patch to one surface of the egg. This will elicit a transient temperature response in the egg (δT, K) as shown by rearranging equation (1):

$$\delta T = \delta Q / C. \tag{3}$$

The basic experimental design tests whether the relationship between the change in added energy from the artificial brood patch and the change in temperature can be altered by the temporal properties of the heat pulse, independently of the quantity of heat in the pulse. If it cannot be, this implies that the egg's thermal capacity is a constant, as would be expected for a gravimetric thermal capacity. However, if it can be altered, this implies that the egg's thermal capacity varies with the temporal properties of the heat pulse, which is the behavior expected for an effective thermal capacity.

Schedule of Heating by the Artificial Brood Patch

The transient pulse of heat was delivered to the egg as part of a controlled schedule of transient heating. Two types of heating schedules were employed. The differences between them are described more fully below. However, both schedules had in common the following three phases (Figs. 1, 2). Phase 1 was a preheating equilibration phase, in which the egg was subjected to an extended period (about 3 h) of a low and steady heat input of 250 mW, sufficient to raise the contact-warmed egg surface to about 10°C above ambient. This phase was intended to allow the egg to come to a thermal steady state. Phase 2 was a heating phase immediately following phase 1. Here, the input of heat from the artificial brood patch was boosted to a higher level for a short time, delivering a pulse of excess heat. During this phase, the egg was transiently warmed. Phase 3 was a relaxation phase, where heat input from the artificial brood patch was returned to that in phase 1. In the relaxation phase, the egg transiently cooled back to the steady state temperatures of phase 1. The duration of phase 3 was about 3 h.

Varying the Phase 2 Heating Impedance

The egg's thermal impedance depends upon the temporal properties of the transient input of heat (Turner 1994*a*). Consequently, heating impedance during phase 2 (and hence effective thermal capacity) can be altered independently of brood patch heat input by changing the rate of heat delivery from the brood patch, which in turn alters the time course of the transient pulse of heat. Two courses of phase 2 heating were used, low impedance heating and high impedance heating. During low impedance heating, the eggs were heated more slowly (400 mW) than they were during high impedance heating (450 mW). This has the effect of shifting the power spectrum during phase 2 heating to lower frequency components (Trimmer 1950), which have overall lower impedances (Turner 1994*a*, 1994*b*, 1994*c*). The converse is true for high impedance heating. In all cases, effective thermal capacity should be smaller during high impedance heating than during low impedance heating (Figs. 1, 2).

Experiment A: Heat Required to Raise Egg Surface Temperature to a Fixed Value

In this set of experiments, phase 2 heating continued until the egg temperature under the brood patch reached a particular "exit temperature" (Fig. 1). In these experiments, the exit temperature was set at 36°C, about 12°–13°C above ambient.

Five variables were measured and compared between high impedance warming and low impedance warming. These, along with their predicted behaviors, are as follows. (1) The heat in joules required to bring the contact-warmed egg surface up to the exit temperature of 36°C (shaded region in Fig. 1). This quantity should be directly proportional to effective thermal capacity and so should be larger during low impedance warming than during high impedance warming. (2) The time in minutes required to bring the contact-warmed egg surface up to the exit temperature of 36°C (Fig. 1). This time should be inversely proportional to the effective thermal capacity and so should be shorter during high impedance heating than during low impedance heating. (3) The relaxation time constant in minutes for the cooling of the contact-warmed egg surface during phase 3. This is the time required for the temperature of the contact-warmed egg surface to return from the exit temperature to within e^{-1} of its preheating equilibrium value. This time is directly proportional to effective thermal capacity and so should be longer following low impedance heating than following high impedance heating. (4) The egg's steady thermal resistance in degrees Celsius per watt is a steady state thermal property of the egg. It is estimated as the ratio of the temperature elevation of the egg above ambient and the brood patch heat input during phase 1. It should not vary with the egg's thermal impedance (Turner 1994*a*, 1994*c*). (5) The transient elevation of temperature in degrees Celsius at the center of the egg during phase

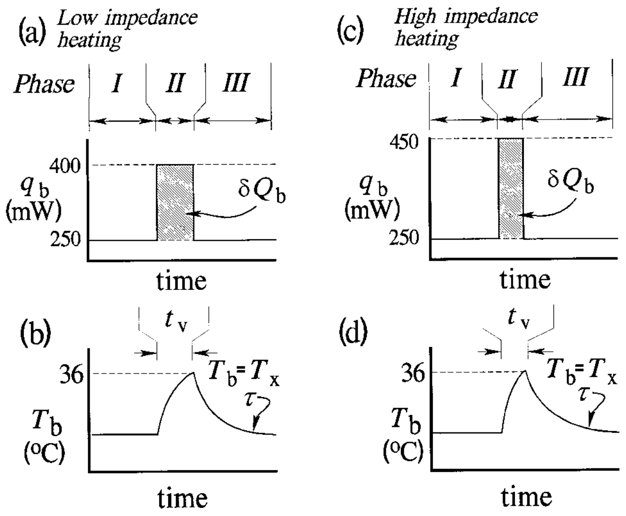

Figure 1. Schematic diagram outlining schedule of heating and expected temperature responses of the egg heated to a particular exit temperature, designated in the text as experiment A. *a* and *c* show the schedules of heating for low impedance heating and high impedance heating, respectively. In both diagrams, phase 1 is the preheating equilibration phase, phase 2 is the heating phase, and phase 3 is the postheating relaxation phase. The shaded portion in each is the quantity of heat (J) added from the brood patch during phase 2 (δQ_b), which is the product of the excess heating rate during phase 2 warming (q_b during phase 2 − q_b during phase 1) and the duration (t_v) of phase 2 warming. *b* and *d* show the expected temperature responses of the contact-warmed surface of the egg for low impedance warming and high impedance warming, respectively. In experiment A, the criterion is to measure the quantity of heat required during phase 2 (δQ_b) to bring the surface temperature of the egg (T_b) up to a particular exit temperature (T_x), set in this experiment as 36°C. The time required to heat the egg's surface is equivalent to the duration of phase 2 (t_v). During phase 3, the egg will cool back to its phase 1 equilibrium temperature at a rate inversely proportional to the time constant for cooling (τ min).

2 warming. Because low impedance heating should involve more of the egg's volume in the transient exchanges of heat, the transient elevation of center temperature should be greater during low impedance warming than during high impedance warming.

Experiment B: Temperature Elevations in Response to a Fixed Quantity of Brood Patch Heat

This set of experiments involved adding to the egg a fixed quantity of heat during phase 2 warming (Fig. 2). This quantity was set at about 250 J, based on the energy requirements for contact-warming observed in experiment A.

Four variables were measured and compared between high impedance warming and low impedance warming. These variables, along with their predicted behaviors, are as follows. (1) The temperature of the contact-warmed egg surface at the end of phase 2 warming. High impedance warming should increase this temperature less than low impedance warming (Fig. 2). (2) The egg's steady thermal resistance. As in experiment A, this quantity should not differ between high impedance warming and low impedance warming. (3) The transient elevation of temperature at the center of the egg during phase 2 warming. Because the heat input from the brood patch in this experiment is always 250 J irrespective of the egg's thermal impedance, one should see the same elevation of central egg temperature during both high impedance warming and low impedance warming. (4) The relaxation time constant for cooling of the contact-warmed egg surface during phase 3. As in experiment A, this time should be greater following low impedance warming than after high impedance warming.

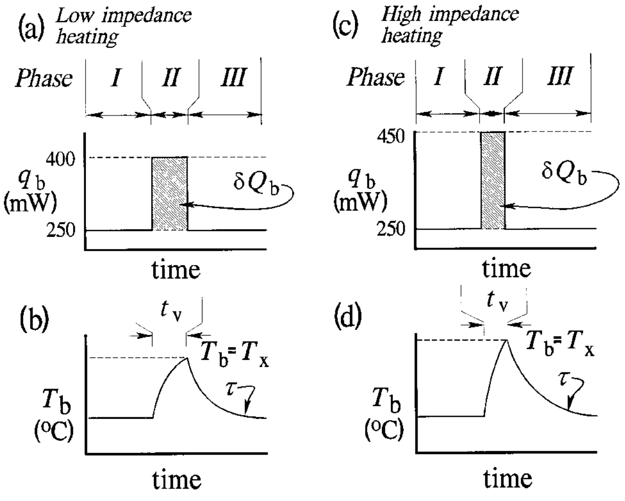

Figure 2. Schematic diagram outlining schedule of heating and expected temperature responses of the egg heated by a particular amount of added heat from the brood patch, designated in the text as experiment B. In all cases, the heat added from the brood patch (δQ_b) is 250 J for both low impedance heating and high impedance heating. Conventions and labeling are as in Figure 1.

The Artificial Brood Patch System

The artificial brood patch system has been described in detail by Turner (1994*a*). It consisted of a Dewar-flask artificial brood patch, custom shaped to fit snugly onto the egg, with the heat dissipation from it controlled by computer through a digitally controlled switching power supply. A particular schedule of heating was programmed into and controlled by the computer (Tandy, Dallas, Tex.). The egg, outfitted with thermocouples, was coupled to the artificial brood patch by a thin layer of dental alginate. Egg temperatures were measured and logged using an amplified analog/digital converting system (Remote Measurement Systems, Seattle, Wash.) controlled by the computer.

Eggs outfitted with the thermocouples and artificial brood patch were placed in a water-jacketed chamber. Wall temperature of the chamber was maintained at approximately 23°C by circulating water through the jacket from a thermostatically regulated water bath.

Developmental Stages of Eggs

Chicken eggs were used in these experiments. Eggs in three different developmental classes were tested: infertile; fertile, middle of incubation (6–12 d incubation); and fertile, end of incubation (13–18 d incubation). Infertile eggs were obtained from a local grocery store. Fertile eggs were obtained from a commercial supplier and incubated at 38°C in an artificial incubator. Fertility and development of the fertile eggs was assessed by periodic candling.

Locations and Measurements of Egg Temperatures

Egg temperatures were measured at two sites in or on the egg, using 32-gauge copper-constantan thermocouples. The contact-warmed egg surface temperature was measured by a thermocouple attached to the egg surface contained within the cup of the artificial brood patch. The thermocouple was attached to the egg surface by embedding it in a small drop of paraffin wax on the eggshell. The thermocouple was placed in the center of the eggshell surface subtended by the chorioallantois, as determined from candling of the egg immediately prior to the experiment. Egg temperature at the center was measured by placing a thermocouple into a glass capillary tube sleeve implanted into the egg. The capillary sleeve ensured the isolation of the thermocouple from the fluid contents of the egg and the reliable placement of the thermocouple in the center of the egg. The capillary sleeve was implanted immediately prior to using the egg in the experiment.

Results

Experiment A: Heat Required to Elevate Egg Surface Temperature to a Fixed Value

Both incubation age and thermal impedance during phase 2 warming had significant effects on the time and energy required to raise the contact-warmed surface of chicken eggs to a particular exit temperature (Tables 1, 2).

The transient flows of energy into an egg clearly were affected by impedance during phase 2 warming. During high impedance warming, about 40% less energy was required to bring the contact-warmed egg surface up to 36°C than was required during low impedance warming (Table 1). This reduction cannot be explained by any effect of heating impedance on the eggs' steady thermal resistances, which were not affected by the rate of heating (Table 1). A transient pulse of heat from the artificial brood patch also penetrated the egg more effectively during low impedance warming, as indicated by the eggs' central temperatures being warmed more than during high impedance warming (Table 1).

The time course of phase 2 warming likewise differed between high impedance warming and low impedance warming. During low impedance warming, the time required to bring the contact-warmed surface up to 36°C was about twice that during high impedance warming (Table 1). The effects extended beyond the actual heating phase. Following low impedance warming during phase 2, the relaxation time constant during phase 3 was about 22% longer than it was following high impedance warming (Table 1).

Incubation age also affected the time and energy requirements of raising the temperature of the contact-warmed surface of the egg (Table 2), mostly through a circulation-dependent reduction of the eggs' steady thermal resistances in the latter third of incubation (Table 2). This reflects a more effective distribution of the transient pulse of heat through the egg when the embryo was older. Heat added to the egg during phase 2 warming warmed the egg's center more in the latter third of incubation than in any other stage (Table 2). Finally, the relaxation time constant was shorter by about 25% in the last third of incubation compared with other incubation stages (Table 2).

Experiment B: Temperature Elevations in Response to a Fixed Quantity of Brood Patch Heat

The temperature response of an egg warmed by the transient addition of 250 J of heat from a brood patch was significantly affected by both incubation stage and thermal impedance during warming (Tables 3, 4).

During high impedance warming, adding 250 J of heat from the brood patch warmed the contact-warmed surface of the egg more than it did during low impedance warming (Table 3). As in experiment A, this cannot be attributed to any variation of the eggs' steady thermal resistances (Table 3). However, the center of the egg was warmed by the same amount, irrespective of thermal impedance (Table 3). Again, as in experiment A, the relaxation time constant was longer following low impedance warming during phase 2 than following high impedance warming (Table 3).

As incubation proceeded, steady thermal resistance dropped as it did in experiment A, and likewise significantly so only in the last third of incubation (Table 4). Also, as the embryo matured, the transient addition of 250 J of heat elevated the temperature of the contact-warmed surface less (Table 4), and this was accompanied by a larger elevation of temperature in the center of the egg (Table 4). Finally, the relaxation time constant was shorter in the last third of incubation than in any other stage of development (Table 4).

Discussion

Estimating the time and energy requirements for intermittently incubating an egg requires a reasonably close estimate of the egg's thermal capacity. Often, the thermal capacity of an egg has been assumed to be simply the product of its specific heat and mass (Kendeigh 1963; Günther 1975; Walsberg and King 1978*a*, 1978*b*; Biebach 1986), that is, a gravimetric thermal

Table 1: Effect of heating rate on the thermal behavior of eggs warmed by a brood patch to an exit temperature of 36°C

	Head added during phase 2 warming (J)	Steady state thermal resistance (°C W^{-1})	Elevation of egg center temperature during phase 2 warming (°C)	Duration of phase 2 warming period (min)	Time constant for cooling during phase 3 relaxation period (min)
Heating rate during phase 2 warming:					
450 mW	180.2	36.13	.785	15.95	12.93
400 mW	295.4	36.52	.958	32.61	15.81
Least significant range	54.1	1.05	.101	5.97	.74
Probability (*P*)	.0045	.5897	.0205	.0003	.0001

Note. Main effects means and probability levels for comparisons between fast heating (high impedance) and slow heating (low impedance). Phase 2 heating continued until the contact-warmed surface temperature of the egg was 36°C (experiment A). Number of eggs used was 48. Means are corrected least squares means, accounting for the variation of steady state thermal resistance. Least significant range was calculated by the method of Sokal and Rohlf (1969) at $P = 0.05$. *P* values are the results of the ANOVA comparing the main effects means.

Table 2: Effect of incubation age on the thermal behavior of eggs warmed by a brood patch to an exit temperature of 36°C

	Head added during phase 2 warming (J)	Steady state thermal resistance (°C W^{-1})	Elevation of egg center temperature during phase 2 warming (°C)	Duration of phase 2 warming period (min)	Time constant for cooling during phase 3 relaxation period (min)
Incubation age:					
Infertile	192.1	37.24	.743	19.17	15.38
Days 6–12	201.0	37.13	.766	21.64	16.02
Days 13–18	321.2	34.60	1.107	32.12	11.71
Least significant range	65.0	1.26	.121	7.18	.89
Probability (*P*)	.0129	.0075	.0001	.0338	.0001

Note. Main effects means and probability levels for comparisons between three incubation ages. Phase 2 heating continued until the contact-warmed surface temperature of the egg was 36°C (experiment A). Number of eggs used was 48. Means are corrected least squares means, accounting for the variation of steady state thermal resistance. Least significant range was calculated by the method of Sokal and Rohlf (1969) at $P = 0.05$. *P* values are the results of the ANOVA comparing the main effects means.

capacity as defined in equation (2). However, when a chicken egg is transiently warmed by an artificial brood patch, its transient temperatures do not behave congruently with this assumption.

One inconsistency is in the magnitude of the transient temperature response to a known input of heat into the egg. Consider the temperature response of the egg to a 250-J pulse of heat from the artificial brood patch (experiment B). Assuming a specific heat for eggs of 3,313 J kg^{-1} K^{-1} (Romanoff and Romanoff 1949), a 57-g chicken egg (the average egg mass in this study) will, according to equation (2), have a gravimetric thermal capacity of 189 J K^{-1}. Assuming perfect transfer of heat into the egg, 250 J should force egg temperature to rise by 1.32°C, bringing the egg surface temperature from its phase 1 temperature of about 9.5°C up to about 10.8°C. The observed rise in temperature was substantially larger, however (Table 3): 250 J added to the egg elevated the temperature of the contact-warmed surface by 3.2°–4.1°C, depending upon the rate of heating used. Clearly, a contact-warmed egg behaved as if it had a thermal capacity roughly one-third to one-half its gravimetric thermal capacity.

Another inconsistency arises from the effect of different rates of heating of the egg. Egg were heated by the brood patch at two different rates, 400 mW or 450 mW, until one of two conditions was met. In experiment A, the heat required to force the contact-warmed surface temperature to a particular exit temperature (36°C) was measured (Tables 1, 2). Experiment B was the converse experiment, in which the temperature increase resulting from adding a fixed quantity of heat (250 J) to the egg was measured (Tables 3, 4). In both experiments,

Table 3: Effect of heating rate on the thermal behavior of eggs heated by a brood patch by 250 J

	Elevation of contact-warmed egg surface above environmental temperature (°C)	Steady state thermal resistance (°C W^{-1})	Elevation of egg center temperature during phase 2 warming (°C)	Time constant for cooling during phase 3 relaxation period (min)
Heating rate during phase 2 warming:				
450 mW	13.62	37.82	.951	10.88
400 mW	12.71	38.15	.897	12.57
Least significant range	.27	1.28	.049	.82
Probability (*P*)	.0001	.7224	.1469	.0066

Note. Main effects means and probability levels for comparisons between fast heating (high impedance) and slow heating (low impedance). Phase 2 heating continued until 250 J excess had been added to the egg (experiment B). Number of eggs used was 42. Means are corrected least squares means, accounting for the variation of steady state thermal resistance. Least significant range was calculated by the method of Sokal and Rohlf (1969) at $P = 0.05$. *P* values are the results of the ANOVA comparing the main effects means. Temperature elevations are to be compared with the phase 1 temperatures, which were on average 9.5°C.

Table 4: Effect of incubation age on the thermal behavior of eggs heated by a brood patch by 250 J

	Elevation of contact-warmed egg surface above environmental temperature (°C)	Steady state thermal resistance (°C W^{-1})	Elevation of egg center temperature during phase 2 warming (°C)	Time constant for cooling during phase 3 relaxation period (min)
Incubation age:				
Infertile	13.72	41.05	.781	12.03
Days 6–12	13.20	39.57	.919	13.08
Days 13–18	12.56	33.34	1.072	10.06
Least significant range	.32	1.54	.059	.98
Probability (*P*)	.0082	.0001	.0003	.0111

Note. Main effects means and probability levels for comparisons between three incubation ages. Phase 2 heating continued until 250 J excess had been added to the egg (experiment B). Number of eggs used was 42. Means are corrected least squares means, accounting for the variation of steady state thermal resistance. Least significant range was calculated by the method of Sokal and Rohlf (1969) at $P = 0.05$. *P* values are the results of the ANOVA comparing the main effects means. Temperature elevations are to be compared to the phase 1 temperatures, which were on average 9.5°C.

if the eggs' thermal capacities were simply the product of mass and specific heat, the eggs' transient temperatures should have behaved the same irrespective of how rapidly heat was added to the egg. In experiment B, for example, a 250-J pulse of heat should have forced egg temperature to rise by the same amount, irrespective of whether the 250 J was added at a rate of 450 mW (i.e., over 9.26 min) or 400 mW (i.e., over 10.42 min). It did not; adding 250 J to the egg at 450 mW raised the contact-warmed egg surface to a higher temperature than when the 250 J was added at 400 mW (Table 3). Clearly, there is some component of the egg's thermal capacity that varies with its heating rate.

There are other inconsistencies; nevertheless, it seems clear that when an egg is being warmed by a brood patch, its gravimetric thermal capacity is not a very good estimate of its true thermal capacity. Assuming that it is may lead to errors, both numerical and conceptual, some potentially serious, others more subtle.

Consider, for example, how one estimates the costs in time and energy to an intermittently incubating bird of periodically rewarming its egg. The most straightforward way would be to estimate the costs from equation (1) or some similar relationship, which has commonly been the case (Walsberg and King 1978*a*, 1978*b*; Biebach 1986). Estimating the costs in this way may overestimate them by 200%–300%, however, because equation (1) assumes a thermal capacity two to three times larger than that which seems to govern the egg's transient temperature response.

In all likelihood, these inconsistencies arise from an overly simplistic conception of how heat flows through a contact-incubated egg. Commonly, the thermal energetics of incubated eggs have been treated using simple resistance or resistance-capacitance models of egg temperature. These typically distribute the mass of the egg into one, or at most a few, discrete nodes in a numerical model (e.g., Walsberg and King 1978*a*, 1978*b*). Often, some of the important parameters governing eggs' thermal energetics, like their thermal conductances or cooling rates, have been derived from eggs cooling uniformly in air (Kendeigh 1963), which imposes an entirely different heat transfer regime upon the egg (Turner 1992). Whenever such models have been tested under controlled conditions, however, they have been found seriously wanting in their ability to quantify the thermal behaviors of contact-incubated eggs. For example, Turner (1992) found that using thermal conductances derived from eggs cooling in air overestimated the energy cost of contact-incubating birds' eggs by roughly 140% under steady state conditions. The results reported here and elsewhere (Biebach 1986; Turner 1994*a*, 1994*b*, 1994*c*) indicate they do no better under transient state conditions.

One reason simple resistance and resistance-capacitance models do not do very well is that they do not account properly for the complex temperature fields that exist in an egg warmed at one of its surfaces, as it would be under a brood patch (Turner 1992, 1994*b*). For example, a resistance-capacitance model that treats the egg as a single node necessarily assumes that temperature is uniform throughout the egg. However, a contact-warmed egg exhibits a complex temperature field emanating from the point of contact with the brood patch (Rahn et al. 1983; Swart et al. 1987; Turner 1992). Because heat flow through the egg depends on these temperature fields, any model that simplifies them necessarily yields errors in the estimated energy costs (Turner 1992).

Consider, for example, the apparently small thermal capacity of a contact-warmed egg. The temperature fields in a contact-warmed egg indicate that heat flows through a relatively small proportion of the egg; heat flows in at the point of contact between the brood patch and egg and tends to leave the egg mostly at the egg surfaces adjacent to the brood patch (Turner

1992). The portions of the egg antipodal to the brood patch tend not to be involved in the heat flows at all. A transient pulse of heat, therefore, would be expected to warm only a small portion of the egg's total mass, that region of the egg close to the brood patch. Concentrating the transient pulse of heat there would make the egg behave as if its thermal capacity was much less than the product of the egg's mass and its specific heat. Thus, the heat required to raise the egg surface temperature to some set value is less than would be expected from the gravimetric thermal capacity, which was the observed result (Table 1). Conversely, the temperature increase in response to a fixed quantity of heat being added to the egg is greater than would be expected from the gravimetric thermal capacity, which also was the observed result (Table 3).

This argument can be extended into a more general model that accounts more fully for the thermal behaviors of the eggs observed in this study. Consider an egg that is warmed by a transient input of heat from a brood patch. Any transient pulse of energy can be dissected into a Fourier series of sinusoidal waves of varying frequency (Trimmer 1950). Each of these sinusoidal components will force onto the egg a sinusoidal variation of temperature (Fig. 3). The actual temperature of the egg would be the sum of the sinusoidal temperature variations for each frequency. In the contact-warmed egg, the amplitude and phase of these sinusoidal temperatures varies with distance from the brood patch, in the manner depicted in Figure 3 (Turner 1994*a*). Compare now the temperatures in two regions of the egg, designated *a,* close to the brood patch, and *b,* distant from and antipodal to the brood patch (Fig. 3). In region *a,* the temperature variation has a large amplitude (i.e., a large unsteady component), while region *b* has a smaller, perhaps negligible, amplitude (i.e., a small or negligible unsteady component).

Because the storage of heat in any object is indicated by its change of temperature, it is clear that region *a* in Figure 3 is storing more heat than is region *b.* While region *b* might have a gravimetric thermal capacity, that is, it has a specific heat, and represents some gravimetric mass, if it is not changing temperature, it is not storing heat; it is effectively at steady state. Consequently, the region *b* is not participating in the transient exchanges of heat between the brood patch and egg; its thermal capacity is effectively not there. The only portions of the egg that capacitatively matter are those that are exhibiting unsteady heat flow (evidenced by their unsteady temperatures), and it is only these portions that will contribute to the egg's effective thermal capacity.

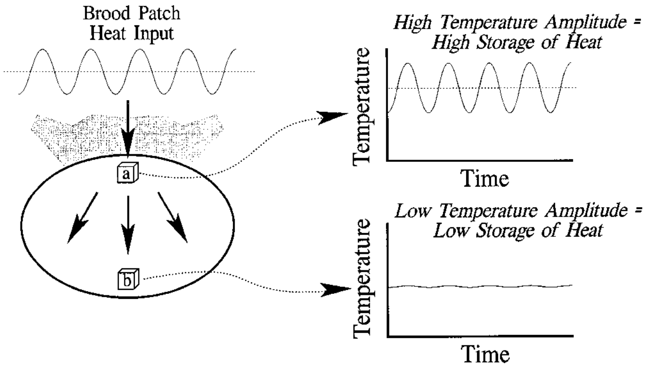

Figure 3. Schematic diagram outlining the thermal behavior of an egg forced by a sinusoidal input of heat from a brood patch. Details of diagram in text.

Thus, we account for the generally smaller apparent thermal capacities in a contact-warmed egg. This model can also account for the effects of heating rate, as seen in Tables 1 and 3. The tendency of a transient pulse of heat to penetrate into the egg is limited by the egg's thermal impedance, which varies with the frequency of the transient pulse (Turner 1994*a,* 1994*b,* 1994*c*). The lower the thermal impedance, the more easily the transient pulse of heat will penetrate into the egg. Empirically, we know that the thermal impedance of contact-warmed eggs goes up with increasing frequency of the heat input from the brood patch (Turner 1994*a*). It follows that the penetration of the transient pulse of heat into the egg will diminish as the frequency of the heat input increases. Thus, as heat input shifts to higher and higher frequencies, the proportion of the egg involved in the transient storage of heat diminishes, making the egg's temperature behave as if its thermal capacity is diminished.

The effect of different heating rates arises then from how these affect the egg's thermal impedance. The Fourier series that describes the pulse of heat can be used to construct a power spectrum that expresses the energy in the different frequency components of the pulse. Heating an egg at a faster rate has the effect of shifting the power spectrum to higher frequencies overall, which in turn results in an overall higher thermal impedance of the egg. This means that joules of heat added quickly to an egg do not engage as large a mass of the egg in the transient flows of heat as would joules of heat added at a slower rate. Rapidly heating an egg, therefore, would make an egg behave as if it had a smaller thermal capacity. A given quantity of heat added quickly would warm the egg surface more than would the same quantity of heat added more slowly, which was the result seen in Table 3. Conversely, less heat would be required to raise the egg surface to a particular temperature if the heat were added rapidly than if the heat were added more slowly, which was the result seen in Table 1.

That the rate of heating is somehow altering the proportion of egg mass that is engaging in transient heat flow is further supported by the observed variation of the time constant for cooling during the postheating relaxation phase (phase 3 in Figs. 1 and 2). The time constant for cooling is the product of the egg's thermal resistance and its thermal capacity (Turner 1985). In all cases, the eggs cooled more slowly after being warmed at 400 mW than they did after being warmed at 450 mW (Tables 1, 3). This variation of time constant was independent of any variation in the eggs' thermal resistances (Tables 1, 3). Thus, a fast rate of heating is making the egg behave as if its thermal capacity was diminished. Again, this can be explained by a thermal impedance effect. Faster heating forces the egg to higher impedance and results in less penetration of the heat into the egg, with involvement of less of the egg's mass in the transient flow of heat. If resistance does not change, this will result in a shorter time constant for cooling, because the apparent thermal capacity is diminished. Again, this was the observed result (Tables 1 and 3).

Thus, the thermal behavior of an egg that is transiently warmed by a brood patch can be better explained by presuming that the egg has an effective thermal capacity that is substantially smaller than its gravimetric thermal capacity and that varies with the temporal properties of the intermittent warming of the egg. The concept of the effective thermal capacity points to intermittent incubation being governed by some complicated and subtle interactions of time and energy.

Consider, for example, the following problem. Among birds that engage in intermittent incubation, some (designated here as "slow intermittent incubators," mostly galliformes and anseriforms) characteristically take one or a few long absences per day, while others (designated here as "fast intermittent incubators," mostly passeriforms) take many short absences per day (Drent 1973). Some birds may even shift between fast and slow intermittent incubation, depending upon the availability of food or favorable climate (F. R. Hainsworth, personal communication). When Drent (1973) used a simple resistance-capacitance model of an egg to analyze the energy costs of rewarming, he concluded that these are always minimized by taking as few long absences per day as possible. A fast intermittent incubator would therefore accrue high energy costs for rewarming its eggs, implying an energetic disadvantage inherent in this strategy.

If there actually is such a disadvantage, then it is reasonable to ask why the strategy of fast intermittent incubation exists. Typically, this has been explained as the outcome of competing behavioral drives. An incubation drive keeps the bird on the nest, and this competes with hunger, thirst, or thermoregulatory drives that prompt the bird to leave the nest. A bird leaves its nest when the hunger, thirst, or thermoregulatory drives override the incubation drive (White and Kinney 1974; Niebuhr 1983; Hogan 1989).

The effective thermal capacity offers an alternative way of looking at this problem. With a simple resistance-capacitance model of cooling and rewarming of an egg, it is straightforward to estimate the energy costs associated with periodically rewarming the egg (Turner 1994*b;* see Appendix). By making some simple assumptions about the time a bird must spend foraging during a day, its rate of temperature change, and how it divides up this time into one or more absences from the nest, it is a simple matter to estimate how energy cost of rewarming varies with number of absences from the nest (Appendix). An example of such an estimation is given in Figure 4, which considers the cost of rewarming a 55-g egg for one to 60 absences d^{-1}, with a total absence (= foraging) time equal to 6 h d^{-1}. In the estimate, Drent's (1973) prediction is clearly in evidence: cost of rewarming is minimized by taking as few long absences from the nest as possible, and cost of rewarming increases with number of absences per day from the nest (Fig. 4).

A very different view emerges, however, if one assumes there is an effective thermal capacity that, as observed in this study, declines with higher frequency of intermittent heat inputs (inset, Fig. 4). Similar to Drent's (1973) prediction, costs are low when numbers of absences are low and durations of absences are long; because the length of the warming-cooling cycle is long, this could be designated low impedance heating (Fig. 4). However, unlike Drent's prediction, rewarming costs also are low when numbers of absences are high and durations of absences are short; because the length of the warming-cooling cycle is short, this could be designated high impedance heating (Fig. 4). Thus, energetic advantage might accrue to fast intermittent incubation that would put this strategy on an energetic par with slow intermittent incubation. This hypothesis could

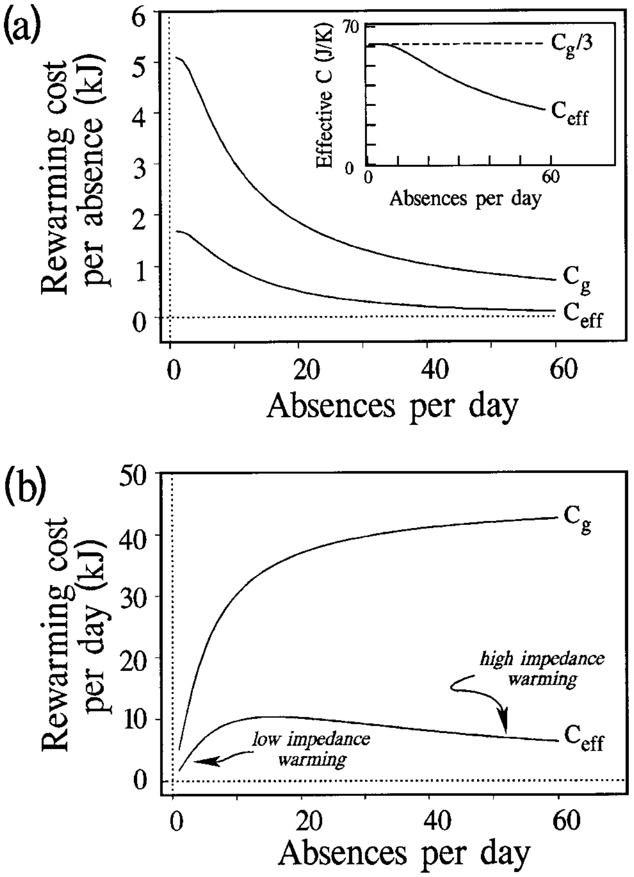

Figure 4. Estimated energy costs of contact rewarming of a 55-g chicken egg as it is affected by variation in the numbers of absences per day from the nest. Details of calculation are given in the Appendix. *a,* The per absence rewarming costs. *b,* The per day rewarming costs. *Inset:* variation of effective thermal capacity with respect to visitation frequency. C_g, gravimetric thermal capacity; C_{eff}, effective thermal capacity.

not have come from a simple resistance-capacitance model of transient egg temperature.

The idea of the effective thermal capacity also suggests some interesting ways that birds might employ impedance effects to manipulate time and energy use during incubation. For example, high impedance heating (low effective thermal capacity) might be usefully employed early on in incubation, when the embryo is small and is automatically positioned near the top of the egg. High impedance heating would confine the brood patch heat to a smaller volume of the egg near the brood patch, which could keep rewarming energy costs low and shorten rewarming time. Alternatively, low impedance heating might come into play later in the incubation period, when the embryo occupies more of the egg's volume.

The development of the embryo within the egg also significantly affects the egg's transient temperature response. That the development of the embryo must have some effect on the warming of an egg has long been suspected. However, the focus has commonly been on the embryo's increasing production of heat, with the implication that rewarming energy costs to the parent will decline as the embryo produces more and more of its own heat (White and Kinney 1974; Walsberg and King 1978*a*, 1978*b;* Vleck 1985).

The results reported here, however, show a different picture, at least in the latter parts of the incubation period. During the last third of incubation, it took more energy to raise the egg surface temperature to 36°C than it did in earlier phases of the incubation period (Table 2). Conversely, 250 J of heat raised egg surface temperature less in the last third of incubation than it did during earlier parts of the incubation period (Table 4).

This no doubt reflects the increasingly important role played by the embryo's developing circulation in distributing heat from the brood patch through the egg. For example, when 250 J was added to the egg from the brood patch, the resulting elevation of surface temperature of the egg declined as the embryos mature. For the eggs in the last third of incubation, the temperature elevation was about 1.2°C less than in infertile eggs (Table 4). This was accompanied by a rise in temperature at the center of the egg that is about 0.25°C greater than in infertile eggs. Clearly, heat from the brood patch was being distributed through the egg more widely as the embryo's circulation developed. The end result will be an energetic cost of intermittent incubation that increases, not decreases, with incubation age, just as it does in steady incubation (Turner 1992).

To conclude, the transient state energetics of the contact-warmed egg appeared to be complex, with warming of the eggs exhibiting many features that typically have not been part of our thinking on this problem. These interesting features arise from impedance effects during warming of the egg, in which the time course and rate of delivery of a transient pulse of heat changes the apparent thermal capacity of the egg. In addition, the circulation of the embryo appears to play a significant role in the contact-warming of the chicken egg, a role that has heretofore not been appreciated.

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Appendix

Estimating Costs of Rewarming a Chicken Egg

The first-order transient temperatures of a warming egg can be described by the equation:

$$T_t = (T_{\mathrm{ret}} - T_{\mathrm{eq,w}})e^{-t/\tau} + T_{\mathrm{eq,w}},$$

where T_{t} is egg temperature at time t, T_{ret} is egg temperature at the time the parent returns to the nest, $T_{\mathrm{eq,\,w}}$ is the equilibrium temperature of the egg warmed by the brood patch, and τ is the time constant for warming. Similarly, the first-order temperatures of a cooling egg can be described by the equation:

$$T_t = (T_{\mathrm{x}} - T_{\mathrm{e}})e^{-t/\tau} + T_{\mathrm{e}},$$

where T_{t} is egg temperature at time t, T_{x} is egg temperature at the time the parent leaves the nest, T_{e} is the equilibrium temperature of the egg exposed to the environment, and τ is the time constant for cooling.

The time spent foraging during a day (t_{f}) will be considered roughly equivalent to the time spent off the nest. Assuming that foraging time is set by the food gathering requirements of the bird, this time could be spent in one long absence per day or in many short absences per day. The time the egg spends cooling during each absence (t_{abs}) will thus be the ratio of the foraging time and the number of absences (n_{abs}):

$$t_{\mathrm{abs}} = t_{\mathrm{f}}/n_{\mathrm{abs}},$$

and the egg will cool during each absence to the return temperature (T_{ret}), which can be estimated by substituting the absence time for t in the first equation.

During each cycle of warming and cooling, the egg temperature thus oscillates between the return temperature and exit temperature. The energy cost of rewarming per visit ($\delta Q_{\mathrm{b,\,v}}$) can be estimated by the product of the difference between these temperatures and the egg's thermal capacity (C):

$$\delta Q_{\mathrm{b,\,V}} = C(T_{\mathrm{x}} - T_{\mathrm{ret}}).$$

The daily cost for rewarming ($\delta Q_{\mathrm{b,\,d}}$) is then the summed costs of rewarming for all visits:

$$\delta Q_{\mathrm{b,\,d}} = \delta Q_{\mathrm{b,\,V}}\, n_{\mathrm{abs}}.$$

In estimating the costs of rewarming depicted in Figure 4, I assume the egg is a chicken egg, stipulating the following parameters: egg mass (M) is 55 g, exit temperature (T_x) is 38°C, time constant for temperature change (τ) is 40 min, foraging time per day (t_f) is 6 h, number of absences per day (n_{abs}) ranges from 1 to 60, equilibrium temperature during warming ($T_{eq,w}$) is 40°C, and environmental temperature (T_e) is 10°C.

For estimating rewarming costs for the egg with a gravimetric thermal capacity, I assumed that the egg's specific heat was 3.3 kJ kg^{-1} K^{-1}, which results in a gravimetric thermal capacity of 182 J K^{-1}.

For estimating rewarming costs for an egg with an effective thermal capacity, a way of relating number of absences (and hence period of heating) to effective thermal capacity is required. I assumed that for one daily absence, effective thermal capacity was one-third the gravimetric thermal capacity, reflecting the values observed in this study. As number of absences is increased, effective thermal capacity declines. Based on previous observations for how period of transient heat input affects the chicken egg's thermal impedance (Turner 1994*a,* 1994*c*), I assumed that effective thermal capacity (C_{eff}) is related to number of absences as follows:

$$C_{eff}[n_{abs}] = C_{eff}[1]\ (1 - e^{-P_{abs}/P_e}),$$

where $C_{eff}[n_{abs}]$ is the effective thermal capacity when number of absences is n_{abs}, so $C_{eff}[1]$ is effective thermal capacity when number of absences is 1, P_{abs} is the period of the absence/visitation cycle ($3{,}600t_f/n_{abs}$), and P_e is the period where $C_{eff}[n_{abs}] = C_{eff}[1]/e$ (600 s). The values calculated for effective thermal capacity are reproduced in the inset in Figure 4.

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